# INVADERS ON THE HORIZON! SCANNING THE FUTURE OF INVASION SCIENCE AND MANAGEMENT

EDITED BY: Ana Sofia Vaz, Ana Novoa, Joana Raquel Vicente,
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PUBLISHED IN: Frontiers in Ecology and Evolution

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88971-640-1
DOI 10.3389/978-2-88971-640-1

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# INVADERS ON THE HORIZON! SCANNING THE FUTURE OF INVASION SCIENCE AND MANAGEMENT

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**Citation:** Vaz, A. S., Novoa, A., Vicente, J. R., Shackleton, R. T., Honrado, J. P., eds. (2021). Invaders on the Horizon! Scanning the Future of Invasion Science and Management. Lausanne: Frontiers Media SA. doi: 10.3389/978-2-88971-640-1

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frontiers
in Ecology and Evolution

EDITORIAL
published: 27 September 2021
doi: 10.3389/fevo.2021.756339

# Editorial: Invaders on the Horizon! Scanning the Future of Invasion Science and Management

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**Keywords: biological invasions, emerging issues, horizon scan, multidisciplinary, technology**

**Editorial on the Research Topic**

**Invaders on the Horizon! Scanning the Future of Invasion Science and Management**

OPEN ACCESS

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*Ana Sofia Vaz*
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***Specialty section:***
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

***Received:*** *10 August 2021*
***Accepted:*** *30 August 2021*
***Published:*** *27 September 2021*

***Citation:***
*Vaz AS, Novoa A, Vicente JR, Honrado JP and Shackleton RT (2021) Editorial: Invaders on the Horizon! Scanning the Future of Invasion Science and Management. Front. Ecol. Evol. 9:756339. doi: 10.3389/fevo.2021.756339*

## INTRODUCTION

In the current era of dynamic human-environment interactions, the phenomenon of biological invasions is a key fingerprint of the Anthropocene (IPBES, 2019). Alongside a changing climate and an increasingly connected world, the rate and number of introduced species, and particularly of established invasive species, is predicted to increase (Seebens et al., 2017). Invasive species are organisms that are introduced (intentionally or accidentally) by humans into regions beyond their natural distributions, where they spread rapidly, representing a major driver of biodiversity and ecosystem change (Stoett et al., 2019), and impact on human welfare, culture, health, and economies (Simberloff et al., 2013).

Anticipating future challenges and opportunities is paramount for adequate strategy development, policy making, risk management, threat identification, and research prioritization in invasion science (Ricciardi et al., 2017). Several studies have been conducted to anticipate future invasion processes and their risks (e.g., Gallardo et al., 2016; Roy et al., 2019; Hughes et al., 2020; Lucy et al., 2020), and thereby pinpoint future monitoring and management measures toward invasive species (e.g., Matlack, 2002; Robertson et al., 2003; Booy et al., 2020).

To effectively anticipate invasions and be prepared for the challenges ahead, some priority issues have been proposed for fostering progress and adjusting the course of invasion research and management (e.g., Caffrey et al., 2014; Ricciardi et al., 2017; Dehnen-Schmutz et al., 2018). Among the proposed priority issues are the development of new technologies to tackle invasive species, the improvement of ecological prediction and knowledge on invasion risks, and the consideration of socio-economic factors in invasion research and management. This Research Topic includes 15 papers exploring these three broad issues, and draws on research papers, reviews and case studies that aim to contribute to advance the way biological invasions can be studied and managed.

## TACKLING INVASIONS WITH NEW TECHNOLOGIES

A set of papers in this Research Topic focus on technological advancements within the fields of genetics, remote sensing, and electric barriers to help with the management of invasive species. Resh et al. show the usefulness of whole genome scanning to determine the source of introduction of invasive species. Using the introduction of the invasive fish *Channa argus* in the United States of America from China as case study, they show how detailed information from whole genome scanning can support the development of targeted strategies to regulate established populations and inhibit further spread. Datta et al. discuss the latest developments of satellite remote sensing and machine learning technologies to improve our capacity to monitor the invasive plant *Eichhornia crassipes* within freshwaters systems. Egly et al. test the efficiency of electric barriers, a potential new technology to manage invasive species, for two invasive invertebrates, *Procambarus clarkii* and *Hyalella azteca*, showing that although the barriers may not slow or prevent spread of invasive invertebrates when attached to water vehicles, they can be useful to prevent the spread of these species through active upstream movement.

## IMPROVING ECOLOGICAL PREDICTION AND KNOWLEDGE

Several papers focus on making predictive ecology more relevant to decision makers. Dinis et al. advance the application of species distribution models to predict the success of the Australian gall-forming wasp, *Trichilogaster acaciaelongifoliae*, as a biocontrol agent for the invasive tree *Acacia longifolia* in Portugal, serving as a framework for similar biocontrol programs in other regions worldwide. Morais et al. use a system dynamic modeling approach to find the cost-effectiveness optimum of control actions toward the invasive shrub *Hakea sericea* under wildfire risk scenarios. Finally, Holenstein et al. model the distribution of 1,602 non-native species in the vicinity of 671 protected areas through time in Norway, highlighting that management efforts should extend beyond the interior of protected areas.

Other papers focus on challenging different hypotheses underlying the invasion process. Using an experimental design in grasslands with the invasive species *Ambrosia artemisiifolia* and *Solidago gigantea*, Yannelli et al. show no evidence to support a limiting similarity effect. Instead, the authors suggest that native communities more effectively suppress invaders that arrived after the natives. Similarly, native communities that produce the most biomass suppress invaders more effectively than native communities that share similar traits with these invaders. Through a multi-species greenhouse experiment with 10 alien invasive plant species in China, Gao et al. find no support for the idea that soil nutrient heterogeneity favors the invasion success of exotic plant species in native plant communities. Other ecological issues pertaining to invasive species, and particularly marine invasions, are also represented in this Research Topic, namely through a review on the potential role of plastic debris as vectors for the introduction of invasive species (García-Gómez, Garrigós et al.), and the observation of rapid invasion processes and impacts caused by the alga *Rugulopteryx okamurae* in Mediterranean and Atlantic waters (García-Gómez, Florido, Olaya-Ponzone, Sempere-Valverde et al.; García-Gómez, Florido, García-Gómez, Florido, de Rada et al.).

## INCLUDING SOCIO-ECONOMIC FACTORS IN INVASION MANAGEMENT

The remaining set of papers presented in this Research Topic focus on the identification of priority invasive species that pose socio-economic risks and impacts. Peyton et al. undertake horizon scanning using expert-elicitation to predict arrivals of invasive alien species that could have adverse human health or economic impacts on the island of Cyprus, and from there, to inform biosecurity policies and communication around invasive species. Likewise, Lenzner et al. conduct a survey among 126 experts in invasion science, suggesting an increasing trend in the spread and establishment of alien species in island systems associated to socio-economic activities and human mediated pathways. Goldsmit et al. adopt a screening assessment tool to identify invasive species of high-risk environmental and economic impacts in Canada, supporting the creation of watch lists to inform adaptive management for preventing the establishment of invaders. Finally, grounded on historical records and paleoenvironmental reconstructions, Costa et al. highlight how trends in international trade, importation of goods, and enhanced connectivity by increasing flights and shipping will probably promote the arrival and spread of several new non-indigenous freshwater species in the Azores archipelago.

## CONCLUDING NOTE

There are no expectations that invasive species will pose fewer challenges in the future. In fact, most predictions suggest the opposite (Seebens et al., 2017), in particular when coupled with other global change drivers like climate change. In order to understand the true complexity of invasion processes and to know how to manage invasive species, it is clear that a multidisciplinary and collaborative approach is needed. A diversity of perspectives grounded on better ecological knowledge, inclusion of socio-economic perspectives and adoption of reliable technologies can elucidate the challenges of invasion science, as well as offer new and more effective ways to manage invasive species and mitigate their impacts. This Research Topic has highlighted the opportunities that the rapidly expanding fields of remote sensing, electric barriers, and genetics bring to the understanding, surveillance, and control of invasions. It has further challenged existing hypotheses and explored new ones to improve knowledge on fast invasions and their interactions with native biota. Additionally, it has emphasized the importance of socio-economic factors in invasion management, namely through the role of humans as vectors of invasions and receivers of their impacts. In a constantly changing world and with rapid advances in science and technology, scanning the future of invasion science may be challenging, yet is imperative to adjust the course of invasion research and management.

## AUTHOR CONTRIBUTIONS

AV, AN, JV, JH, and RS jointly wrote and edited the article. All authors contributed to the article and approved the submitted version.

## FUNDING

The authors acknowledge support from the Ministerio de Ciencia, Innovación y Universidades in Spain [contract reference FJC2018-038131-I], the Portuguese Foundation for Science and Technology [contract references DL57/2016/ICETA/EEC2018/13 and 2020.01175.CEECIND], the Czech Science Foundation [EXPRO grant no. 19-28807X], and the Czech Academy of Sciences [long-term research development project RVO 67985939].

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 17 July 2020
doi: 10.3389/fevo.2020.00238

# Moving Away From Limiting Similarity During Restoration: Timing of Arrival and Native Biomass Are Better Proxies of Invasion Suppression in Grassland Communities

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A challenge in many restoration projects, in particular when establishing *de novo* communities, is the arrival and later dominance of invasive alien plants. This could potentially be avoided by designing invasion-resistant native communities. Several studies suggest achieving this by maximizing trait similarity between natives and potential invaders (“limiting similarity”), but evidence supporting this approach is mixed so far. Others pose that the relative time of arrival by native and invasive species (“priority effects”) could play a stronger role, yet this factor and its interaction with trait similarity is not fully understood in the context of ecological restoration. Thus, we hypothesized that multi-trait similarity would increase suppression of invasive species by native communities, and that the effect would be stronger when natives arrive first. We established two distinct communities of native central European grassland species based on native–invasive trait similarity, and then tested the introduction of invasive *Ambrosia artemisiifolia* and *Solidago gigantea* separately when arriving in the native communities at two times, i.e., sown either at the same time as the natives or 2 weeks after. For the traits selected, our data did not provide evidence for a limiting similarity effect, but rather supported priority effects. Both native communities more effectively suppressed invaders that arrived after the natives. In addition, the native community that produced the most biomass suppressed both invasive species more than the most ecologically similar community. This effect of biomass revealed that prioritizing native–invader ecological similarity can fail to account for other community characteristics that affect invasion resistance, such as biomass. Instead, native communities could be designed to enhance priority effects through the inclusion of early and fast developing species. We conclude that native community composition plays a significant role in

OPEN ACCESS

**Edited by:**
*Ana Sofia Vaz,*
*University of Granada, Spain*

**Reviewed by:**
*Christoph Kueffer,*
*ETH Zürich, Switzerland*
*Pilar Castro-Díez,*
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**Specialty section:**
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

**Received:** *21 April 2020*
**Accepted:** *01 July 2020*
**Published:** *17 July 2020*

**Citation:**
*Yannelli FA, MacLaren C and Kollmann J (2020) Moving Away From Limiting Similarity During Restoration: Timing of Arrival and Native Biomass Are Better Proxies of Invasion Suppression in Grassland Communities.*
*Front. Ecol. Evol. 8:238.*
*doi: 10.3389/fevo.2020.00238*

the establishment success by invasive species, and resource pre-emption seems more significant than trait similarity. In terms of grassland restoration, native species should be selected based on plant traits related to fast emergence and early competitiveness.

**Keywords: biotic resistance, limiting similarity, priority effects, restoration ecology, revegetation**

## INTRODUCTION

According to the latest report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, human activities have significantly altered 75% of the global land surface leading to a sharp rise in extinctions (IPBES, 2019). Land-use change is often associated with ecosystem degradation such as soil erosion or the invasion of alien species, which have negative impacts on biodiversity (IPBES, 2019). The report also stressed the importance of ecological restoration of degraded habitats as a promising strategy to mitigate negative effects on biodiversity as well as its associated ecosystem services. However, a common problem during restoration is the presence of invasive alien species, which jeopardize the success of many projects. In particular, during the establishment of target plant communities, often the slow development of natives favors colonization by alien species, especially in scarcely vegetated sites.

Thus, new approaches are needed to suppress biological invasions during the re-introduction of native vegetation. A promising method is to use a trait-based framework to assemble resistant communities with species that outcompete incoming invasive alien plants (Laughlin, 2014; Yannelli et al., 2018). This approach can be useful to prevent the establishment of such species during early phases of ecological restoration, to ensure the success of the project and the effective use of economic resources (Funk et al., 2008). Yet, though often not considered, the selection of suitable plant traits can be challenging given that other factors might act in concert determining competition outcomes during community assembly (Byun et al., 2018).

At the community level, competition for limiting resources, depicted by niche overlap of native and alien species, can be a significant mechanism that modulates the biotic resistance of plant communities (MacDougall et al., 2009). According to this, alien species would only be able to invade communities consisting of ecologically dissimilar species, a concept described by the "limiting similarity hypothesis" (Shea and Chesson, 2002; Funk et al., 2008). Several studies have explored this concept by using a set of plant functional traits for comparing native and invasive species with respect to ecological similarity (Byun et al., 2013; Yannelli et al., 2018; Catford et al., 2019; Fagúndez and Lema, 2019). There is some evidence that trait similarity between native and invasive species can modulate invasion success, particularly in artificial communities, but results have been conflicting so far (Price and Pärtel, 2013; Yannelli et al., 2018).

For instance, when Yannelli et al. (2017b) tested the effect of multi-trait similarity using European grassland species and two invasive plants (*Ambrosia artemisifolia* and *Solidago gigantea*), they found that the dominance of an ecologically similar native species could suppress the invasives. In a follow-up study, Yannelli et al. (2018) confirmed that while an ecologically similar community suppressed *S. gigantea*, fast seedling emergence and canopy development of the native communities overruled the effects of ecological similarity. In other words, temporal differences in traits that confer an advantage in resource exploitation (i.e., niche pre-emption), were more important for invasion suppression than ecological similarity. The question arising is whether functional similarity is a poor predictor of invasive plants suppression, or if temporal dynamics might influence the strength of such effects. Though poorly explored in terms of restoration, timing of arrival can have a significant effect on community composition and invasion suppression (Hess et al., 2019). Namely, temporal aspects, such as the early emergence of certain species in the community could modulate the effects of niche overlap, leading to mixed results found when testing how effective functional similarity is for restoration.

Early colonizers control the establishment of later-arriving species by occupying safe sites for establishment, regulating their persistence by changing the biotic and abiotic conditions of the restored ecosystem (Helsen et al., 2016). For example, the resource uptake by early emerging species can generate so-called "priority effects" leading to fitness inequalities among early- and late-emerging species (Hess et al., 2020). Priority effects could be beneficial for restoration if they arise from early native colonizers that enhance biotic resistance, or could be detrimental if invasive species are able to colonize first and then dominate. That is, early arriving plants, whether native or invasive, can pre-empt the available resources such as space, nutrients and light, thus reducing establishment opportunities for late-arriving individuals. Such effects can ultimately lead to dominance by the first colonizers (Fukami, 2015), and potentially to the failure of restoration projects.

Thus, even if the composition of the restored native community is manipulated to maximize overall ecological similarity with potential invaders, relative timing of arrival mediated by priority effects would have a stark impact on restoration success. Indeed, invasive species often have high early germination rates and fast seedling development, resulting in a temporal advantage over natives (Wainwright et al., 2012; Wainwright and Cleland, 2013). As indicated by previous research, this means that in order to assure resistance to an invasive species during restoration, community design should not only seek to increase the ecological similarity between native and invasive species, but also needs to ensure that priority effects benefit the natives. However, relative effects of interactions between priority effects and ecological similarity during community assembly have not been well explored in previous studies (Hess et al., 2019).

In this contribution we examine the potential roles of ecological similarity and priority effects with respect to the success of invasive species during early restoration. We do so in a controlled glasshouse environment, but from the perspective of applied restoration. We apply the concept of limiting similarity by designing, *a priori*, native communities that are either more or less similar to the invasive species according to information from plant trait databases. This reflects the information on ecological similarity of native and invasive species likely available to land managers seeking to restore native communities, who may not have extensive resources for on-site characterization of species traits. We test for priority effects by either planting both native and invasive species at the same time, or by planting the invasive species later than the native species. In practice, this scenario could result from land managers timing the planting of native species before the date that invasive species germinate, or from short-term control of invasive species following the planting of native species (Young et al., 2017). We also assess how limiting similarity and priority effects, thus applied, could interact in terms of whether the timing of arrival of invasive species affects their success when arriving in either an ecologically similar or dissimilar native community.

We selected grassland species commonly used in restoration projects, and the two invasive plant species *Ambrosia artemisiifolia* L. and *Solidago gigantea* Aiton. Ecological similarity between native and invasive species was evaluated by classifying them into groups based on functional traits. In a greenhouse experiment, we composed native communities based on plants from the same functional group as the invasive species or from a different group, and then introduced the invasive species to these similar and dissimilar native communities at different arrival times. We hypothesized that: (i) that native communities with a greater ecological trait similarity to the invasive species will more successfully suppress the invader; (ii) native communities will exert stronger suppression on the invasive species due to resource pre-emption when the natives establish earlier; and (iii) that these two factors positively interact to increase the strength of suppression. By designing functionally similar communities with this method we aim to help managers, who are typically in charge of implementing restoration programs, to be able to plan *a priori* which natives are the ones likely to suppress invaders.

## MATERIALS AND METHODS

### Species, Seed Material and Traits Selection

The two invasive alien plant species *Ambrosia artemisiifolia* and *Solidago gigantea* are problematic in many parts of Europe (Kowarik, 2003). *Ambrosia artemisiifolia* was introduced as seed contaminant and is currently present in most European countries albeit with different abundances (Essl et al., 2015). This annual pioneer occurs at disturbed habitats such as roadsides, waste places, construction sites, agricultural fields, abandoned fields, and urban ruderal habitats. In heavily invaded regions it causes crop-yield losses, and its pollen is highly allergenic (Gerber et al., 2011). *Solidago gigantea* was initially introduced to Europe as an ornamental, but has naturalized in many countries, developing dense monospecific stands that inhibit native vegetation (Weber and Jakobs, 2005).

Seeds of *A. artemisiifolia* were collected near river Danube in Vienna, E Austria (48°16′01′′N, 16°22′10′′E), and those of *S. gigantea* were gathered along river Isar in Freising, S Germany (48°23′57′′N, 11°45′16′′E). The native competitors were commercially produced species for restoration purposes, selected from a pool of 28 species with a frequency $\geq$10% occurrence in more than 100 surveys of calcareous grasslands in the north of Munich, Germany (Conradi and Kollmann, 2016). The seed material of these species was supplied by Johann Krimmer (Pulling, Germany) based on local provenances. Species nomenclature follows Wißkirchen and Haeupler (1998).

In order to categorize the study species into functional groups we utilized eight traits, namely, canopy height at maturity, shoot morphology (rosette, hemi-rosette, or non-rosette plants), life form (*sensu* Raunkiaer, 1934), morphology of vegetative organs (rhizome, runner, pleiocorm, and tuft), leaf dry matter, specific leaf area (SLA), seed mass and plant longevity (annual or perennial). These traits are known to be related to different stages such as dispersal, establishment, growth, persistence, as well as the species' competitive ability (Westoby et al., 2002; Funk et al., 2008; Pérez-Harguindeguy et al., 2013). For example, shoot morphology relates to the plant capacity to ground cover, plant height influences resource capitalization such as light but it also affects plant fecundity, SLA and leaf dry matter have found to affect resource allocation and photosynthetic rate, and seed mass is highly associated to early competitiveness and survival (Pérez-Harguindeguy et al., 2013). Longevity was included as a proxy for temporal niche overlaps. Traits categories are rarely clear-cut, but we considered that including some that might seem redundant, would increase the chances of successfully portraying resource use. Trait information was obtained from the databases BiolFlor and LEDA (Klotz et al., 2002; Kleyer et al., 2008).

### Functional Groups and Community Composition

We transformed non-numerical traits to numerical units following Yannelli et al. (2017b). Functional groups were devised by means of cluster analysis, using Gower's similarity coefficient among species and the Ward linkage method (Pla et al., 2012). The analysis yielded three functional groups according to species trait similarities (FG1, FG2, and FG3), with both invasive species falling into FG2 (**Supplementary Figure S1** and **Supplementary Table S1**). We used a MANOVA test to confirm that the three functional groups were significantly different ($F$ = 13.6, $P$ < 0.0001). All analyses of the functional grouping were performed using Infostat (Di-Rienzo et al., 2013).

Previous results from Yannelli et al. (2017b) showed that FG1 has highest, FG3 intermediate and FG2 lowest suppression success. Though not tested at that point, we found indications that early developing of some natives species might modulate the effect of trait similarity as a predictor of invasive species suppression. Therefore, we decided to only use FG1 and FG2 in order to devise native communities for testing the three hypotheses, given FG1's previous success and FG2 potentially being the most similar community. In this study though, we randomly selected nine species that were known to germinate well from each functional group to avoid a richness effect due to lack of emergence (**Table 1**).

## Experimental Design

We performed an additive experiment using a fully randomized design with the treatments "functional group identity of the community" and "time of arrival." The functional group identity treatment had three levels, namely communities composed with native species from either FG1 or FG2, and a control with no natives ("FG1," "FG2," "control"). Specifically, there was a control for each invasive species and timing treatments, consisting of pots in which natives were not sown, and invasives were sown as a monoculture at the different times of arrival. Time of arrival was defined by whether the invasive species was sown at the same time as the natives or 2 weeks later ("same arrival" and "late arrival"). Treatment combinations were tested with the two invasive species separately, and each treatment combination was replicated five times (60 trays in total).

Sowing densities of 3 g m$^{-2}$ were used for native species as is common practice in restoration projects (Kiehl et al., 2010), and 1 g m$^{-2}$ for both invasive species, comparable with densities in soil seed banks (Minchin, 1987; Yannelli et al., 2017b). We filled 40 × 30 × 6 cm$^3$ plastic trays with peat-based substrate (EinheitsErde®, Einheitserdewerke Werkverband e.V., Altengronau, Germany; N, 180 g m$^{-3}$; P, 240 g m$^{-3}$; K, 240 g m$^{-3}$; pH 5.8) and scattered the seeds of native species on top of the soil. The invasive species were sown simulating a seed rain at the same time as the natives or after 2 weeks without disturbing the establishing community for the late arrival treatment. We supplied water daily from above until germination and then switched to watering on demand for 1 h from below the trays.

We carried out the experiment in an unheated greenhouse at the Centre of Greenhouses and Laboratories Dürnast, School of Life Sciences Weihenstephan, Technical University of Munich (48°24′N, 11°41′E). The experiment lasted for 8 weeks starting in June 2014, and had an average temperature of 21 ± 6°C.

**TABLE 1 |** Species composition, families, and functional groups included in the two selected experimental communities.

| Functional group | Species | Family |
|---|---|---|
| FG1 | *Achillea millefolium* | Asteraceae |
| | *Agrostis capillaris* | Poaceae |
| | *Brachypodium pinnatum* | Poaceae |
| | *Briza media* | Poaceae |
| | *Festuca rubra* | Poaceae |
| | *Helictotrichon pubescens* | Poaceae |
| | *Poa angustifolia* | Poaceae |
| | *Potentilla tabernaemontani* | Rosaceae |
| | *Prunella grandiflora* | Lamiceae |
| FG2 | *Buphthalmum salicifolium* | Asteraceae |
| | *Festuca ovina* | Poaceae |
| | *Hieracium pilosella* | Asteraceae |
| | *Sanguisorba minor* | Rosaceae |
| | *Betonica officinalis* | Lamiaceae |
| | *Centaurea scabiosa* | Asteraceae |
| | *Dactylis glomerate* | Poaceae |
| | *Trifolium pratense* | Fabaceae |
| | *Campanula rotundifolia* | Campanulaceae |

## Measurements and Data Analyses

The experiment was terminated after 8 weeks, when *A. artemisiifolia* started flowering to decrease work hazards due to its highly allergenic pollen. At this time, we identified and visually estimated the percentage cover of all plant species growing in the trays for each treatment combination. We then harvested the biomass by cutting all plants 1 cm aboveground and separating natives from invasive species. All plant material was oven-dried for 3 days at 65°C and subsequently weighted.

Aboveground biomass data was log (*ln*) transformed to meet the assumption of a normal distribution. We performed two-way ANOVA to assess differences in invasive biomass among the treatments for each invasive species separately (model: invasive biomass − community identity × time of arrival). *Post hoc* pairwise comparisons were made using the Bonferroni correction. We calculated the overall native community weighted mean trait distance (CWMTD) difference to both invaders weighted by each species cover and assessed its correlation with native biomass. For this, we used the distances calculated using all traits included in the definition of functional groups, as explained in section "Functional Groups and Community Composition." As a proxy for niche similarity, given that we did not measure the traits during the experiments (Yannelli et al., 2017b), we calculated phylogenetic distances by constructing a phylogenetic tree using a tree of all angiosperms as a backbone (Zanne et al., 2014), and calculated distances with the R package *pez* (**Supplementary Figure S2**) to obtain the community weighted distances based on plant cover (CWMPD). We then checked for correlations among potential explanatory variables to avoid collinearity and found that trait and phylogenetic distance differences were highly correlated (Pearson c = 0.81, $P < 0.001$). Given that we found a moderate correlation native biomass and CWMTD (Pearson c = 0.65, $P < 0.01$), we tested which variable was a better predictor of invasive species suppression and selected the native biomass because of its better fit (model: invasive biomass − native biomass × time of arrival).

# RESULTS

All native species selected for our communities were perennials and hemicryptophytes. FG1 was overrepresented by species from the family Poaceae (all but two species) and runners, while FG2 included more families. The rest of the traits were evenly represented in both communities. Although FG2 was supposed to be more like both invasive species than FG1, there were still trait differences between this community and the invasive species (**Table 2**).

**TABLE 2 |** Community weighted means (CWM ± SE) of each numerical trait selected calculated for the two communities (FG1, 2) and average values of the same traits for both invasive alien species (*Ambrosia artemisiifolia* and *Solidago gigantea*).

| Characteristics | FG1 | FG2 | *Ambrosia artemisiifolia* | *Solidago gigantea* |
|---|---|---|---|---|
| | CWM | CWM | | |
| Seed mass (mg) | 0.16 ± 0.03 | 1.60 ± 0.45 | 3.18 | 0.06 |
| Canopy height maturity (m) | 0.33 ± 0.01 | 0.39 ± 0.04 | 0.80 | 1.38 |
| Leaf dry matter (mg) | 222.9 ± 9.86 | 218.2 ± 7.47 | 153 | 308 |
| Specific leaf area ($mm^2$ $mg^{-1}$) | 24.3 ± 1.41 | 26.2 ± 1.25 | 32.10 | 20.30 |
| Proportion runner | 0.39 ± 0.10 | 0.03 ± 0.02 | 0 | 0 |
| Proportion forbs | 0.23 ± 0.05 | 0.13 ± 0.04 | 1 | 1 |
| Proportion grasses | 0.01 ± 0.01 | 0.10 ± 0.04 | 0 | 0 |

We found that functional group identity of the invaded community, time of arrival and their interactions had a significant effect on aboveground biomass of the two invasive species, 8 weeks after sowing. When the invasive *A. artemisiifolia* arrived late, the lowest biomass was found under competition with the FG1 community [mean $ln(\text{mass}) + SE = -3.5 + 0.5$], followed by FG2 [mean $ln(\text{mass}) + SE = 1.3 + 0.3$] and the control [mean $ln(\text{mass}) + SE = 1.4 + 0.7$; **Figure 1** and **Supplementary Tables S2, S3**; ANOVA: interaction $F = 19.4$, $P < 0.001$]. When arriving at the same time, *A. artemisiifolia* biomass did not differ among the functional group communities [FG1 mean $ln(\text{mass}) + SE = 4.2 + 0.2$, FG2 mean $ln(\text{mass}) + SE = 4.5 + 0.1$, control mean $ln(\text{mass}) + SE = 4.61 + 0.1$]. In *S. gigantea*, aboveground biomass was lowest at late arrival in the FG1 community [mean $ln(\text{mass}) + SE = -2.8 + 0.9$], followed by FG2 late arrival [mean $ln(\text{mass}) + SE = -0.2 + 0.5$], and with no significant differences among the other treatment combinations [late arrival control mean $ln(\text{mass}) + SE = 2.1 + 0.2$, same arrival FG1 mean $ln(\text{mass}) + SE = 2.3 + 0.1$, same FG2 mean $ln(\text{mass}) + SE = 3.7 + 0.1$, same control mean $ln(\text{mass}) + SE = 3.6 + 0.2$; **Figure 1** and **Supplementary Tables S2, S3**; ANOVA: interaction $F = 10.6$, $P < 0.001$].

In terms of CWMTD and CWMPD, FG2 was the community with less average distance to both invaders compared to FG1, confirming our initial calculations for designing the communities (**Table 3**). When we assessed the effect of the native species biomass and time of arrival on the invasive species, we found that both variables and their interaction significantly affected biomass of *A. artemisiifolia*, and only time of arrival and the interaction with native biomass for *S. gigantea*. Specifically, performance of both invasive species decreased as the biomass of the native species increased, when native and invasive were sown at the same time (**Figure 2** and **Supplementary Table S4**; Linear model $_{A.artemisiifolia}$: adjusted $R^2 = 0.9$, $P < 0.0001$; Linear model $_{S.gigantea}$: adjusted $R^2 = 0.8$, $P < 0.0001$). When the invasive species arrived late, invasive biomass was consistently lower than when arriving at the same time as the natives.

## DISCUSSION

This study tested whether using limiting similarity to design communities, priority effects and/or their interactions play a role in the suppression of the invasives *A. artemisifolia* and *S. gigantea* during establishment of native grassland communities. With our experimental design and species selection we found evidence for

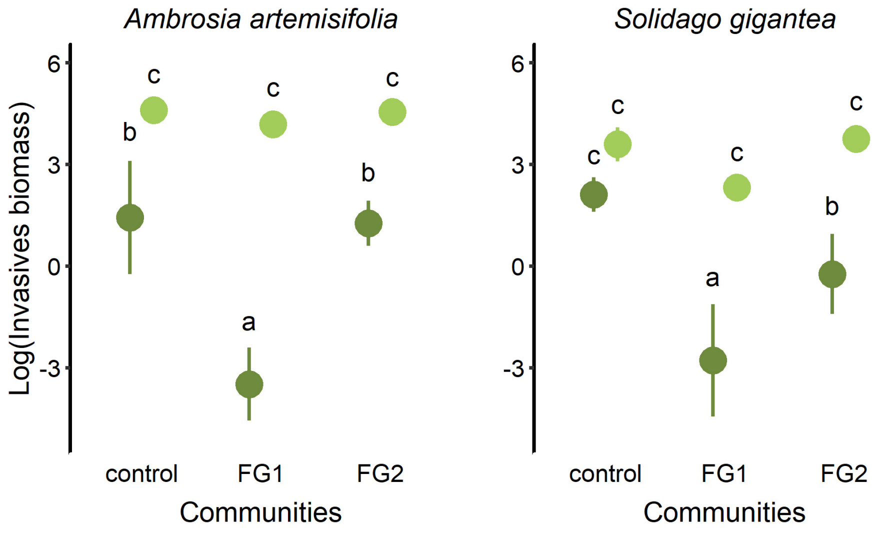

**FIGURE 1 |** Effect of the community type and time of arrival on biomass of the invasive alien *Ambrosia artemisiifolia* and *Solidago gigantea* 8 weeks after sowing (control, monoculture of the invasive plant species; FG1, functional group 1; FG2, functional group 2). Light green symbols indicate simultaneous seeding of native and invasive species, and dark green symbols show results for late arrival of invasive species. ANOVA: interaction $F_{A.artemisiifolia} = 19.4$, $P < 0.001$; $F_{S.gigantea} = 10.6$, $P < 0.001$; letters indicate significant differences among treatments ($P < 0.05$).

**TABLE 3 |** Overall native community weighted mean trait (CWMTD ± SE) and phylogenetic (CWMPD ± SE) distances calculated for the two communities (FG1,2) to both invasive alien species (*Ambrosia artemisiifolia* and *Solidago gigantea*).

| Invasive spp. | Variable | Functional group | Mean distance | SE |
|---|---|---|---|---|
| *Ambrosia artemisiifolia* | CWMTD | FG1 | 0.71 | 0.08 |
| | | FG2 | 0.38 | 0.03 |
| | CWMPD | FG1 | 70.53 | 11.04 |
| | | FG2 | 52.57 | 5.47 |
| *Solidago gigantea* | CWMTD | FG1 | 0.77 | 0.04 |
| | | FG2 | 0.21 | 0.02 |
| | CWMPD | FG1 | 83.37 | 5.81 |
| | | FG2 | 52.21 | 5.74 |

priority effects, with both invasive species disadvantaged (i.e., producing less biomass) by arriving 2 weeks later than the native communities. However, there was no evidence that limiting similarity offered an effective strategy to suppress invasive species, at least in terms of the trait-based design considered in this study. While FG2 was the community considered to be most ecologically similar to both invasive plants, FG1 was more successful in resisting invasion as also observed by Yannelli et al. (2017b). Based on our data, the biomass of the native community was a better predictor of invasive species suppression than CWMTD.

Our results agree with other studies indicating that priority effects can control the establishment of invasive species in plant communities (Dickson et al., 2012; Stuble and Souza, 2016; Delory et al., 2019). For instance, Delory et al. (2019) reported that the invasive species *Senecio inaequidens* had lower biomass when arriving later into a grassland community. However, contrary to their findings, we found that the strength of the priority effect depends on both the composition of the native community and the identity of the invasive species (Young et al., 2017). Namely, we found that FG1 suppressed both *A. artemisifolia* and *S. gigantea* when these species arrived late, while FG2 only exerted a suppression effect on late-arriving *S. gigantea*, and to a lesser extent than FG1 (**Figure 1**).

Differences in community effects and invasive species responses may have begun at planting, with differences in resource availability and sowing densities as reflected by seed masses (**Table 2**). *Ambrosia artemisifolia* has significantly larger seeds compared to *S. gigantea*, which has been previously found to result in taller seedlings, allowing them to avoid early competition for light (Yannelli et al., 2017a). However, because sowing quantities for native seed mixtures were calculated as total weights (as it is commonly done in restoration projects), the overall smaller seeds of the species included in FG1 resulted in higher sowing densities compared to FG2. Previous studies have shown a correlation between seed density of seed mixtures and establishment success, later leading to higher biomass production (Yannelli et al., 2017a, 2018; Byun et al., 2020). Indeed, there is evidence that biomass production by the native communities was important in our experiment, with FG1 having more biomass than FG2 in the presence of *A. artemisifolia*. In contrast, when *S. gigantea* arrives late, both FG1 and FG2 produced a similar

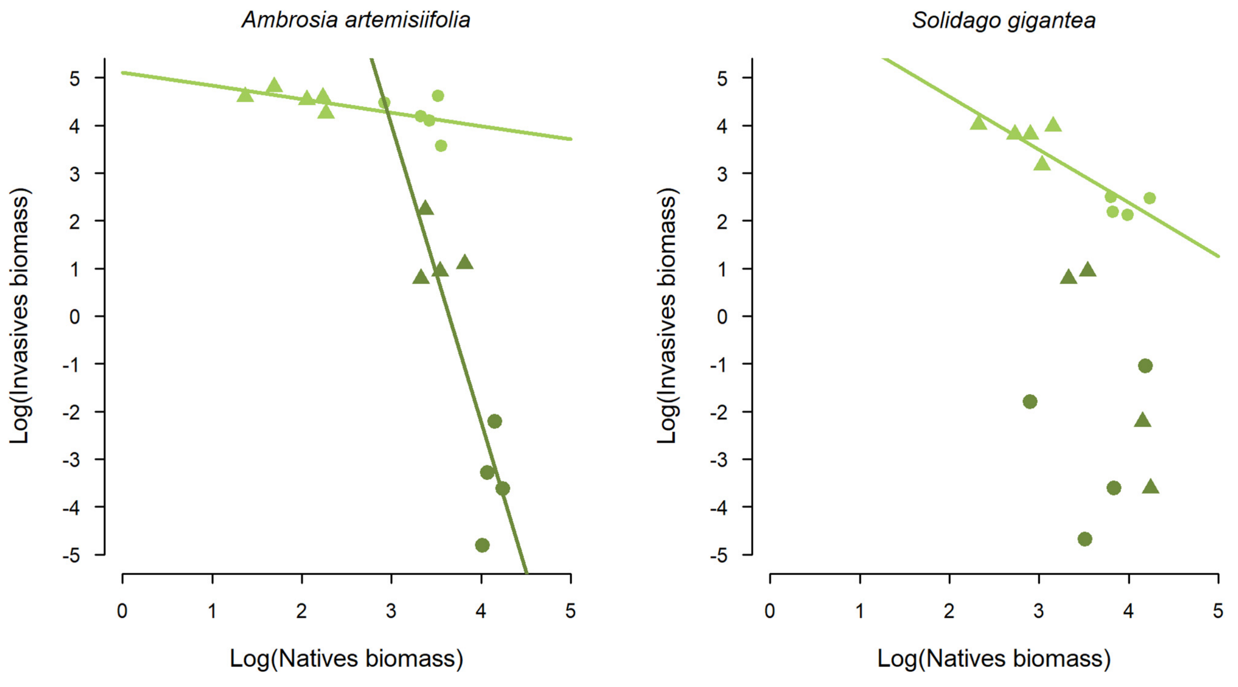

**FIGURE 2 |** Native species biomass effect on the invasive alien *Ambrosia artemisiifolia* and *Solidago gigantea*. Linear model $_{A.artemisiifolia}$: adjusted $R^2 = 0.96$, $P < 0.0001$; Linear model $_{S.gigantea}$: adjusted $R^2 = 0.91$, $P < 0.0001$. *Ln* biomass values for the FG1 communities are indicated in dots, with triangles for the FG2 community. Light green symbols indicate simultaneous arrival of native and invasive species, dark green symbols show results for late arrival of the invasive species.

amount of biomass, which may explain why both communities suppressed this invasive species.

Biomass production reflects resource acquisition of plants and can thus be an indicator of niche pre-emption by early arriving individuals. Studies comparing the relative priority effects of native and invasive species generally find that invasives create stronger priority effects, and that these species typically have faster early growth and biomass production than the native species (Delory et al., 2019; Hess et al., 2019). Invasive species, thus, seem to benefit more from early arrival than native species, as these traits allow them to pre-empt more niche space in a shorter time than natives. Likewise, when invasive and native species arrive simultaneously, species that can establish first and quickly produce a canopy to capitalize on the available resources have an advantage compared to slower ones, independently on whether they are native or invasive (Yannelli et al., 2018). In terms of native target communities for restoration, this can be translated in that faster-growing native communities tend be more effective in suppressing invasive species (Byun et al., 2013). Similar findings have been observed in agriculture, with more productive crop mixes capable of greater resource capture and more effective weed suppression (Finney et al., 2016; MacLaren et al., 2019). Therefore, our results suggest that FG1 was more successful than FG2 to suppress both invasive species due to greater niche pre-emption in the 2 weeks before the invasive species were sown.

It has been hypothesized that, for a given amount of biomass, greater niche pre-emption would occur when early- and late-arriving species are ecologically similar (Vannette and Fukami, 2014). Ecologically similar native species would be expected to capture more of the particular resources required by the invasive species due to greater niche overlap, and so would further suppress the invasive species via limiting similarity. We did not find evidence for this based on our definition of functional similarity. In the presence of *S. gigantea*, biomass production by both native communities was similar, yet the least similar community (FG1) was still more effective at suppressing *S. gigantea*. This indicates that FG1 may suppress invasive species through other mechanisms in addition to the resource capture, such as allelopathy or modification of the soil biota (Price and Pärtel, 2013). For instance, one of the species dominating FG1, *Achillea millefolium* L., has been reported to have allelopathic effects (Verma et al., 2017). Nevertheless, with our experimental design we cannot pinpoint the degree that any of these factors would play in this setting.

That FG1 was more effective at suppressing invasive species than FG2 counters our hypothesis that an ecologically more similar community would more effectively suppress the invasive species via limiting similarity. It should be noted, however, that two important issues arose from the *a priori* trait-based design of the different communities in this study. Firstly, the ecological similarity between the native and invasive species was constrained by the trait space occupied by the native species. The native communities were not highly similar to either invasive species with regard to any particular trait (**Table 2**), which may have prevented us from detecting an effect of ecological similarity. It has been shown though that some plants may be invasive precisely because they possess traits that native plants do not (Divíšek et al., 2018) and so it may be frequently difficult, if not impossible, to design native communities that are sufficiently similar to invasive species to suppress them. Secondly, the *a priori* trait-based design of communities in our study led to other differences between FG1 and FG2 apart from their similarity to the invasive species. These included biomass and sowing density, which can also affect invasion suppression, and thus may have confounded or counteracted any effect of ecological similarity (for example, FG1 had a higher biomass than FG2). Thus, our study did not directly test whether ecological similarity reduced invasion, but has led to the perhaps more practical finding that using limiting similarity as a basis to design restoration communities can unintentionally create other vulnerabilities to invasion if, for example, the resulting community produces less biomass.

Furthermore, similarity in resource capture may not be adequately represented by the functional traits selected in our study, or by the use of trait measurements from databases (see discussion in Yannelli et al., 2017a, 2018). It is possible that FG1 was more similar to both invasive species than FG2 in terms of key traits of early growth and resource capture that were not included in the analysis. Fitness inequalities can emerge when certain species within a functional group can make early use of resources, resulting in competitive hierarchies (Hess et al., 2020). In this regard, Yannelli et al. (2017b) showed that suppression could also be explained by competition with the close relative of both invasive species *Achillea millefolium*. Nevertheless, data from this experiment show that phylogenetic distance differences were highly correlated with trait distance differences, supporting the idea that the traits were not the problem, but rather that other mechanisms might be at play at this stage. One key aspect to consider is that the limiting similarity hypothesis assumes that resources are limited, thus leading to biotic filtering through competition to be the force behind invasive plants suppression. The abiotic conditions of our experiment (e.g., substrate and moisture) may have not portrayed these limiting conditions. If there are still enough available resources, instead of competition-related traits, environmental filters can lead to the success of species with traits associated to an environmental optimum (Funk et al., 2008).

Taken together, our results indicate that the best practice for establishing community resistant to arriving alien invasive species would be to capitalize on priority effects resulting from utilizing early emerging, fast-growing native species at high densities that can quickly develop highly productive communities (**Figure 3**). It is unclear whether limiting similarity could further increase invasion resistance, but we found it to be an impractical basis for the design of restoration communities. Achieving high native-invader ecological similarity was difficult, and prioritizing ecological similarity at the expense of community biomass is counterproductive. These findings should be considered alongside studies spanning longer terms and located in different environments, as our study provides a snapshot of early growth dynamics between native and invasive species in a controlled environment, which may not predict the long-term outcome of a restoration project.

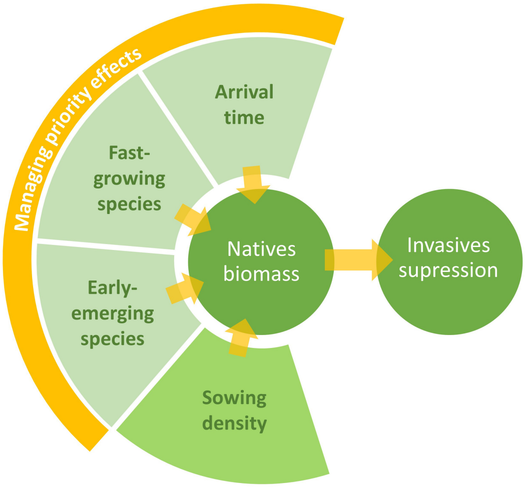

**FIGURE 3 |** Management recommendations for restoration based on our experiment results. We advise to enhance priority effects when designing seed-mixtures, for instance by selecting early emerging and/or fast-growing native species. Increased native species biomass could also be accomplished by assuring that native species dominate the early community. If possible, the use of high sowing density of natives is also encouraged.

## CONCLUSION AND IMPLICATIONS FOR MANAGEMENTS

The approach taken to designing two functionally similar communities in this study aimed to mimic the knowledge available and constraints experienced by land managers implementing restoration programs. It is unlikely that detailed trait information would be available for all species at a given site, so land managers could rely on trait databases to select species. Armed with this trait information, two key community characteristics that land managers could influence are the composition of the native community and its arrival timing relative to invasive species. We found that managing priority effects to advantage native species can increase suppression of invasive species, but that aiming for trait-based ecological similarity can bias other aspects of the community which may reduce invasion resistance, such as total biomass, functional diversity, and phylogenetic diversity. The practical application of limiting similarity is further constrained by difficulties in assessing ecological overlap, and whether it is possible to compose a sufficiently ecologically similar native community within the trait space occupied by a given set of native species (Price and Pärtel, 2013; Divíšek et al., 2018; Yannelli et al., 2018; Hess et al., 2020).

Thus, restoration strategies focused on ensuring priority effects and fast biomass production could be effective. Although priority effects vary between different native and invasive species, and may thus not always be predictable, there are a variety of options for using priority effects in favor of native species in the field (Young et al., 2017; Hess et al., 2019). Plant traits in restoration communities could also be optimized to enhance priority effects, or other significant ecosystem functions (Ostertag et al., 2015), rather than ecological similarity. Based on our results, we suggest that characteristics such as early emergence and fast development can create priority effects, benefiting natives and suppressing invasive species (**Figure 3**).

Finally, we note that these results should be cautiously extrapolated to other contexts as field conditions, where abiotic conditions may significantly change the outcome of native-invasive plant interactions due to other factors becoming limiting. In our experiment there were no resource limitations (i.e., soil nutrients and moisture) or disturbances. Other mechanisms might be more important under conditions such as stress due to extended drought in roadsides, or the opposite with very high nutrient inputs in former agricultural lands. However, given that grasslands are highly dynamic through time, our recommendation of favoring priority effects is pertinent for this early stage of active restoration.

## DATA AVAILABILITY STATEMENT

The datasets generated during this study are available as **Supplementary Information**.

## AUTHOR CONTRIBUTIONS

FY and JK conceived the experiment. FY carried out the experiment, collected, and analyzed the data. All authors were discussed and interpreted the results. FY and CM drafted the manuscript, which was improved by contributions of all authors. All authors approved the submitted version.

## FUNDING

FY was funded by scholarship financed by the European Commission through the Erasmus Mundus Arcoiris program, and a research grant from Dr.-Ing. Leonhard-Lorenz-Foundation.

## ACKNOWLEDGMENTS

We thank Johann Krimmer and Gerhard Karrer for providing the seed material. We are also grateful to Wolf-Christian Saul for suggestions on the figures; and Katie Wolcott, Holger Paetsch, Robert Hansel, Ivonne Jüttner, and the staff at Greenhouse Laboratory Centre Dürnast, for technical help. We thank the two reviewers CK and PC-D for their input to improve this manuscript. We acknowledge support by the Open Access Publication Initiative of the Freie Universität Berlin.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00238/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 04 September 2020
doi: 10.3389/fevo.2020.00280

# What Will the Future Bring for Biological Invasions on Islands? An Expert-Based Assessment

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Biological invasions are a major threat to global biodiversity with particularly strong implications for island biodiversity. Much research has been dedicated towards understanding historic and current changes in alien species distribution and impacts on islands and potential changes under future climate change. However, projections of how alien species richness and impacts on islands might develop in the future are still lacking. In the absence of reliable projections, expert-based assessments are a valuable tool to investigate the importance of different drivers and pathways and the distributions of potential impacts of future biological invasions. These insights can guide subsequent quantification efforts and inform invasive species management and policy. In this study, we performed a survey among 126 experts in invasion science ranging from scientists to managers and decision makers with a focus on island systems until the mid-21st century. The survey revealed that out of 15 drivers, six were considered important by almost all respondents (>90%). Of these, trade and transport was identified as most important at the introduction stage (99.2%) and land use/cover change as most important at the establishment (96.8%) and spread (95.2%) stage. Additionally, the experts considered that alien species were more likely to be introduced (93.7%) and spread (78.6%) as stowaways than through any other pathway. In general, respondents agreed that the impacts of alien species will increase on all types of islands, particularly on oceanic islands, followed by atolls and continental islands. Within islands, terrestrial ecosystems were assumed to be impacted more severely than marine ecosystems. Finally, the survey hints toward the potential for effective communication,

OPEN ACCESS

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**Reviewed by:**
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**Specialty section:**
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *20 May 2020*
***Accepted:*** *10 August 2020*
***Published:*** *04 September 2020*

scientific research and increased pro-active management of alien species on islands to reduce their future consequences. Given the major threat represented by invasive alien species on islands, these results provide crucial insights relevant for global and regional conservation efforts.

**Keywords: biodiversity change, biological invasions, drivers, islands, expert-based approach, plausible futures, scenarios, survey**

# INTRODUCTION

Biological invasions have been identified as one of the major threats to biodiversity worldwide and are an important facet of global environmental change (Maxwell et al., 2016; IPBES, 2018). Islands are hotspots of both endemic (Myers et al., 2000; Kier et al., 2009) and alien species richness (Bellard et al., 2017; Dawson et al., 2017; Essl et al., 2019a) with a subset of alien species – invasive alien species (IAS) – causing negative impacts on biodiversity and driving many recent extinctions (Tershy et al., 2015; Bellard et al., 2016). Current knowledge of the mechanisms driving biological invasions on islands, and of the threats IAS pose on island biota, largely relies on information from several well studied regions (e.g., Macaronesian Islands, Hawaii; e.g., Levine and D'Antonio, 1999; Daehler, 2006; Kueffer et al., 2014), while research in many other island regions is often less extensive or even lacking.

Two issues are crucial in understanding island invasions for conservation and scientific purposes: (i) a comparison of trends in alien species richness in mainland and island regions (Seebens et al., 2018); (ii) how environmental and socio-economic factors could change in relative importance over time for driving future invasions. Improved understanding of these issues should lead ultimately to better knowledge on how invasion impacts could change over time in magnitude and geographical distribution (Lenzner et al., 2019). Answers to these questions are complex, as drivers of biological invasions may change distinctly across taxa, habitats and island regions (Latombe et al., 2019b).

Assessments of potential future invasions and impacts of alien species require the use of scenarios of future trajectories for various facets of specific systems, such as invasion pathways or other drivers of alien species richness, composition, abundance and impact. For most other key drivers of biodiversity change such scenarios have already been established. These include climate change (Moss et al., 2010; IPCC, 2014), land-use change (Hurtt et al., 2009), sea-level rise (Wetzel et al., 2012; Hinkel et al., 2014) and human population change (Lutz et al., 2014). However, comprehensive long-term scenarios are still missing for biological invasions (Lenzner et al., 2019). One reason for the lack of scenarios for potential future states of biological invasions is their complex nature and until recently a lack of comprehensive global datasets (Courchamp et al., 2017). Moreover, biological invasions have arisen from a complex interplay of environmental, socio-economic and societal changes that are difficult to project using classical modeling techniques, like static habitat suitability models, population dynamic models or cellular automata (see Buchadas et al., 2017; Capinha et al., 2018; Lenzner et al., 2019). To overcome such multi-disciplinary challenges, combining classical forecasting techniques with expert-based assessments has proven to be a promising approach (e.g., through qualitative surveys; Berg et al., 2016; Symstad et al., 2017; Reside et al., 2018).

Here, we present the outcome of an expert survey with the aim to identify the importance of different drivers and pathways of biological invasions on islands in the 21st century. Further, based on the knowledge of experts on island ecology and conservation, we aim to gain a better understanding of potential future impacts of biological invasions on islands. The identification of these aspects of biological invasions in the future is crucial for subsequent quantification efforts. Specifically, we focus on three overarching questions: (1) Which drivers will contribute most strongly to alien species richness increase during the introduction, establishment and spread phases of the invasion process? (2) Which pathways will substantially increase alien species richness during the introduction and spread phases of the invasion process? (3) How strongly will different island contexts be affected by an increase in alien species richness?

# MATERIALS AND METHODS

## Driver Selection

A set of 15 major drivers of biological invasions was selected during a workshop on scenarios for biological invasions held in Vienna, Austria in October 2016. A comprehensive list of drivers of biological invasions based on an extensive literature search was compiled prior to the workshop. This list was then provided to a group of invasion scientists with complementary backgrounds in related fields (e.g., land-use change, systems analysis, global environmental change), who assessed the importance of each driver and identified a set of 15 most relevant ones for future biological invasions. For the selection procedure, each workshop participant identified three most important drivers for future invasions and the highest ranked drivers were selected. This set of drivers underlies complementary assessments of biological invasion scenarios that are currently under development (Essl et al., 2019b, 2020; Roura-Pascual et al., under review). We adopted this updated list of 15 drivers and classified them into three thematic groups: (i) environmental change drivers (climate change; ocean acidification; eutrophication and pollution; biodiversity loss and degradation), (ii) socio-economic activity drivers (trade and transport; land use/cover change; socio-economic change; demography and migration) and (iii) society and technology (awareness, values and lifestyle; recreation and tourism; communication and outreach; technology and innovation; cooperation, legislation and agreements; IAS science;

IAS management). For the description of individual drivers and their rationale as provided in the questionnaire, see **Table 1**.

## Survey Design

The questionnaire was divided into four sections: (1) drivers of biological invasions, (2) pathways of biological invasions, (3) effects of alien species richness increases related to three island contexts (i.e., types, systems and habitats), and (4) personal background and expertise of respondents. Section 1 contained questions related to three thematic groups of drivers (see above). For each thematic group, we asked the survey respondents to indicate which of the drivers will strongly increase alien species richness on islands within the 21st century in each of the three main stages of invasion (i.e., introduction, establishment and spread). In section 2, we asked which pathways will substantially increase alien species richness in the introduction and spread stages on islands within the 21st century. The pathways are based on Hulme et al. (2008) and include six categories: stowaway, escape, contaminant, release, corridor, unaided. Section 3 related to the respondents' projection of how strongly an increase in invasive alien species richness in the 21st century will affect different island types (oceanic islands, continental islands and atolls), island systems (marine, freshwater, terrestrial) and habitats (e.g., wetlands, agricultural land; see the full list in **Supplementary Material S2**). Finally, section 4 aimed at collecting background information on the level and area of expertise of the respondents (focal taxonomic groups, geographic regions, island types, and socio-economic status of

**TABLE 1 |** Overview table of the 15 drivers used in the survey and their rationale on how they might affect biological invasions.

| Driver | Rationale |
|---|---|
| **Environmental Change** | |
| Climate Change | Climate change is likely to change mean temperatures, change precipitation patterns etc. and increase the frequency, magnitude and distribution of extreme events, causing disturbances that may create opportunities for alien species. These changes are likely to interact synergistically with biological invasions, although substantial variation exists among taxa and geographic regions. |
| Ocean Acidification | Increasing CO2-levels will increase ocean acidification, thereby affecting water chemistry and native biota |
| Eutrophication and Pollution | Anthropogenic input of pollutants and nutrients via fertilization, run off and atmospheric deposition affect many ecosystems, often promoting opportunistic species. |
| Biodiversity Loss and Degradation | Downgrading and loss of (near-) natural ecosystems, loss of species and functional groups, and positive feedbacks (facilitation, invasional meltdown) may have distinct implications on species compositions. |
| **Socio-Economic Activity** | |
| Trade and Transport | Key features of trade and transport such as the type of goods that are transported, the volumes that are traded, the means and velocity of transport, and the routes of transport are likely to change in the future. Emerging modes of trading (e.g., via internet) that are more difficult to regulate may become more relevant for biological invasions. Trade includes also specific high-risk pathways such as pet and horticultural trade, wood products, ballast water and biofouling, and the emergence of new trade routes that are becoming accessible due to climate change (Arctic shipping routes) or economic interests (Suez Canal and Panama Canal extension, Nicaragua Canal). |
| Land Use/Cover Change | Demand for food supplies, clothing, housing, etc. and for new materials (e.g., for bioenergy production) will likely increase in the 21st century. The resulting changes in land-use (incl. the intentional use of IAS) and land-use intensity may cause losses of ecosystems, degradation of used ecosystems, increase fragmentation and disturbance of ecosystems, and alter resource dynamics. |
| Socio-Economic Change | The level of socio-economic activities (as measured by per capita GDP or similar metrics) is correlated with a wide range of changes of the environment (e.g., resource and energy uses, human mobility, land use) that may be relevant for determining the success of biological invasions. |
| Demography and Migration | Changes in the size and distribution of human populations and migration of humans may influence biological invasions via a range of correlated relevant impacts. |
| **Society and Technology** | |
| Awareness, Values and Lifestyle | The awareness and values of the citizens, stakeholders, business, NGOs and politicians toward biological invasions is important for establishing and implementing invasive alien species (IAS) policies and management. Includes also the views of people who are opposing actions on IAS on ethical grounds (e.g., animal-right movements) or because they consider it unwarranted. |
| Recreation and Tourism | (Outdoor) recreation (incl. gardening, hunting, fishing, hiking) and tourism may impact on biological invasions in a range of different ways. |
| Communication and Outreach | The way, tone and intensity of communication on biological invasions with(in) the wider public and decision makers may influence the public perception of and action on invasive alien species (IAS). |
| Technology and Innovation | The general level of innovation and the extent to which new technologies are introduced, accepted and become widely applied may have substantial implications for biological invasions (e.g., biocontrol safety). |
| Cooperation, Legislation and Agreements | The level of political and institutional cooperation (within and between nations) and the ensuing legislation and agreements on biosecurity and biological invasions, their relationship with other relevant topics (e.g., trade agreements), and the level of implementing these policies. |
| IAS Science | Scientific research on invasive alien species (IAS) may improve the understanding of the invasion process of IAS, improve management techniques, increase data availability on alien species etc. Further, research priorities may be more or less relevant for IAS management and policy. |
| IAS Management | The comprehensiveness and level of implementation of invasive alien species (IAS) management, and the available resources and institutional capacities may be important for the level of biological invasions. |

*Within the questionnaire, the drivers were grouped in three subcategories: (i) environmental change, (ii) socio-economic activity, and (iii) society and technology.*

their study area) and personal information (gender, age, country of home institution).

The questionnaire was implemented using Google Forms©. The respondents had to answer all questions (i.e., they were not able to skip a questions) in the provided order and could only switch to the next page once all questions had been answered. Introductory text and guidance were provided for each question where necessary (see survey layout in **Supplementary Material S2**). Survey responses were in the form of a Likert scale (e.g., strongly disagree < disagree < neutral < agree < strongly agree, or low < medium < strong). The link to the online survey was distributed among the 262 participants of the 3rd International Conference of Island Biology 2019 on La Réunion Island.[1] The survey was sent out twice during the conference and once after the conference (July 2019). Additionally, to reach an even wider audience, the survey was circulated once through relevant mailing lists (August 2019), namely the Island Conservation Network mailing list (Island-L; islands-l@listserv.bgci.org) which has 382 subscribers (as of February 2020) and the ALIENS-L mailing list (aliens-l@list.auckland.ac.nz) of the Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission with 1449 subscribers (as of February 2020).

## Data Preparation and Statistical Analysis

For two of the questions concerning their personal background and study system, the respondents were given the option to provide free text additions to their answers. Where possible, we integrated the additional information on personal background into the default categories, whereas the answers stating a role in policy or government-related positions were assigned to a new additional category named "policy." For the question on study systems, we likewise added an additional post-survey category named "island-like system"; this category encompassed respondents who stated they work with island-like systems (e.g., fragmented landscapes) but not "true" islands. We provide the original data and their category assignment in the **Supplementary Table S1**.

To assess the agreement between respondents on the importance of the different drivers, pathways and island characteristics for each stage of invasion, we fitted proportional odds models with a logit-link function using the '*clm*'-function in the package 'ordinal' (Christensen, 2019) in the statistical programming software R version 3.6.1 (R Core Team, 2019). Individual models were run for each invasion stage for section 1 (three models: introduction, establishment and spread) and 2 (two models: introduction and spread) of the survey. Survey responses were modeled as a function of the individual categorical drivers of invasion. Similarly, three different models were run for section 3 to assess how island types, systems and habitats might be affected in the future. Again, survey responses were modeled as a function of the individual categorical drivers of invasion. Model fit was assessed visually and none of the models violated the proportional odds assumption.

To assess the agreement or disagreement of respondents with the postulated contribution of drivers to future invasions, we evaluated whether given answers differed statistically from a neutral assumption of random answers. To this end, we introduced an additional factor level (i.e., formally a new driver) which was assumed to be assessed at random by all respondents, i.e., we assigned an equal number ($n$ = 25) of responses to the response options "strongly disagree," "disagree," "agree" and "strongly agree" and 26 responses to the neutral response option to resemble the 126 respondents of the survey. We then used this dummy category as a reference level and all the other drivers were tested on whether they differed significantly from it. A significantly higher odds ratio was interpreted as agreement with the postulated effect, a non-significantly different one as neutral and a significantly lower odds ratio as disagreement.

# RESULTS

## Personal Background and Expertise

In total, 126 responses were obtained. If fully attributed to either of the channels through which we distributed the survey, this would equate to response rates of 48% of the conference participants, 32% of the members of the Island-L mailing list, or 9% of the Aliens-L mailing list. The gender ratio among the respondents was 74 men to 50 women with two respondents not providing this information (option "prefer not to say"). The age ranged from <25 ($n$ = 3) to >65 ($n$ = 10) years of age with most people in the age class of "36–45" ($n$ = 51). The responses regarding the location of home institution (which was an open-text question) sometimes included only a country or an island group, which might have somewhat distorted the true picture as many islands are administrative units of certain countries; meanwhile, four participants did not provide a clear answer that could be assigned to a country or island group. Overall, home institutions were distributed across the world with participants situated on islands within all major ocean realms, as well as on all continents, but most participants had their home institutions in Europe ($n$ = 42) followed by mainland United States ($n$ = 28). However, most researchers worked on North Pacific Islands ($n$ = 37), North Atlantic Islands ($n$ = 37), Indian Ocean Islands ($n$ = 33) and islands in the South Pacific Ocean ($n$ = 26). Fewest worked on South Pacific Islands ($n$ = 14), Southern Ocean Islands ($n$ = 6), and Arctic Ocean Islands ($n$ = 1). Finally, 19 respondents indicated that they worked at a global scale. Within their study regions, respondents mainly worked with oceanic islands ($n$ = 108), followed by continental islands ($n$ = 39) and atolls ($n$ = 16). Most islands studied by the respondents are situated in developed countries ($n$ = 85), followed by developing ($n$ = 40) and emerging ($n$ = 39) ones (see the questionnaire in **Supplementary Material S2** for definitions of the socio-economic background of the study regions). Most respondents indicated that their professional background was in conservation management ($n$ = 80), followed by applied research ($n$ = 55), basic research ($n$ = 52), policy ($n$ = 21), other stakeholders ($n$ = 4) and interested citizens ($n$ = 3). Finally, respondents working in the marine realm had highest expertise with vertebrates,

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[1] https://ib2019.sciencesconf.org/

followed by invertebrates, plants and microorganisms. In the terrestrial realm, highest expertise was indicated for plants, followed by vertebrates, invertebrates and microorganisms. All data on personal information and scientific background and expertise are summarized in **Supplementary Figure S1**.

## Drivers of Increase in Alien Species Richness

For the introduction stage, respondents almost uniformly pinpointed trade and transport (99.2% agreement) as an important driver of future alien species richness, followed by recreation and tourism (92.9% agreement) and demography and migration (92.8% agreement), and with some respondents indicating distance by land use/cover change (80.2% agreement), socio-economy (76.2% agreement) climate change (68.3% agreement) and biodiversity loss and degradation (68.2% agreement). The remaining drivers were not considered to contribute to the increase in alien species richness at the introduction stage, i.e., the agreement for these drivers was <50% and the odds ratio of agreement to their contribution was not significantly higher as for the dummy category (see **Figures 1**, **2A** and **Table 2A**).

At the establishment stage, the main drivers of the increase in alien species richness were considered to be land use/cover change (96.8% agreement), biodiversity loss and degradation (96.0% agreement), climate change (93.7% agreement), and demography and migration (85.7% agreement) as well as socio-economy (80.2% agreement), recreation and tourism (74.6% agreement), eutrophication and pollution (73.8% agreement) and trade and transport (65.9% agreement). The remaining drivers were considered to not contribute substantially to alien species richness increase at the establishment stage, with <50% agreement and odd ratios that did not deviate significantly from the dummy category (see **Figures 1**, **2B** and **Table 2B**).

At the spread stage, the drivers of alien species richness were considered to be land use/cover change (95.2% agreement), climate change (91.3% agreement), biodiversity loss and degradation (91.3% agreement), demography and migration (88.9% agreement), recreation and tourism (86.5% agreement), trade and transport (86.5% agreement), socio-economy (81.0% agreement) and eutrophication and pollution (68.2% agreement). The remaining drivers were considered not to contribute substantially to alien species richness increase at the spread stage, with <50% agreement and non-significantly deviating odd ratios from the dummy category (see **Figures 1**, **2C** and **Table 2C**).

Across invasion stages, two drivers – technology and innovation and awareness, values and lifestyle – consistently showed no clear trend, i.e., not deviating significantly from the dummy category. For technology & innovation respondents disagreed slightly more with their importance as a driver of alien species richness (introduction: 30.2% agreement and 38.9% disagreement; establishment: 28.6% agreement and 41.3% disagreement; spread: 27.0% agreement and 41.3% disagreement; see **Figure 2** and **Table 2**), whereas for awareness, values and lifestyle, the results were more balanced (introduction: 38.9% agreement and 35.7% disagreement; establishment: 35.7% agreement and 33.3% disagreement; spread: 34.9% agreement and 32.5% disagreement; see **Figure 2** and **Table 2**).

## Pathway Contribution to Increased Alien Species Richness

For the introduction stage, respondents consistently agreed that all six pathways will substantially contribute to an increase in alien species richness, i.e., > 50% agreement and significantly higher odd ratios than for the dummy category for all of them. The responses identified strongest agreement for species introductions as stowaway (93.7% agreement), followed by escapes (89.7% agreement), contaminants (86.5% agreement), release (74.6% agreement), corridor (67.5% agreement) and unaided (65.9% agreement).

For the spread stage, respondents agreed again to all introduction pathways increasing alien species richness. Strongest agreement was provided for stowaway (78.6% agreement), escape (74.6% agreement) and corridor (71.4% agreement), followed by contaminant (69.8% agreement), unaided (65.9% agreement) and release (64.3% agreement). The overall agreement on pathway contributions to alien species richness was stronger at the introduction rather than the spread stage. See **Figure 3** and **Table 3** for the answer structure and model outputs.

## Effects of Increase in Alien Species Richness Increase

All respondents agreed that each island type would be affected by a future increase in alien species richness, with oceanic islands being affected more strongly (85.7% strong effects) than atolls (57.1% strong effects) and continental islands (52.4% strong effects).

The respondents were also consistently convinced that an increase in invasive alien species richness will have ecological implications across different types of island systems. Strongest effects were expected for terrestrial (81.8% strong effects), freshwater (69.0% strong effects) and marine systems (65.9% strong effects).

Across habitats, strongest effects were suggested for terrestrial coastal habitats (70.6% strong effects), wetlands (67.5% strong effects), dry forests (60.3% strong effects), marine habitats (57.1% strong effects), and settlements (52.4% strong effects). Least strong effects were anticipated for mountain and alpine habitats (43.6% strong effects; odds ratio = 3.6; $p$-value = 0.004) and (semi-)deserts (25.4% strong effects; odds ratio = 0.8; $p$-value = 0.346). For information on the answer structure and model outputs for all impact related analyses see **Figure 4** and **Table 4**.

# DISCUSSION

Our study identifies six drivers that, according to experts, should substantially contribute to alien species richness increase on islands during the 21st century. At the introduction stage these drivers are mainly related to socio-economic activities like trade and transport, recreation and tourism and demography and

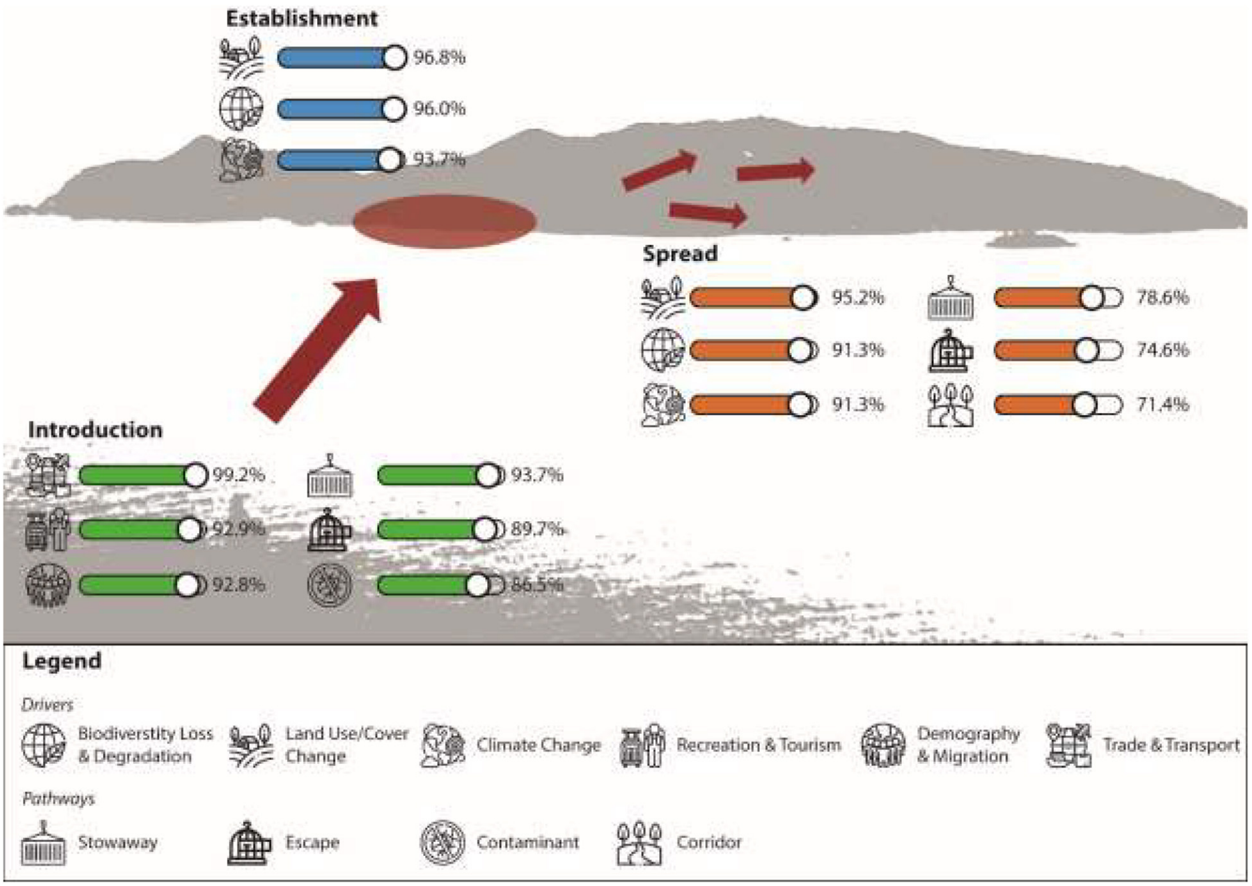

**FIGURE 1 |** Summary of the three main drivers of alien species richness for all invasion stages and the three main pathways of alien species introduction and spread contributing to substantially to an increase of alien species richness. Values are given for the percent of combined answers in the categories "agree" and "strongly agree." Icons are made by "Freepik" from "www.flaticon.com."

migrations. At the establishment and spread stage the drivers change and mainly include environmental and anthropogenic change drivers, namely land use/cover change, biodiversity loss and degradation and climate change (**Figure 1**). Major pathways assumed to substantially increase future alien species richness at the introduction stage are stowaways, escapes and contaminants. At the spread stage the first two pathways remain similar, with contaminants being third in importance (**Figure 1**). All results are discussed in more detail in the following sections.

## Drivers and Pathways

Per definition, alien species are distributed by human agency to regions outside their native range and hence their introduction is inherently tied to the movement of commodities and people around the world (Essl et al., 2018). Thus, respondents unanimously identified socio-economic activity drivers such as trade and transport, demography and migration and recreation and tourism as major drivers of future alien species richness on islands. As current scenarios of global trade assume that traded commodities will double or increase more than 4-fold between 2015 and 2050 (ITF, 2017), the numbers of species introductions are likely to increase for islands in the future. Additionally, the global trade network is projected to change over the course of the 21st century, including a stronger integration of hitherto less well integrated regions, which would change the frequencies, volumes and travel times of traded goods (World Trade Organisation, 2013). With changing frequencies and volumes of traded goods, propagule pressure and colonization will increase, and shorter travel times will increase the survival probability of transported propagules, all contributing to higher alien species richness in respective regions (Seebens et al., 2015; Sardain et al., 2019). Furthermore, the respondents identified stowaways and contaminants as the leading pathways, which is in line with what has been observed in other studies (Hulme, 2009; Pergl et al., 2017). The outlined changes in global trade are not exclusive to islands but apply to all regions worldwide. However, islands typically have high volumes of imports as most commodities are not produced on the islands themselves, which together with higher invasibility compared to mainland regions increases their invasion risk (Hulme, 2009; Moser et al., 2018; OECD, 2018). Hence, on islands the proportion of unintentionally introduced alien species will likely increase. Given the isolated nature of islands, biosecurity measures are more easily implemented compared to mainland

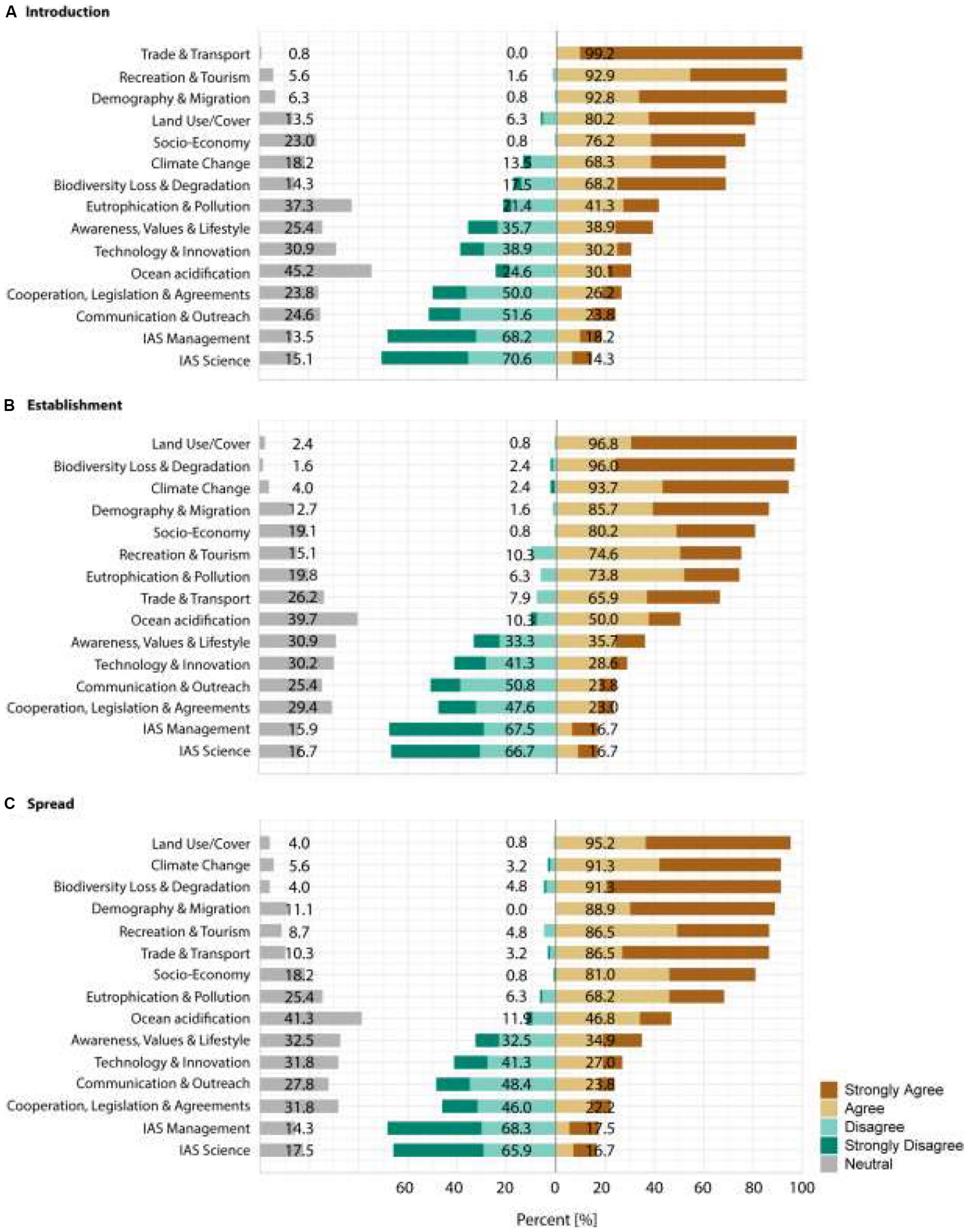

**FIGURE 2 |** Summary of the answers provided by the 126 respondents for the first section of the survey. Respondents were asked which of the drivers will significantly increase alien species **(A)** introductions, **(B)** establishment and **(C)** spread to/on islands in the 21st century. Answers were provided on a 5-point Likert scale with the categories: strongly disagree, disagree, neutral, agree and strongly agree. Shown is the percentage of agreement with each of the categories. Values are given for the percent of answers in the neutral category and for the disagreement and agreement categories grouping the respective two answer possibilities.

**TABLE 2 |** Proportional odds models analyzing if the 15 drivers of biological invasions addressed in the survey significantly increase alien species (A) introduction, (B) establishment, and (C) spread on islands in the 21st century.

**(A)**

| | **Introduction** | | |
|---|---|---|---|
| | **Odds Ratio** | ***CI*** | ***p*** |
| **Predictors** | | | |
| Awareness, Values and Lifestyle | 1.1 | 0.69–1.76 | 0.68 |
| Climate Change | 3.75 | 2.34–5.99 | <0.001 |
| Biodiversity Loss and degradation | 5.03 | 3.09–8.18 | <0.001 |
| Communication and outreach | 0.6 | 0.37–0.95 | 0.03 |
| Cooperation, legislation and agreements | 0.62 | 0.39–0.99 | 0.04 |
| Demography and migration | 13.61 | 8.31–22.27 | <0.001 |
| Eutrophication and Pollution | 1.55 | 0.98–2.45 | 0.06 |
| IAS management | 0.25 | 0.15–0.40 | <0.001 |
| IAS science | 0.23 | 0.14–0.37 | <0.001 |
| Land Use/Cover change | 6.69 | 4.16–10.77 | <0.001 |
| Ocean Acidification | 1.14 | 0.72–1.79 | 0.58 |
| Recreation and tourism | 7.55 | 4.74–12.03 | <0.001 |
| Socio-Economic change | 5.8 | 3.63–9.26 | <0.001 |
| Technology and Innovation | 0.83 | 0.53–1.32 | 0.43 |
| Trade and transport | 74.48 | 37.85–146.58 | <0.001 |
| **Threshold coefficients:** | | | |
| Strongly disagree\| Disagree | 0.12 | 0.08–0.17 | <0.001 |
| Disagree\| Neutral | 0.55 | 0.39–0.78 | 0.001 |
| Neutral\| Agree | 1.84 | 1.30–2.61 | 0.001 |
| Agree\| Strongly agree | 8.41 | 5.86–12.07 | <0.001 |

**(B)**

| | **Establishment** | | |
|---|---|---|---|
| | **Odds Ratio** | ***CI*** | ***p*** |
| **Predictors** | | | |
| Awareness, values and lifestyle | 1.05 | 0.65–1.68 | 0.84 |
| Climate change | 13.01 | 7.96–21.25 | <0.001 |
| Biodiversity loss and degradation | 29.69 | 17.40–50.67 | <0.001 |
| Communication and outreach | 0.58 | 0.36–0.92 | 0.02 |
| Cooperation, legislation and agreements | 0.58 | 0.36–0.92 | 0.02 |
| Demography and migration | 10.24 | 6.28–16.69 | <0.001 |
| Eutrophication and pollution | 4.25 | 2.66–6.80 | <0.001 |
| IAS management | 0.23 | 0.14–0.38 | <0.001 |
| IAS science | 0.25 | 0.15–0.40 | <0.001 |
| Land Use/Cover change | 23.77 | 14.18–39.87 | <0.001 |
| Ocean acidification | 2.11 | 1.33–3.35 | 0.002 |
| Recreation and tourism | 4.4 | 2.74–7.07 | <0.001 |
| Socio-Economic change | 6.21 | 3.87–9.99 | <0.001 |
| Technology and innovation | 0.73 | 0.46–1.17 | 0.19 |
| Trade and transport | 4.2 | 2.60–6.78 | <0.001 |
| **Threshold coefficients:** | | | |
| Strongly disagree\| Disagree | 0.12 | 0.08–0.17 | <0.001 |
| Disagree\| Neutral | 0.5 | 0.35–0.71 | <0.001 |
| Neutral\| Agree | 1.82 | 1.27–2.59 | 0.001 |
| Agree\| Strongly agree | 11.17 | 7.69–16.22 | <0.001 |

*(Continued)*

**TABLE 2 |** Continued

**(C)**

| | **Spread** | | |
|---|---|---|---|
| | **Odds Ratio** | ***CI*** | ***p*** |
| **Predictors** | | | |
| Awareness, Values and Lifestyle | 1.11 | 0.69–1.78 | 0.66 |
| Climate Change | 10.79 | 6.64–17.52 | <0.001 |
| Biodiversity Loss and Degradation | 22.9 | 13.51–38.80 | <0.001 |
| Communication and Outreach | 0.59 | 0.37–0.95 | 0.03 |
| Cooperation, Legislation and Agreements | 0.61 | 0.38–0.97 | 0.04 |
| Demography and Migration | 14.28 | 8.67–23.51 | <0.001 |
| Eutrophication and Pollution | 3.65 | 2.29–5.81 | <0.001 |
| IAS Management | 0.24 | 0.15–0.39 | <0.001 |
| IAS Science | 0.25 | 0.16–0.41 | <0.001 |
| Land Use/Cover Change | 15.54 | 9.46–25.54 | <0.001 |
| Ocean Acidification | 1.93 | 1.22–3.05 | 0.01 |
| Recreation and Tourism | 7.2 | 4.48–11.56 | <0.001 |
| Socio-Economic Change | 6.33 | 3.95–10.15 | <0.001 |
| Technology and Innovation | 0.72 | 0.45–1.15 | 0.17 |
| Trade and Transport | 13.97 | 8.46–23.08 | <0.001 |
| **Threshold coefficients**: | | | |
| Strongly disagree\| Disagree | 0.12 | 0.09–0.18 | <0.001 |
| Disagree\| Neutral | 0.5 | 0.35–0.71 | <0.001 |
| Neutral\| Agree | 1.86 | 1.31–2.65 | 0.001 |
| Agree\| Strongly agree | 9.78 | 6.77–14.14 | <0.001 |

regions, and prevention measures are preferred and most cost-efficient in the context of islands (Leung et al., 2002; Russell et al., 2017).

The identified main drivers of future invasions differ between the introduction and the establishment stages. The drivers associated with the environment (e.g., climate change and biodiversity loss and degradation) and human activity (e.g., land use/cover change, socio-economy or demography and migration) become prevalent at the establishment stage. Anthropogenic habitat destruction has indeed been shown to strongly increase alien species richness and abundance across habitats, at the expense of native species richness (Sanchez-Ortiz et al., 2019). Other anthropogenic disturbances like infrastructure development additionally increase alien species establishment (Alexander et al., 2016; Haider et al., 2018), and urban and artificial environments already hold a high diversity of alien species, often buffering them from adverse environmental conditions (Strubbe and Matthysen, 2009). Finally, anthropogenic habitat transformation (IPBES, 2018), future climate change (Bellard et al., 2013; Harter et al., 2015), and socio-economic activity (Hulme, 2009; Seebens et al., 2015) also indirectly promote the establishment of new alien species through the loss of native biodiversity.

Overall, the participants assessed alien species spread to be promoted by a combination of drivers relevant at the introduction and establishment stages. The respondents particularly agree that land use/cover change, biodiversity loss and degradation and climate change will strongly contribute

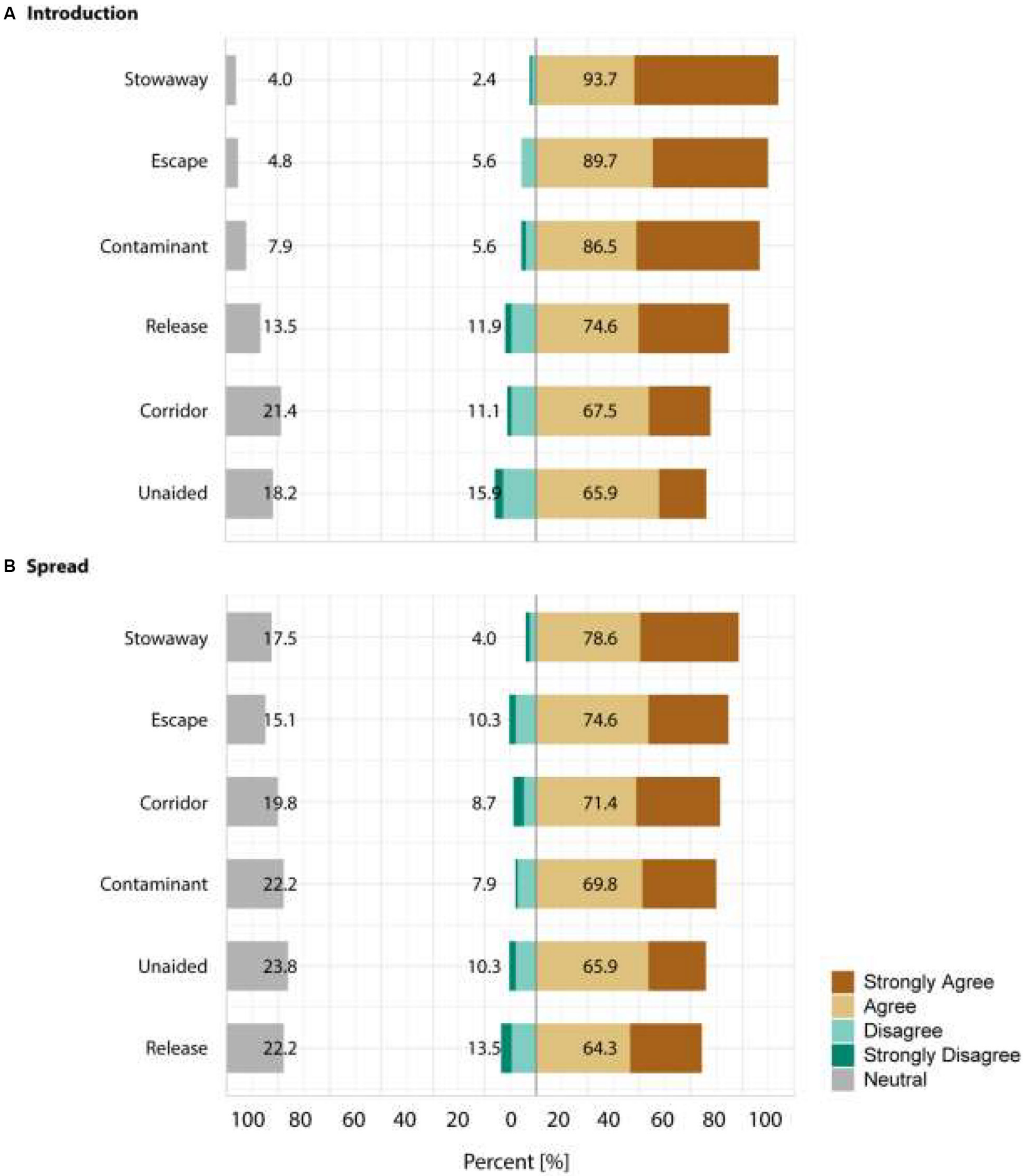

**FIGURE 3 |** Summary of the answers provided by the 126 respondents for the second section of the survey. Respondents were asked which pathway will significantly increase alien species **(A)** introductions and **(B)** spread to/on islands in the 21st century. Answers were provided on a 5-point Likert scale with the categories: strongly disagree, disagree, neutral, agree, and strongly agree. Shown is the percentage of agreement with each of the categories. Values are given for the percent of answers in the neutral category and for the disagreement and agreement categories grouping the respective two answer possibilities.

to an increase of alien species richness in the future. These drivers are closely followed by the same drivers related to the movement of people (e.g., recreation and tourism) and goods (e.g., trade and transport) that are most important at the introduction stage. This assumption appears intuitive, as with ongoing anthropogenic pressure and disturbance more suitable

**TABLE 3 |** Proportional odds models, analyzing which pathway will significantly increase alien species (A) introductions and (B) spread to/on islands in the 21st century.

| | Introduction | | | Spread | | |
|---|---|---|---|---|---|---|
| | **Odds Ratio** | ***CI*** | ***p*** | **Odds Ratio** | ***CI*** | ***p*** |
| **Predictors** | | | | | | |
| Contaminant | 9.15 | 5.59–14.97 | <0.001 | 3.99 | 2.49–6.39 | <0.001 |
| Corridor | 3.27 | 2.05–5.23 | <0.001 | 4.43 | 2.75–7.13 | <0.001 |
| Escape | 8.79 | 5.39–14.31 | <0.001 | 4.49 | 2.80–7.22 | <0.001 |
| Release | 4.9 | 3.03–7.95 | <0.001 | 3.3 | 2.06–5.30 | <0.001 |
| Stowaway | 13.34 | 8.08–22.01 | <0.001 | 6.04 | 3.74–9.74 | <0.001 |
| Unaided | 2.67 | 1.68–4.26 | <0.001 | 3.15 | 1.98–5.02 | <0.001 |
| **Threshold coefficients:** | | | | | | |
| Strongly disagree\| Disagree | 0.15 | 0.10–0.23 | <0.001 | 0.16 | 0.10–0.23 | <0.001 |
| Disagree\| Neutral | 0.57 | 0.40–0.81 | 0.002 | 0.49 | 0.35–0.70 | <0.001 |
| Neutral\| Agree | 1.49 | 1.05–2.12 | 0.026 | 1.74 | 1.22–2.48 | 0.002 |
| Agree\| Strongly agree | 9.93 | 6.78–14.54 | <0.001 | 9.16 | 6.29–13.33 | <0.001 |

habitat for alien species opens up, and increased movement of people and goods then facilitates secondary spread of species within and between island groups. Similar to the introduction phase, unintentional dispersal pathways (i.e., stowaways and contaminants) appear to be most relevant for alien species richness increases at the spread stage.

The strong support for demography & migration across invasion stages as one of the main drivers for alien species on islands is indicative of complex dynamics with other drivers, especially tourism. This appears to contradict future projections of human population trends on islands, which indicate an earlier saturation or even a decrease of human population sizes in island regions like the Caribbean, Oceania or the group of small island-developing countries compared to continental regions (United Nations et al., 2019). Additionally, many small island states face increasing threats of climate change driven sea-level rise, leading to forced migration (Kelman, 2010; Bellard et al., 2014). Emigration often leads to the abandonment of agricultural and highly modified regions and ecosystems. The subsequent succession in these areas often favors the establishment of alien species that are better adapted to human-modified landscapes compared to native species (Rey Benayas et al., 2007; Plieninger et al., 2014). However, many islands are tourist destinations with more people projected to arrive in the future. This emerging economic incentive might result in more people remaining or returning to islands, which would slow down expected demographic trends. Cumulative effects of demography and migration and recreation and tourism with the subsequent development of infrastructure (e.g., roads and hiking trails; Haider et al., 2018; Liedtke et al., 2020) might foster future establishment of alien species as these structures have been shown to be introduction pathways (Toral-Granda et al., 2017). Additionally, cultivation of alien species near tourist accommodations and in public green spaces further increases the probability that these species might jump the fence and establish new populations outside gardens (Cowie et al., 2008; van Kleunen et al., 2018). In several instances, charismatic alien species have as well adopted an economic value for the local community because they attract tourists (Jarić et al., 2020). The relevance of both drivers is in agreement with our study results.

The respondents have different perceptions on the role of technology and innovation for different invasion stages in the future. While there is a tendency toward technology optimism, meaning that technological development will not result in an increase of alien species richness, about one third of respondents have the opposite opinion. This ambivalence in responses might suggest that technological development can have strongly diverging effects on biological invasions. On the one hand, environmental DNA (eDNA) is already used for early detection and rapid response to alien species introductions (Thomsen and Willerslev, 2015; Dougherty et al., 2016). Especially in aquatic systems, eDNA is a highly effective tool to detect alien species at low population densities (Dejean et al., 2012). On islands, the use of eDNA methods will very likely result in better biosecurity effectiveness due to increased early detection rates and improved IAS surveillance (Herder et al., 2014; Tingley et al., 2019). Smart applications for reporting nature observations are used in citizen science projects to detect, monitor and manage alien species (Mannino and Balistreri, 2018; Roy et al., 2018; Johnson et al., 2020) and satellite data are used via remote sensing for alien species mapping and management (Henderson and Dawson, 2009; Robin et al., 2011; Rocchini et al., 2015; Rivas-Torres et al., 2018). On the other hand, e-commerce has resulted in increased alien species introductions and has emerged as a new pathway of introductions that is difficult to manage (Lenda et al., 2014; Humair et al., 2015), which likely explains why the divergence in opinion was higher for the introduction than for the two other stages of invasion. Furthermore, upon the initial introduction of goods to major transportation hubs, secondary spread of alien species might be facilitated by more localized trade with higher transportation frequencies resulting from increased automation using, for example, block chain techniques, reduced transit times, and new consumer good distribution techniques (McKinsey Global Institute, 2019).

A similarly ambiguous assessment was provided for the effects of awareness, values and lifestyle on alien species richness

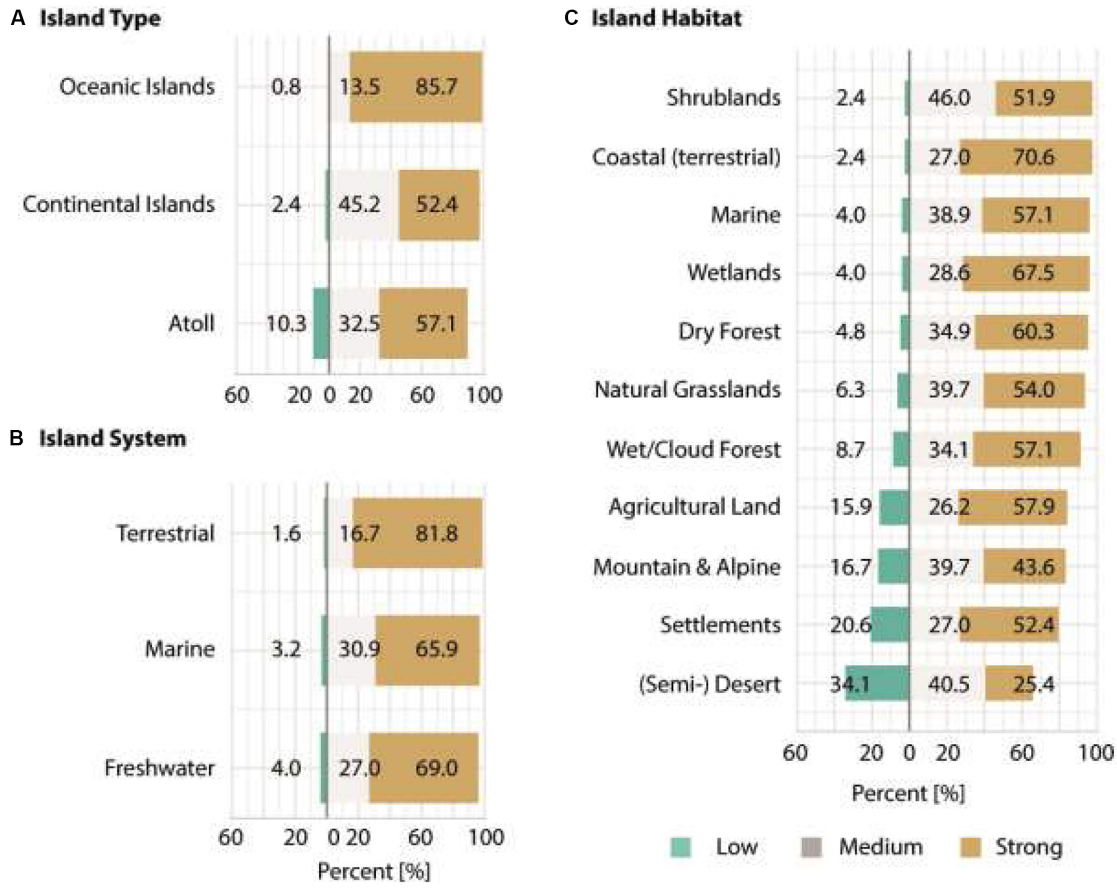

**FIGURE 4 |** Summary of the answers provided by the 126 respondents for the third section of the survey. Respondents were asked how strongly an increase in alien species richness in the 21st century will affect different **(A)** island types, **(B)** island systems, and **(C)** island habitats. Answers had to be provided on a 3-point Likert scale with the categories: low, medium, strong. Shown are the percentage results for each of the categories.

across invasion stages. Prevention of introduction and post-introduction early detection and rapid response are the most effective management options against alien species introduction (Reaser et al., 2020), which is reflected in the responses, showing that this driver has the lowest contribution toward the increase of alien species richness at the introduction stage. At later stages, building awareness might be more difficult, as many alien species that were introduced a long time ago, may have been incorporated culturally or economically into local communities and are now being perceived as "native." For example, the prickly pear (*Opuntia ficus-indica*) was introduced to the Macaronesian islands as an economically important fodder and to obtain red and purple pigment (Prance and Nesbit, 2005). Nowadays prickly pear occurs across all islands and is even used to advertise the beauty of the islands to tourists. Another aspect related to peoples' values toward alien species might lie in their perception of a species based on its charisma (Jarić et al., 2020) and in several instances, alien species management plans have failed due to strong opposition of the general public and activist groups (e.g., Bertolino and Genovesi, 2003; Verbrugge et al., 2013). Finally, there can be important discrepancies in the perception of alien species between archipelagos and even between islands within an archipelago, with people in more remote islands tending to see more benefits in alien species (Meyer and Fourdrigniez, 2019). It is hence important to include all relevant stakeholders in the decision-making process for managing alien species as well as transparently communicating such actions and their relevance to the general public (Novoa et al., 2018; Shackleton et al., 2019). Especially on islands, where native biodiversity is a major economic pillar, such societal transformations with respect to awareness, values and lifestyle are crucial and feasible. However, it is likely that efforts toward societal transformation will not show their result within the near future, a delay, which probably motivated the ambivalent responses in our study.

Finally, the survey shows consensus in that knowledge generation (i.e., IAS science), dissemination (i.e., communication and outreach) and pro-active actions (i.e., IAS management) does not substantially increase future alien species richness. For a long time, islands have been at the forefront of biological research, dating back to Charles Darwin and Alfred Russel Wallace. They have provided valuable testing grounds for theory development and conservation planning (Whittaker and Fernandez-Palacios, 2007). Given their isolated nature and limited spatial extent, biosecurity measures are

**TABLE 4 |** Proportional odds models, analyzing how strongly an increase in alien species richness in the 21st century will affect different **(A)** island types, **(B)** island systems, and **(C)** island habitats.

**(A) Island type**

| | **Odds Ratio** | ***CI*** | ***p*** |
|---|---|---|---|
| **Predictors** | | | |
| Atoll | **3.54** | **2.16–5.81** | **<0.001** |
| Continental Island | **3.43** | **2.12–5.57** | **<0.001** |
| Oceanic Island | **16.47** | **8.88–30.58** | **<0.001** |
| **Threshold coefficients:** | | | |
| Low\| Medium | **0.37** | **0.26–0.54** | **<0.001** |
| Medium\| Stron | **2.7** | **1.87–3.91** | **<0.001** |

**(B) Island system**

| | **Odds Ratio** | ***CI*** | ***p*** |
|---|---|---|---|
| **Predictors** | | | |
| Freshwater | **5.98** | **3.56–10.04** | **<0.001** |
| Marine | **5.31** | **3.19–8.83** | **<0.001** |
| Terrestrial | **11.86** | **6.64–21.18** | **<0.001** |
| **Threshold coefficients:** | | | |
| Low\| Medium | **0.38** | **0.27–0.56** | **<0.001** |
| Medium\| Strong | **2.6** | **1.79–3.76** | **<0.001** |

**(C) Island habitat**

| | **Odds Ratio** | ***CI*** | ***p*** |
|---|---|---|---|
| **Predictors** | | | |
| Agricultural Land | **3.28** | **2.01–5.37** | **<0.001** |
| Mountain and Alpine | **2.01** | **1.25–3.24** | **0.004** |
| Wet/Cloud Forest | **3.61** | **2.22–5.87** | **<0.001** |
| Coastal (terrestrial) | **6.71** | **4.02–11.20** | **<0.001** |
| Dry Forest | **4.3** | **2.64–7.01** | **<0.001** |
| Marine | **3.89** | **2.40–6.31** | **<0.001** |
| Natural Grassland | **3.37** | **2.08–5.44** | **<0.001** |
| (Semi-) Deserts | 0.8 | 0.50–1.28 | 0.35 |
| Settlements | **2.46** | **1.51–4.01** | **<0.001** |
| Shrubland | **3.32** | **2.07–5.34** | **<0.001** |
| Wetlands | **5.73** | **3.46–9.48** | **<0.001** |
| **Threshold coefficients:** | | | |
| Low\| Medium | **0.37** | **0.26–0.53** | **<0.001** |
| Medium\| Strong | **2.67** | **1.89–3.79** | **<0.001** |

substantially easier to implement compared to mainland regions. For example, on the Galapagos Islands, where nature-based tourism is a vital part of the local economy, IAS management is a top priority, with the highest allocated budget of 2.5 million US$/yr in a study of 21 protected areas globally (González et al., 2008; Self et al., 2010; Shackleton et al., 2020). Similarly, New Zealand has some of the strictest biosecurity protocols regarding IAS and an ambitious governmental program ("Predator-Free NZ") aiming to eradicate a selection of invasive predators by 2050 (Russell et al., 2015). This strong history of research communication and acknowledgment of the risk of alien species might contribute to a slowdown of future alien species richness increases on islands even though this conclusion cannot be drawn directly from our survey (see limitations section below for a short discussion).

## Effects of Increases in Alien Species Richness

Most respondents agree that effects of increases in alien species richness will occur mainly on oceanic islands, followed by atolls and continental islands. Oceanic islands show a higher degree of endemism and more disharmonic floras and faunas than the other island types (König et al., 2019; Taylor et al., 2019). This disharmony and proportion of endemism increases with island isolation (Kier et al., 2009; König et al., 2017) and at the same time isolation has been shown to increase island invasibility (Moser et al., 2018). Continental islands, on the other hand, have a more diverse set of native biota including functional guilds usually underrepresented or absent on oceanic islands and thus might be less affected by alien species introductions (Atkinson, 1989; Apanius et al., 2000). However, their proximity to the mainland generally leads to higher anthropogenic use (e.g., higher population sizes) and socio-economic exchange with the mainland (e.g., trade) and higher propagule pressure due to close proximity compared to more distant (usually oceanic) islands, facilitating species introductions (Ficetola and Padoa-Schioppa, 2009).

Respondents assumed strong impacts across all island systems (marine, freshwater and terrestrial) with the latter experiencing most dramatic impacts. While most anthropogenic activity is undoubtedly directed toward terrestrial ecosystems, all systems are tightly interconnected with strong cascading effects across all island ecosystems (Graham et al., 2018). Lower assumed impacts in marine regions might result from the fact that marine regions are less isolated from similar regions than terrestrial island regions and thus are less prone to biological invasions (results only including 17 participants out of 126 with high expertise for at least one marine taxonomic group provide a similar ranking; see **Supplementary Figure S2**). However, marine alien species introductions via the pet trade like the lionfish in the Caribbean (*Pterois volitans* and *P. miles;* Ricardo et al., 2011) have been shown to dramatically affect local environments and species communities (Ballew et al., 2016), highlighting the need to monitor and manage alien species in marine systems. It is noteworthy, that data availability on IAS and their management is particularly scarce in the marine realm (Ojaveer et al., 2015; Latombe et al., 2019a) and that therefore, our results may be influenced by this lack of knowledge and the lower taxonomic expertise of the survey participants as compared to other systems.

Lastly, island habitats that will likely experience the strongest assumed impacts in the future are coastal regions, wetlands and dry forests. Coastal habitats on islands are exposed to highest anthropogenic pressures, with major cities and transportation hubs and highest population densities found there (Russell et al., 2017; Andrew et al., 2019). Dry forest ecosystems tend to be situated close to coastal regions, especially on tropical and subtropical islands (Janzen, 1988). During the initial human colonization, many dry forest ecosystems were degraded and thus became highly vulnerable to species invasions (Janzen, 1988;

Barbé et al., 2015), a trend that will likely persist in the future. Wetlands are probably even more vulnerable to alien species introduction and establishment than other habitats, as native wetland biodiversity (especially amphibians) is highly endemic (Duellman and Trueb, 1994; Inger, 2001). The introduction of invasive species to island wetlands, such as the cane toad (*Bufo marinus*) in the Pacific and Hawaiian Islands (Eldredge, 2000; Ellison, 2009), are a serious threat to local biodiversity. For all other habitats, the respondents agree that at least medium but mainly strong impacts are likely to occur in the future. The only exceptions are agricultural land and settlements, which are probably assumed to be already highly invaded with strong impacts and consequently impacts are assumed to be low in the future, as well as mountain and alpine and (semi-) desert habitats. For the latter two, the survey did not provide a clear trend in impact severity. While both habitats provide environmental conditions that might not suit many alien species, mountains are an attractive destination for tourists who can introduce species to these habitats (Seipel et al., 2012; Alexander et al., 2016).

### Limitations of the Survey

Our study aims to provide a global picture of future drivers of alien species richness on islands by targeting a large panel of diverse respondents. Necessarily, such generality imposes trade-offs with respect to the level of detail in the questions asked and the framing of the drivers, to make them applicable across regions and systems. In section 1, the drivers are defined in a broad sense (see **Table 1**) and it is thus impossible to disentangle their effects at fine scales. For example, climate change encompasses many relevant facets like temperature changes, changes in precipitation patterns or the shifts in extreme event severity or frequency or alterations of oceanic currents and ocean chemistry. All these aspects are very important at the local and regional level, however will very likely vary dramatically between different regions of the world. Follow-up studies that target specific island regions with a more differentiated and context specific set of drivers are necessary to draw such conclusions. An interesting angle would for example be to discriminate between different taxonomic groups, which was not addressed in this study. Our study nonetheless provides a valuable synthesis on which drivers to look at more specifically.

In section 1, we asked the participants to provide an assessment of the degree of their (dis)agreement that certain drivers would increase alien species richness in the future. Disagreement does not necessarily imply the opposite effect, i.e., that the driver leads to a decrease in alien species richness. This is especially relevant for a set of drivers related to communication, management and research, and technology and innovation, for which the participants disagreed with a positive effect of the drivers on alien species richness. We interpreted this result as the expression of a negative relationship between these drivers and species richness, rather than the absence of a relationship. Although this assumption cannot be directly inferred from the survey results, it is based on the similarity in expertise between the co-authors of this study and the respondents and is supported by the existing body of literature.

Expert surveys are only as representative as the sample of respondents that take part in it and the same survey among a different group of experts might produce diverging results. We acknowledge that the participants' background is skewed toward European and Northern American institutions, expertise in terrestrial systems and plants and vertebrates, a reoccurring bias in ecological research (e.g., Troudet et al., 2017; Nuñez et al., 2019). For example, the results regarding alien species richness effects on island types or systems mirror to some degree the expertise of the respondents. We thus cannot exclude any bias in the answers given but are confident of the validity of the results following our discussion and the link to existing literature. Overall, our sample size of 126 participants is substantial and the participants represent all important island regions, major taxonomic groups and relevant scientific fields. We additionally include the answer structure to the survey including only respondents with specific expertise (e.g., for taxonomic groups or realms; **Supplementary Figure S2**).

## CONCLUSION

Our survey provides a comprehensive expert-based assessment of the future importance of drivers, pathways of biological invasions on islands and their effects in different contexts. Experts across different fields of expertise and with varying backgrounds have high confidence that the movements of goods and people and related activities like tourism and recreation will continue to be the major drivers of alien species introduction and subsequent spread in the future. Additionally, biotic and abiotic factors, such as land use/cover change, biodiversity loss and climate change, are acknowledged to play crucial roles in the increase of alien species richness on islands after introduction.

In the meantime, the responses from our survey suggest that experts do not expect a silver bullet that will provide a mid-term solution to alien species-related issues. Technological innovation might play out either way, supporting or restricting alien species introduction and spread. Societal processes like changes in awareness, lifestyles and values are considered to have little to no substantial effects within the next few decades. However, transformation of societal norms is crucial in the long term, and this is supported by a consensus among the respondents. The adoption of strict biosecurity measures and pro-active communication regarding the threats from alien species is believed to lead toward effective prevention and management of biological invasions.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

BL and FE designed the research. BL performed the analysis with input from GL, CC, and FE. BL led the writing of the initial manuscript with input by GL, CC, and FE. BL designed the questionnaire with input by SDHI, HS, PW, GL, CC, and FE. All other authors contributed to writing and commented on the manuscript. All authors contributed to the article and approved the submitted version.

## FUNDING

BL, FE, DM, SD, GL, FC, CD, AT, MG, IK, HS, and NR-P appreciate funding by the BiodivERsA-Belmont Forum Project "Alien Scenarios" (BL, FE, DM, SD, and GL: FWF project no: I 4011-B32; NR-P: AEI PCI2018-092966; MG and IK: BMBF/PT DLR 01LC1807C; HS: BMBF/PT DLR 01LC1807A). FC, CD, and AT were also supported by the AXA Chair in Invasion Biology.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00280/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor declared a past co-authorship with several of the authors, BL, FC, and FE.

*Citation: Lenzner B, Latombe G, Capinha C, Bellard C, Courchamp F, Diagne C, Dullinger S, Golivets M, Irl SDH, Kühn I, Leung B, Liu C, Moser D, Roura-Pascual N, Seebens H, Turbelin A, Weigelt P and Essl F (2020) What Will the Future Bring for Biological Invasions on Islands? An Expert-Based Assessment. Front. Ecol. Evol. 8:280. doi: 10.3389/fevo.2020.00280*

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 19 October 2020
doi: 10.3389/fevo.2020.576667

# Can Niche Dynamics and Distribution Modeling Predict the Success of Invasive Species Management Using Biocontrol? Insights From *Acacia longifolia* in Portugal

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**Specialty section:**
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

**Received:** *26 June 2020*
**Accepted:** *25 September 2020*
**Published:** *19 October 2020*

**Citation:**
*Dinis M, Vicente JR, César de Sá N, López-Núñez FA, Marchante E and Marchante H (2020) Can Niche Dynamics and Distribution Modeling Predict the Success of Invasive Species Management Using Biocontrol? Insights From Acacia longifolia in Portugal. Front. Ecol. Evol. 8:576667. doi: 10.3389/fevo.2020.576667*

Biological invasions are among the major contemporary threats to biodiversity. Biocontrol has a long history as a safe and effective strategy for the control of invasive species in several world regions, yet the life history and ecological requirements of biocontrol agents are often poorly understood. Species distribution models and assessments of niche overlap and dynamics constitute a way to quantify and compare ecological niches and are widely used for predicting biological invasions. While these tools can also be valuable to predict the effectiveness of biocontrol programs and anticipate whether biocontrol agents can establish on areas targeted for control, they remain underutilized for this purpose. In this work, species distribution models and comparisons of niche dynamics are used to predict the success of the ongoing biocontrol program for *Acacia longifolia* in Portugal, and potentially along the Mediterranean Basin, using the Australian gall-forming wasp *Trichilogaster acaciaelongifoliae*, previously released in South Africa. Niches of both the invasive plant and the biocontrol agent were found to be highly similar and to remain conserved through the introduction process. Distribution models identify suitable climatic areas for *A. longifolia* in 19% of the Mediterranean Basin and predict successful establishment of *T. acaciaelongifoliae* in 41% of the suitable area for *A. longifolia,* despite excluding a few locations where very recent establishment occurred. These results allow us to quantify the risk of future *A. longifolia* invasion and potential success of biocontrol, as well as establish a comparative framework for similar programs being considered in other regions of the world dealing with *A. longifolia* invasions.

**Keywords: biological invasions, biocontrol, distribution modeling, niche conservatism, *Acacia longifolia*, *Trichilogaster acaciaelongifoliae***

## INTRODUCTION

Biological invasions are among the major contemporary threats to biodiversity (IPBES, 2019). Specifically, invasive plants cause changes in ecosystem services and functionality, with negative impacts at different levels, e.g., at the level of plant and soil communities and nutrient dynamics (Marchante et al., 2008a,b; Le Maitre et al., 2011; Vilà et al., 2011; Simberloff et al., 2013; Zhang et al., 2019) which are often difficult to reverse or mitigate without active restoration efforts (Le Maitre et al., 2011). Control of invasive species is frequently prohibitively expensive and labor-intensive (Marais et al., 2004). Understanding biological invasion processes is essential for informing decision-making and optimizing the allocation of limited resources. Correlative approaches based on geographic occurrence data (such as species distribution models and multivariate environmental assessments of niche overlap) are valuable to quantify and compare ecological niches and are widely used to predict and improve management of biological invasions (e.g., Broennimann et al., 2007; Vicente et al., 2010, 2011, 2016; Petitpierre et al., 2012; Guisan et al., 2014).

Biological control (hereafter biocontrol) has a long history (over a century) as a safe and effective strategy for the control of invasive plant species (Clewley et al., 2012) in several regions of the world, such as South Africa, Australia, or United States. Yet, the biocontrol of invasive plants was only recently (less than a decade ago) initiated in Europe (Shaw et al., 2018). Classical biocontrol consists on the deliberate introduction of a natural enemy of the target invasive species into a new region invaded by the latter with the objective of mitigating its competitive advantage. Biocontrol agents should be highly specific in order to minimize interactions with native biodiversity in the regions where they are introduced. They should also be able to establish viable populations in the invaded areas. Considering this, it follows that the chances of success of a biocontrol agent are likely to be improved when the ecological requirements for its successful establishment and long-term persistence are similar to those of its target. These requirements, due to their explicitly geographically-oriented and scenopoetic nature, fall within the Grinnellian definition of the ecological niche (*sensu* Peterson et al., 2011). Consequently, the similarity in ecological requirements between species can be characterized using the related concept of niche overlap (*sensu* Warren et al., 2008). Despite this, very few studies so far have explicitly compared biocontrol agents and their respective targets in terms of niche overlap (but see Sun et al., 2017).

*Acacia longifolia* is a *Leguminosae* native to southeastern Australia which has become highly invasive in several exotic locations. Currently, invasive populations of *A. longifolia* are established beyond its native range in south-western Australia (Costello et al., 2000; Impson et al., 2011), as well as in New Zealand, South Africa, Chile, United States (California), Spain (Galicia), and Portugal (EFSA Panel on Plant Health, 2015). Large long-lived seed banks and the ability to germinate following disturbances (particularly fire) are common traits in the *Acacia* genus which account for its high invasive ability (Richardson and Kluge, 2008; Passos et al., 2017). Invasions by *A. longifolia* are associated to changes in soil communities and nutrient cycles (Marchante et al., 2008a,b), disturbance of plant (Costello et al., 2000; Marchante et al., 2003, 2015), and plant-gall communities (López-Núñez et al., 2017), nutrient and water cycling (Werner et al., 2010), and fire regimes. Many of these effects tend to persist after removal, hindering restoration efforts (Marchante et al., 2009, 2011a). Mechanical and chemical control of invasive *Acacia* species is often highly demanding in terms of resources, time and labor (Marais et al., 2004). Reduction of seed banks is particularly problematic, yet essential for the long-term management of invasive plants with high seed production (Richardson and Kluge, 2008). Biological control is consequently often proposed as a valuable and indispensable asset for the management of *Acacia* invasions (Marais et al., 2004; Richardson and Kluge, 2008; Wilson et al., 2011).

*Trichilogaster acaciaelongifoliae* is a gall-forming wasp endemic to Australia. Like all gall-forming insects, it is a highly specific endoparasite which requires successful interaction with its host to complete the life cycle, making it an ideal candidate for biocontrol programs due to the extremely low risk of detrimental interactions with species other than its preferred host, and its inability to expand beyond the distribution of its host (Dennill et al., 1993; Marchante et al., 2011b). Currently, only two programs using *T. acaciaelongifoliae* to control *A. longifolia* exist in the world. It was first introduced in South Africa in 1982 and 1983 (Dennill, 1985, 1988, 1990; Dennill and Donnelly, 1991; Dennill et al., 1993) where it quickly became established through most of the range of *A. longifolia,* successfully decreasing the reproductive potential (89–95%) and vegetative growth (53%) of its target and causing *A. longifolia* mortality in stressful situations (Dennill, 1985, 1988; Dennill and Gordon, 1990). Owing to the success of *A. longifolia* biocontrol in South Africa, a similar program was initiated in Portugal (Marchante et al., 2011b), with the first release of *T. acaciaelongifoliae* in the wild taking place recently, in 2015 (Marchante et al., 2017). As of 2018, four populations of *T. acaciaelongifoliae* established in Portugal, and it is expected that they will maintain the current trend of population growth and expansion, eventually reaching all areas of the country invaded by *A. longifolia* (Marchante et al., 2017). While the program was initiated in Portugal, the agent may potentially spread to other regions of the Mediterranean Basin where adequate environmental conditions are available.

Understanding how the niches of a biocontrol agent and its target species relate in their native distribution may be insufficient to predict the success of biocontrol. The possibility of niche shifts during introduction into new environments (Guisan et al., 2014) may promote niche divergence between the two species, creating a mismatch in environmental space which, when transported to geographic space, can result in inability of the biocontrol agent to establish in areas targeted for control.

This work aims to characterize the realized niches of *A. longifolia* and *T. acaciaelongifoliae* and test the adequacy of *T. acaciaelongifoliae* as a biocontrol agent for *A. longifolia* in Portugal as a function of niche overlap. To accomplish this, we characterize and compare the realized niches of the host plant and of the biocontrol agent in their native and introduced ranges. We also test the hypothesis of niche shifts by comparing realized niches between native and introduced ranges for both species.

We then project the environmental affinities of *A. longifolia* and *T. acaciaelongifoliae* into geographical space using species distribution models, in order to predict the success of the biocontrol program primarily in Portugal but ultimately in the geographically and climatically proximate Mediterranean Basin.

## MATERIALS AND METHODS

### Occurrence Records

A database of *A. longifolia* and *T. acaciaelongifoliae* occurrence records was compiled from the Global Biodiversity Information Facility[1], Atlas of Living Australia[2], South Australian Museum[3] provided upon request by Doctor Peter Hudson, Australian National Insect Collection[4] provided upon request by Doctor Juanita Rodriguez, Invasive Plants in Portugal – Invasoras.pt[5] (Marchante et al., 2017), Southern Africa Plant Invaders Atlas (Henderson, 1999), literature references (Dennill, 1985, 1987; Prinsloo and Neser, 2007; Lado, 2008; Henriksen et al., 2017, 2019); and data provided by authors and collaborators (see section "acknowledgments"). Data collection for *A. longifolia* and *T. acaciaelongifoliae* was independent and no records were shared among the two datasets.

Occurrence data were considered until June 2018. *A. longifolia* records were included taking into account the species *sensu lato* (i.e., including subspecies *A. longifolia longifolia*, *A. longifolia floribunda* and *A. longifolia sophorae*, all considered hosts of *T. acaciaelongifoliae*). In June 2018, *T. acaciaelongifoliae* was still narrowly distributed in Portugal, and thus occurrence records in this area were not considered for subsequent analyses. Records outside the native area (southeastern Australia) and the introduced areas of interest (South Africa and Portugal) were excluded. Uncertain or duplicate records were also excluded. Records with less positional accuracy than 10 km were excluded to maximize geographic coverage while minimizing the loss of spatial precision (Gutiérrez-Rodríguez et al., 2017). To reduce potential sampling bias and spatial autocorrelation, a declustering approach (e.g., Vale et al., 2016; Dinis et al., 2019) was performed using the R package *ecospat* (Di Cola et al., 2017), which consisted of delimiting a 10 km buffer around each record and, when two or more buffers overlapped, removing one of the records randomly. This process was repeated until all remaining records per species had a distance of at least 10 km among them. Clustering was quantified before and after the declustering treatment to ensure an effective decrease in the level of clustering (e.g., Dinis et al., 2019). This was done by calculating the Nearest Neighbor Index in ArcMap 10.1 (Environmental Systems Research Institute, 2012). The final database consisted of 1493 and 140 occurrences for *A. longifolia* and *T. acaciaelongifoliae*, respectively (**Supplementary Table 1**). Occurrences were then further subdivided by geographical areas of interest (southeastern Australia, South Africa, and Portugal; **Figure 1**).

### Bioclimatic Variables and Study Area

The native distributions of *A. longifolia* and *T. acaciaelongifoliae* were represented by southeastern Australia. South Africa and Portugal were selected to represent areas of *A. longifolia* invasion because they are the areas where biocontrol programs with *T. acaciaelongifoliae* are ongoing. The Mediterranean Basin (slightly expanded to include also northern Spain) was selected for model projections for two reasons. First, it is the geographical area of which Portugal is part and *A. longifolia* occurs with invasive potential in several countries in the region (Spain, France, Italy, Lorenzo et al., 2010); at the same time, if *A. longifolia* is present, this creates the possibility of natural dispersion of *T. acaciaelongifoliae*. Second, climatic similarity with the global distribution of *A. longifolia* and *T. acaciaelongifoliae* (predominately in areas of Mediterranean climate) is expected to maximize analogy of predictors.

Nineteen bioclimatic variables representing average contemporary conditions (1970–2000) were obtained from Worldclim v2.0[6] (Hijmans et al., 2005) at a spatial resolution of 10 × 10 km, to ensure consistency with the minimum positional accuracy of the occurrence data. Other scenopoetic candidate variables, such as topography, were considered but ultimately excluded under the assumption that they would not be informative at this spatial resolution, while variables related to soil composition and vegetation cover/structure were excluded due to being dynamically linked to the presence of the target species, consequently falling outside the scope of the Grinnellian niche (Peterson et al., 2011). The temporal extent of the Worldclim dataset overlaps with the collection dates for most occurrence records used in this work, and was therefore selected as an adequate representation of climatic conditions available to the target species upon the time of observation.

Background and training areas were defined by clipping bioclimatic layers to a 200 km buffer surrounding the minimum convex polygon which includes all occurrence records. Buffer size was selected taking into account coarse distributional patterns, topography, vegetation zones, and the limits of climatic regions according to the Köppen-Geiger climate classification (Köppen, 1900) and aims to represent the habitats and areas which the species may have reasonably sampled in each region (Barve et al., 2011) and prevent biases in the sampling of background data, which are known to occur when using overly broad or restrictive training areas (VanDerWal et al., 2009; Anderson and Raza, 2010). This was done separately for each species in each relevant area of distribution, i.e.: for *A. longifolia* in its native range in southeastern Australia as well as the invasive ranges in South Africa and Portugal; and for *T. acaciaelongifoliae* in its native and introduced ranges in southeastern Australia and South Africa, respectively. Analyses were also performed combining the multiple native and introduced/invaded ranges for each species (Australia, South Africa and Portugal for *A. longifolia*, Australia and South Africa for *T. acaciaelongifoliae*,

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[1] https://www.gbif.org/en/

[2] https://www.ala.org.au/

[3] http://www.samuseum.sa.gov.au/

[4] https://www.csiro.au/en/Research/Collections/ANIC

[5] http://www.invasoras.pt

[6] http://www.worldclim.org

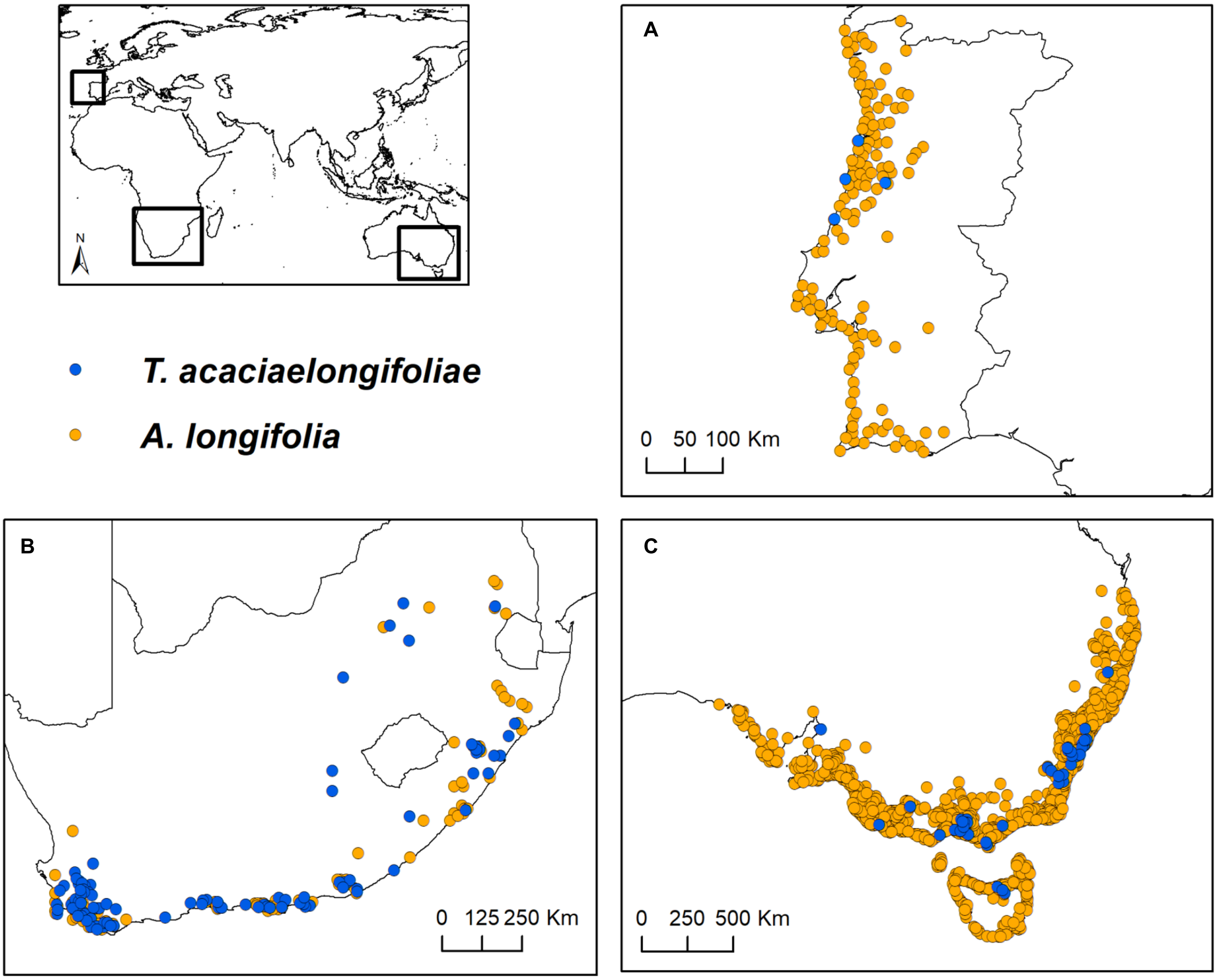

**FIGURE 1 |** Study areas and occurrence records of *Acacia longifolia* and *Trichilogaster acaciaelongifoliae* used in this work. **(A**; top right): Portugal; **(B**; bottom left): South Africa; and **(C**; bottom right): southeastern Australia. *Trichilogaster acaciaelongifoliae* records from Portugal are merely indicative and were not included in any analyses due to their low number and recent establishment.

**Figure 2**). All operations were performed in ArcMap 10.1 (Environmental Systems Research Institute, 2012).

## Niche Overlap

Ecological niches were compared between *A. longifolia* and *T. acaciaelongifoliae*, as well as between different native and introduced areas of each species' distribution (**Figure 2**). For *A. longifolia*, niches were compared between the native range in Australia and the two invaded ranges in South Africa and Portugal. For *T. acaciaelongifoliae*, comparisons took into account only the native and introduced distributions in Australia and South Africa, respectively. All three distribution areas for *A. longifolia* were compared, to avoid assumptions about introduction pathways. Niches were compared in multivariate environmental space using the PCA-env technique (Broennimann et al., 2012). This approach allows for pairwise comparisons of niches between groups, and consists of three steps: (1) calculation of density of occurrences along a multivariate environmental space for both target groups; (2) measurement of the overlap between density distributions of the two groups in environmental space (niche overlap), as defined by Schoener's D metric (Schoener, 1970); and (3) statistical tests of niche equivalency (whether niche overlap is constant when randomizing occurrences among both groups) and niche similarity (whether the niche of one group is more similar to the other than would be expected by chance given the available environmental background), using a permutation-based framework (Warren et al., 2008; Broennimann et al., 2012).

Representation of niches as densities along environmental space allows the quantification of differences in the densities of groups, which can be expressed as niche stability (proportion of niche B overlapping with niche A), niche expansion (proportion of niche B non-overlapping with niche A), and niche unfilling [unique proportion of niche A (i.e., non-overlapping with niche B); Guisan et al., 2014]. These metrics were developed to compare

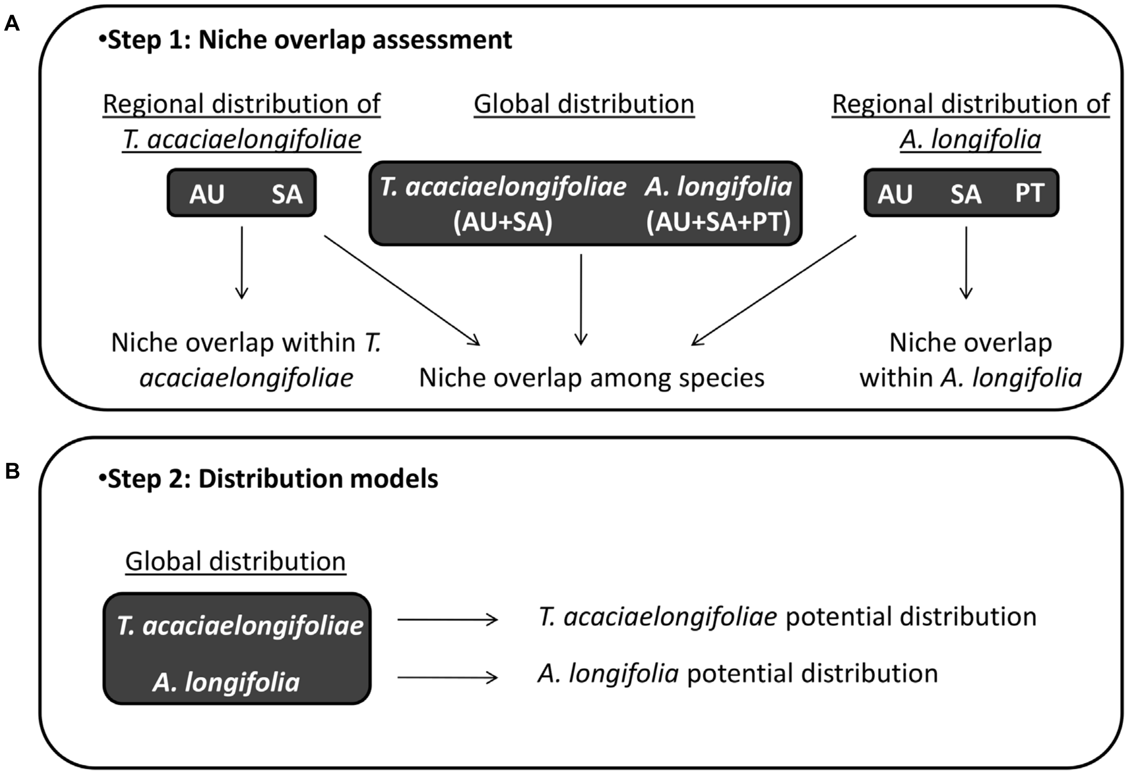

**FIGURE 2 |** Workflow for niche overlap assessments and distribution modeling. Panel **(A**; top): Regional species distribution datasets were compared to assess niche conservatism for *Acacia longifolia* and *Trichilogaster acaciaelongifoliae.* Niche overlap among species was quantified (overlap), tested (equivalency and similarity), and characterized (stability, expansion, and unfilling) to assess ecological overlap in environmental space. Panel **(B**; bottom): Distribution modeling was used to project ecological overlap into geographic space and predict the potential ability of *T. acaciaelongifoliae* to establish in areas susceptible to *A. longifolia* invasion in the Mediterranean basin. Acronyms: AU: Australia, SA: South Africa, and PT: Portugal.

native and exotic niches, and represent the proportion (0–1) of the realized niche that remains constant (stability), is gained (expansion), or is lost (unfilling) during introduction/invasion. Application outside of an explicit comparison of native vs introduced ranges (such as when comparing two unrelated taxa like *A. longifolia* and *T. acaciaelongifoliae*) requires an arbitrary assignment of each group to either niche A or B, which will alter the order in which niche expansion and unfilling are calculated but will not affect the final results or interpretation. Background areas for each group were spatially delimited using the same areas used for calibration of niche models. For each pairwise comparison, background areas of the two groups under comparison were merged. Environmental space was defined by the 19 bioclimatic variables available from Worldclim v2.0 (Hijmans et al., 2005), at a resolution of 10 × 10 km. Though several of these variables are correlated in geographic space, the PCA-based approach addresses this by creating an orthogonal linear combination of the original variables. This approach allows the inclusion of all available bioclimatic variables, maximizing the environmental variance under consideration for niche assessments and minimizing assumptions about variable importance. Given what little is known about the ecology of *T. acaciaelongifoliae,* we opted to minimize such assumptions. Niche overlap was calculated and niche equivalency and similarity tests were performed among regions for each species, and across species. We also calculated metrics of niche stability, expansion and unfilling using the same framework. For all tests among species, *A. longifolia* was considered as group A and *T. acaciaelongifoliae* as group B. All analyses were performed in the R package *ecospat* (Di Cola et al., 2017).

## Species Distribution Models

Based on the evidence for niche conservatism for both *A. longifolia* and *T. acaciaelongifoliae* (see Results section), species distribution models were calibrated using all available records for southeastern Australia, South Africa and (for *A. longifolia*) Portugal. This allows maximization of the number of occurrence records used to train the models and a better sampling of relevant environmental gradients. To avoid overparametrization, distribution models were developed using a subset of the bioclimatic variables used for niche overlap analysis. This approach precludes direct comparison between the two methods. Consequently, we treat the distribution models strictly as niche-based tools for predicting distributions rather than accurate representations of the niches, relying solely on the niche overlap tests for any inferences regarding the dynamics and relationships of niches. Spatial correlation between bioclimatic variables was assessed in ArcMap 10.1 (Environmental Systems Research Institute, 2012), and multicollinearity was assessed by calculating the Variance Inflation Factor (VIF) using the *usdm* package in R (Naimi et al., 2014). When two or more variables were highly correlated, preference was given to the one with the most biological sense. A set of five and six slightly correlated (Pearson's $r < 0.7$) and non-collinear variables (VIF $< 5$; e.g., Vicente et al., 2013) were selected to create models for *T. acaciaelongifoliae* and *A. longifolia*, respectively, (**Table 1**). An ensemble modeling approach was performed in the R package *biomod2* (Thuiller et al., 2009) using a combination of seven modeling techniques: Generalized Linear Models (GLM), Generalized Boosting Models (GBM), Flexible Discriminant Analysis (FDA), Classification Tree Analysis (CTA), Multivariate Adaptive Regression Splines (MARS), Random Forests (RF), and Maximum Entropy (MAXENT). Models were created using 5 datasets of 1000 pseudoabsences randomly distributed through the training areas, and 8 replicates were performed for each combination of pseudoabsence dataset and modeling algorithm, for a total of 280 models per species. Each model was calibrated setting aside 30% of available presence records for model evaluation. The resulting testing datasets were used to evaluate model discrimination by calculating the area under the curve of the receiver operating characteristic curve (AUC), and ensemble models across all modeling techniques were created for each species (e.g., Petitpierre et al., 2017), using the mean of all models where AUC $> 0.7$. Individual models were projected for the Mediterranean Basin and binary ensemble models were created using the Maximized Sum Threshold criteria (MST; Cantor et al., 1999), implemented in *biomod2* under the "binary.meth = 'ROC'" argument (Thuiller et al., 2009). This method selects the threshold which maximizes the sum of sensitivity and specificity. We opted to use this approach due to its good general performance in comparative studies and particularly for its superior performance with low-prevalence datasets and ability to minimize omission errors, which are generally more costly in conservation applications such as identifying areas under risk of biological invasion (Liu et al., 2005; Jiménez-Valverde and Lobo, 2007). The importance of environmental variables for each model was determined by average permutation importance (Phillips et al., 2006).

# RESULTS

## Niche Characterization

Niche overlap among *A. longifolia* was overall low between the three regions (less than 0.5, with 0 corresponding to no overlap and 1 to complete overlap), with the greatest overlap occurring between *A. longifolia* in South Africa and Portugal (0.416; **Table 2**). Niche equivalency, i.e., whether niche overlap remains constant when randomizing occurrences among groups, was found in all pairwise tests except for *A. longifolia* in Australia vs. Portugal and South Africa vs. Portugal. Niche similarity, i.e., whether groups are more similar than expected considering available background, was found in all pairwise tests. Similar niche dynamics were found for all *A. longifolia* comparisons, with predominant niche stability ($>0.89$), analogous niches across regions and very little expansion into novel areas of environmental space during introduction. Niche unfilling, i.e., areas of environmental space present in original range but not after introduction, ranged between 0.2 and 0.26 for all pairs except South Africa vs. Portugal, which had very little unfilling ($<0.01$). For *T. acaciaelongifoliae* in Australia vs. South Africa, niche unfilling was of similar magnitude to *A. longifolia* (0.25), but niche expansion was much more pronounced (0.56), with a corresponding decrease in niche stability (0.44; **Table 2**).

For comparisons between *A. longifolia* and *T. acaciaelongifoliae*, niche overlap ranged between 0.53 (in Australia) and 0.85 (in South Africa). The niches of the two species were found to be equivalent and similarity was not rejected in any pairwise test. Niche stability was higher than 0.96 in all comparisons, with corresponding low values of niche expansion from *A. longifolia* to *T. acaciaelongifoliae* ($<0.04$). Niche unfilling from *A. longifolia* to *T. acaciaelongifoliae* was lowest in South Africa (0.05) and highest in Australia (0.23; **Table 2**). All significant ($p$-value $< 0.01$) niche similarity tests corresponded to values of overlap greater than the distribution

**TABLE 1 |** Variable ID and minimum, maximum, and mean values across model training areas for *Acacia longifolia* and *Trichilogaster acaciaelongifoliae* of ecogeographical variables used in model creation.

| | | ***Acacia longifolia*** | | | ***Trichilogaster acaciaelongifoliae*** | | |
|---|---|---|---|---|---|---|---|
| | | **Min** | **Max** | **Mean** | **Min** | **Max** | **Mean** |
| BIO2 | Mean diurnal range (C°) | | | | 5.28 | 18.04 | 12.37 |
| BIO3 | Isothermality (%) | 33.02 | 62.67 | 48.95 | 36.18 | 63.39 | 49.77 |
| BIO4 | Temperature seasonality | 201.10 | 634.90 | 426.80 | | | |
| BIO6 | Min temperature of coldest month (C°) | −6.15 | 13.42 | 3.18 | | | |
| BIO9 | Mean temperature of driest quarter (C°) | 0.50 | 25.03 | 15.93 | | | |
| BIO13 | Precipitation of wettest month (mm) | | | | 20.00 | 299.00 | 91.38 |
| BIO14 | Precipitation of driest month (mm) | 1.00 | 119.00 | 26.93 | 2.00 | 119.00 | 25.85 |
| BIO15 | Precipitation seasonality | | | | 8.55 | 87.14 | 39.22 |
| BIO19 | Precipitation of coldest quarter (mm) | 11.00 | 842.00 | 174.60 | | | |

*Variables are represented only for the species in which they were utilized for model creation.*

of pseudoreplicates, indicating that the groups are more similar than expected considering the available background.

## Species Distribution Models

All 280 models per species had AUC values above 0.7 and were thus included in the ensembles. AUC values for *A. longifolia* models ranged between 0.79 and 0.94, with a weighted average of 0.90 ± 0.02 (±SD). AUC of models for *T. acaciaelongifoliae* ranged between 0.71 and 0.92, with a weighted average of 0.85 ± 0.04 (±SD; **Table 3**).

Temperature seasonality (BIO4), minimum temperature of the coldest month (BIO6), and precipitation of the coldest quarter (BIO19) were the most important variables for the *A. longifolia* models, with marginal contributions from the remaining variables. Variable importance for *T. acaciaelongifoliae* was less straightforward, with all variables contributing somewhat to the models, yet isothermality (BIO3) and mean diurnal range of temperature (BIO2) were the variables with the most explanatory power (**Table 3**).

Suitable areas for *A. longifolia* were predicted through the Atlantic coast of the Iberian Peninsula and Morocco, in some areas extending up to 280 km inland (**Figure 3**). Suitability for *A. longifolia* was also identified in northern Spain, southern France, some areas of the Italian and Balkan peninsulas (particularly along the Adriatic coast), most of the Mediterranean coast of North Africa and the Middle East and all Mediterranean archipelagos. *T. acaciaelongifoliae* is predicted to have suitable climatic conditions in most of the Iberian coastline (except for a gap of approximately 300 km in northern Portugal), the entirety of the coastline of Morocco, most of the Mediterranean areas of Libya, Egypt, Israel, and Palestine and areas in the Adriatic coast and in the islands of Cyprus, Sicily and the Aegean sea (**Figure 3** and **Supplementary Figure 1**). In total, 19% of the total area of the Mediterranean basin was predicted to be suitable for *A. longifolia*, and 41% of the area identified as suitable for *A. longifolia* is also predicted as suitable for *T. acaciaelongifoliae*. Currently established population of *T. acaciaelongifoliae* were all correctly identified as suitable by the modeling approach used, with the exceptions of the population located in the city of Coimbra (**Figure 3** and **Supplementary Figure 1**) and a few very recently observed populations in the northern coast (not shown).

# DISCUSSION

## Niche Dynamics of *A. longifolia* and *T. acaciaelongifoliae*

While there are differences in niche dynamics between different ranges of *A. longifolia* and *T. acaciaelongifoliae*, the results are overall consistent with niche conservatism during the invasion/introduction process, respectively. Evidence for niche similarity on all cases suggests that observed differences in niches are related to differences in habitat availability and/or introduction pathways between Australia, South Africa and Portugal. Comparisons between Australia and South Africa revealed contrasting patterns for the two species, with *A. longifolia* invasion being associated with niche stability, and *T. acaciaelongifoliae* introduction being associated with strong niche expansion. It's unlikely that this reflects actual expansion of *T. acaciaelongifoliae* into new environments in

**TABLE 2 |** Niche overlap and dynamics between all pairs of native (AU: Australia) and introduced (SA: South Africa; PT: Portugal) *Acacia longifolia* (Al) and *Trichilogaster acaciaelongifoliae* (Ta).

| | Pairs | PC1 | PC2 | Niche overlap (D) | Equivalency (sig = non-eq.) | Similarity A- > B | Similarity B- > A | Expansion | Stability | Unfilling |
|---|---|---|---|---|---|---|---|---|---|---|
| *Acacia longifolia* | AU-PT | 44.27 | 20.19 | 0.18 | 0.001* | 0.052 | 0.07 | 0.084 | 0.916 | 0.257 |
| | AU-SA | 37.24 | 26.64 | 0.33 | 0.263 | 0.012 | 0.009* | 0.102 | 0.898 | 0.211 |
| | SA-PT | 45.01 | 19.67 | 0.416 | 0.001* | 0.011 | 0.013 | 0.06 | 0.94 | 0.004 |
| *Trichilogaster acaciaelongifoliae* | AU-SA | 37.24 | 26.64 | 0.157 | 0.987 | 0.141 | 0.134 | 0.561 | 0.439 | 0.254 |
| Among species | AlSA-TaSA | 35.02 | 27.08 | 0.846 | 0.604 | 0.004* | 0.005* | 0.039 | 0.961 | 0.053 |
| | AlAU-TaAU | 48.96 | 22.37 | 0.526 | 0.94 | 0.094 | 0.084 | 0.001 | 0.999 | 0.227 |
| | AlAll-TaAll | 39.71 | 24.08 | 0.556 | 1 | 0.09 | 0.09 | 0.013 | 0.987 | 0.106 |

*Comparisons are made within each species and between the two species considering the native (AU) and introduced (SA) ranges where both occur. Tests between the two species considering the full range where they occur (AU, SA and PT for A. longifolia; AU and SA for T. acaciaelongifoliae) are also presented (AlAll-TaAll). Percentage of explained variation of the two first principal component (PC1 and PC2), niche overlap (Schoener's D), p-values of equivalency and similarity tests ($p < 0.01$, significant values marked with *) and indices of niche expansion, stability and unfilling are presented. All tests of niche similarity presented null distributions lower than the observed overlap, indicating niche similarity.*

**TABLE 3 |** Number of occurrence records (N), average (and SD) Area Under the Curve (AUC) and average (and SD) permutation importance of each ecogeographical variable across all 280 species distribution model replicates for *Acacia longifolia* and *Trichilogaster acaciaelongifoliae.* *Indicate highest contributing variables.

| | N | AUC | BIO3 | BIO4 | BIO6 | BIO9 | BIO14 | BIO19 |
|---|---|---|---|---|---|---|---|---|
| *Acacia longifolia* | 1493 | 0.897 (0.022) | 0.045 (0.033) | 0.238* (0.089) | 0.178* (0.089) | 0.072 (0.052) | 0.042 (0.051) | 0.350* (0.094) |
| | N | AUC | BIO2 | BIO3 | BIO13 | BIO14 | BIO15 | |
| *Trichilogaster acaciaelongifoliae* | 140 | 0.846 (0.040) | 0.501* (0.109) | 0.527* (0.113) | 0.251 (0.153) | 0.343 (0.296) | 0.261 (0.236) | |

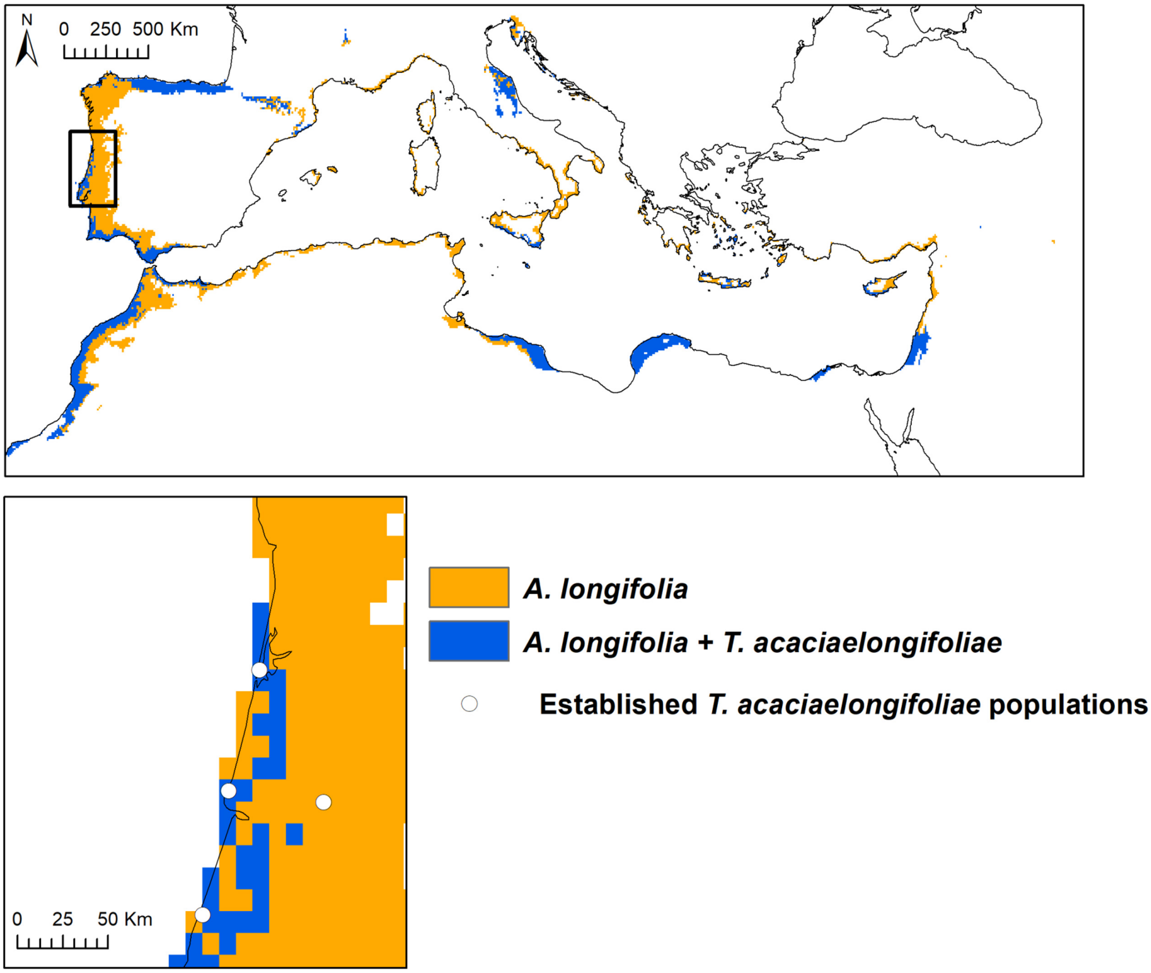

**FIGURE 3 |** Spatial overlap between model predictions of suitability for *Acacia longifolia* and *Trichilogaster acaciaelongifoliae* in the Mediterranean region. *Trichilogaster acaciaelongifoliae* model was constrained to areas of predicted suitability for *A. longifolia* to prevent classification of suitability in areas where the species cannot persist due to lack of its host plant. Bottom: Populations of *T. acaciaelongifoliae* already established in Portugal as of 2018

South Africa, as its dependency on *A. longifolia* would require the host plant to do the same, which is rejected by the evidence. Rather, non-climatic factors such as biotic interactions are likely to constrain the distribution of *T. acaciaelongifoliae* in Australia, where the species is native and as such suffers higher levels of parasitism and competes with other bud-feeding insects (Neser, 1984). Despite present, the lower level of such interactions in South Africa (Manongi and Hoffmann, 1995; Seymour and Veldtman, 2010) may have allowed the species to expand into previously unoccupied areas of niche space which are nonetheless contained within the realized niche of *A. longifolia*. The evidence for niche expansion may also reflect the low number of occurrence records for *T. acaciaelongifoliae* in Australia, which thus fail to fully represent the realized niche. Gall-forming insects, particularly in native regions where they coexist with their hosts often in equilibrium, are frequently overlooked and understudied organisms, despite the importance of several species as biocontrol agents (Dennill, 1988; Harris and Shorthouse, 1996) or pests (Gil-Tapetado et al., 2018; Ferracini et al., 2019). This resulted in a relatively reduced dataset in Australia, vulnerable to spatial biases, which are known to affect niche estimates (Graham et al., 2008; Sánchez-Fernández et al., 2011). Regardless, the evidence for niche conservatism allowed us to combine the *T. acaciaelongifoliae* occurrence records for Australia and South Africa for the development of niche models, minimizing the effect of spatial biases.

The very high niche overlap between *A. longifolia* and the gall-former *T. acaciaelongifoliae* is consistent with the high specificity of *T. acaciaelongifoliae* with its host plant (Dennill et al., 1993; Marchante et al., 2011a). The realized niche of *T. acaciaelongifoliae* is found to be almost fully contained within the niche of *A. longifolia* on all regions where the two species co-occur (reflected in high niche stability and near zero niche expansion). In South Africa, niches of the two species were found to be more similar than expected given the available environmental background and niche unfilling was found to be the lowest among all interspecies comparisons. This suggests a near total colonization by *T. acaciaelongifoliae* of all environments where *A. longifolia* occurs, which has been reported by some authors (J. Hoffmann, personal communication). It also indicates that the aforementioned expansion of *T. acaciaelongifoliae* in South Africa in the absence of substantial negative biotic interactions took place exclusively within the range of *A. longifolia,* highlighting the high specificity of *T. acaciaelongifoliae* which is a key factor in its reliability as a biocontrol agent. Australia had the lowest niche overlap and highest niche unfilling among all interspecies comparisons, highlighting that *T. acaciaelongifoliae* is not known to occur (or reported) in many of the environments where *A. longifolia* is present in its native range. Again, this likely reflects non-climatic influences hindering the ability of *T. acaciaelongifoliae* to successfully colonize all *A. longifolia* habitats.

## Implications for the Management of *A. longifolia* Including Biocontrol

The predicted suitable area for *A. longifolia* in the Mediterranean basin far exceeds the current distribution. Besides environmental conditions, introduction histories are known to greatly influence species distributions (Donaldson et al., 2014). One of the main pathways for *A. longifolia* introduction in Portugal was for sand binding of coastal dunes (Marchante et al., 2003). This coastal introduction, associated with habitat connectivity and dispersal constraints, may account for the current species distribution which is not known to extend as far inland as predicted by our model (with a few exceptions in some particular locations). This hypothesis seems likely when considering that *A. longifolia* (*sensu lato*) is known to occur much further inland in its native distribution than in Portugal (Court et al., 2020). Likewise, in South Africa, where *A. longifolia* was introduced also to stabilize inland slopes (Dennill and Donnelly, 1991), the species is present as far inland as 500 km, demonstrating that it can become established far from coastal climate given the adequate means of dispersal. Regardless, we cannot dismiss the possibility that factors not included in the models, such as biotic interactions or non-climatic abiotic variables, may constrain the distribution of *A. longifolia* beyond the model's prediction. The current model predicts risk of *A. longifolia* invasion in most of the Mediterranean and, especially, Atlantic coastline of the Mediterranean Basin region. Areas of current *A. longifolia* invasion in the region besides Portugal include north-western Spain (Community of Galicia), which is correctly predicted as climatically suitable. *A. longifolia* is currently present, even if not yet considered as invasive, in several countries which are predicted as having suitable areas for the establishment of the species, namely France, Italy, Greece and Turkey (Akanil and Middleton, 2010; EFSA Panel on Plant Health, 2015). Our results suggest that particular care should be taken to prevent *A. longifolia* invasion in these regions where the species is already present within an area of suitable environment. The model for *A. longifolia* identified a small area of suitability in the southern Pyrenees Mountains, a region characterized by montane conditions that are uncharacteristic for the species. Species distribution models have a limited ability to extrapolate beyond the environmental conditions available in the training area and may produce unexpected results when environmental homology between training and projection areas is not assured (Elith and Leathwick, 2009). Despite our efforts to maximize homology by restricting the model projections to the Mediterranean Basin, mountain ranges in the region are likely to include extreme conditions which lead to extrapolation, resulting in less reliable predictions in these areas.

*Trichilogaster acaciaelongifoliae* is predicted to find suitable climate in a significant part of the potential *A. longifolia* distribution area. Current areas of *A. longifolia* invasion where *T. acaciaelongifoliae* is not predicted to find suitable conditions are located in the coastline of northern Portugal and Galicia, as well in the most inland areas of Portugal. Nevertheless, the existence of a well-established population of *T. acaciaelongifoliae* in the Portuguese city of Coimbra and very recent (2019; López-Núñez et al., in prep.) establishment in northern areas of Portugal (classified as unsuitable by the model) indicates that the approach used in this work may not be sufficient to fully characterize the niche of this species. Partial inconsistencies amongst modeling outputs and field observations occur in other studies (e.g., Gallien et al., 2012; Fischbein et al., 2019) for several reasons. In our study, agreement between model predictions and known distributions in the Mediterranean Basin was higher for *A. longifolia* than for *T. acaciaelongifoliae*, likely reflecting the difference in number and quality of occurrence records between the two species. Moreover, this may be explained by the fact that the biocontrol agent was only recently (2015) introduced in Portugal (Marchante et al., 2017), still not having enough time to spread and establish across the suitable area. Furthermore, the life history of *T. acaciaelongifoliae* is characterized by a near-total existence as an endoparasite, and as such the microenvironmental conditions and interactions with the host plant are likely to be better predictors of the species' ability to form viable populations than macroclimatic factors. Despite the identification of ecogeographical variables that have a limiting effect on *T. acaciaelongifoliae*, the environmental triggers required for completion of this species' life cycle are still poorly understood. *T. acaciaelongifoliae* has shown to be sensitive to such triggers, as the change in hemisphere (and consequent temporal mismatch between the species' life cycle and seasonal queues) upon introduction to Portugal resulted in low establishment success in the first years (Marchante et al., 2017, López-Núñez et al., in prep.). Identifying these triggers is fundamental to properly assess the long-term robustness of effective biocontrol of *A. longifolia* mediated by *T. acaciaelongifoliae*. Ultimately, mechanistic approaches to modeling which integrate microhabitat and biotic interactions between host and parasite as well as an explicit understanding of how these factors contribute to the life cycle of *T. acaciaelongifoliae* (Palhas et al., in prep.) are expected to better approximate the fundamental niche and, when integrated with correlative approaches such as the one presented in this work, allow for more accurate predictions.

Despite the limitations described above, the high niche overlap between the two species shows promise regarding the effectiveness of *T. acaciaelongifoliae* for biocontrol of

*A. longifolia* in other invaded areas worldwide. Particularly in New Zealand, where such a program is being considered (Northland Conservancy Department of Conservation, 2005; Northland Regional Council, 2019), distribution modeling approaches such as the one presented here may offer insight on whether and where biocontrol has a chance to be effective.

## CONCLUSION

Predictive modeling is widely used for the prevention and management of biological invasions. The ability to predict invasion risk beforehand enables the application of preventive measures which are generally more cost-effective than attempting to eradicate already established invasive populations (Rejmánek et al., 2013). We have developed a predictive mapping of suitable areas for *A. longifolia* establishment in the Mediterranean basin, from which several areas potentially under invasion risk were identified in southern Europe. These areas represent priority targets for preventive measures in order to prevent future invasions. However, areas predicted as suitable are unlikely to share a similar risk of invasion. We uncovered a likely important role of introduction pathways in shaping the current distribution of *A. longifolia* across its invasive range. Understanding landscape permeability to dispersal and identifying dispersal corridors, which can be accomplished by connectivity analysis (e.g., Gonçalves et al., 2016) can potentially improve risk mapping.

Distribution models and assessments of ecological overlap are not frequently used to inform the implementation of biocontrol programs. The potential of these approaches for quantifying the adequacy of a biocontrol agent in terms of ecological overlap with the target species and ability to establish in target areas should not, however, be underestimated. Despite the limited data available for *T. acaciaelongifoliae*, we were able to identify substantial overlap between the biocontrol agent and the target invasive plant. We also uncovered an important role of biotic interactions constraining the realized distribution of *T. acaciaelongifoliae* in its native range. In the absence of such interactions in the introduced range, the species may be able to explore previously unavailable parts of its fundamental niche, potentially being able to colonize even more of the distribution of *A. longifolia* than predicted by the current model. These are promising predictions for the future of *A. longifolia* biocontrol in Portugal and in the Mediterranean basin, but also in other regions dealing with *A. longifolia* invasions.

## DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/**Supplementary Material.**

## AUTHOR CONTRIBUTIONS

All authors contributed to the study design. MD and NC collected the data. MD performed the analyses with important contributions from JRV, NC, and FL-N. MD wrote the manuscript with important contributions from all authors.

## FUNDING

This work was supported by European funds FEDER and Portugal 2020/POCI and national funds by Portuguese Foundation for Science and Technology through project INVADER-IV (PTDC/AAG-REC/4896/2014) and CFE-Centre for Functional Ecology-Science for People & the Planet's Strategic Plan (UIDB/04004/2020). FL-N is supported by FCT Ph.D. grant SFRH/BD/130942/2017. JRV was supported as a post-doc researcher at ICETA CIBIO/InBIO by national funds through FCT – Foundation for Science and Technology, DL57/2016/ICETA/EEC2018/13.

## ACKNOWLEDGMENTS

The authors would like to thank Alan Wood, Kristine French, Tony Rebelo, Pride Mudavanhu, and Andy Sheppard for providing occurrence records.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.576667/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 21 October 2020
doi: 10.3389/fevo.2020.566281

# Horizon Scanning to Predict and Prioritize Invasive Alien Species With the Potential to Threaten Human Health and Economies on Cyprus

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**Specialty section:**
This article was submitted to
Biogeography and Macroecology,
a section of the journal
Frontiers in Ecology and Evolution

**Received:** 27 May 2020
**Accepted:** 12 August 2020
**Published:** 21 October 2020

**Citation:**
Peyton JM, Martinou AF, Adriaens T, Chartosia N, Karachle PK, Rabitsch W, Tricarico E, Arianoutsou M, Bacher S, Bazos I, Brundu G, Bruno-McClung E, Charalambidou I, Demetriou M, Galanidi M, Galil B, Guillem R, Hadjiafxentis K, Hadjioannou L, Hadjistylli M, Hall-Spencer JM, Jimenez C, Johnstone G, Kleitou P, Kletou D, Koukkoularidou D, Leontiou S, Maczey N, Michailidis N, Mountford JO, Papatheodoulou A, Pescott OL, Phanis C, Preda C, Rorke S, Shaw R, Solarz W, Taylor CD, Trajanovski S, Tziortzis I, Tzirkalli E, Uludag A, Vimercati G, Zdraveski K, Zenetos A and Roy HE (2020) Horizon Scanning to Predict and Prioritize Invasive Alien Species With the Potential to Threaten Human Health and Economies on Cyprus. Front. Ecol. Evol. 8:566281. doi: 10.3389/fevo.2020.566281

Invasive alien species (IAS) are known to be a major threat to biodiversity and ecosystem function and there is increasing evidence of their impacts on human health and economies globally. We undertook horizon scanning using expert-elicitation to predict arrivals of IAS that could have adverse human health or economic impacts on the island of Cyprus. Three hundred and twenty five IAS comprising 89 plants, 37 freshwater animals, 61 terrestrial invertebrates, 93 terrestrial vertebrates, and 45 marine species, were assessed during a two-day workshop involving 39 participants to derive two ranked lists: (1) IAS with potential human health impacts (20 species ranked within two bands: 1–10 species or 11–20 species); and, (2) IAS with potential economic impacts (50 species ranked in three bands of 1–10, 11–20, and 21–50). Five species of mosquitoes (*Aedes aegypti*, *Aedes albopictus*, *Aedes flavopictus*, *Aedes japonicus,* and *Culex quinquefasciatus*) were considered a potential threat to both human health and economies. It was evident that the IAS identified through this process could potentially arrive through many pathways (25 and 23 pathways were noted for the top 20 IAS on the human health and economic impact lists respectively). The Convention on Biological Diversity Level II (subcategory) pathways *Contaminant on plants*, *pet/aquarium/terrarium species (including live food for such species)*, *hitchhikers in or on aeroplanes*, *hitchhikers in or on ship/boats,* and *vehicles* were the main pathways that arose across both lists. We discuss the potential of horizon scanning lists to inform biosecurity policies and communication around IAS, highlighting the importance of increasing understanding amongst all stakeholders, including the public, to reduce the risks associated with predicted IAS arrivals.

**Keywords: prevention, non-native species, negative impact, environmental management, introduction pathways, communication**

## INTRODUCTION

Invasive alien species (IAS), species introduced either intentionally or unintentionally by humans outside of their native range, and causing negative impacts to biodiversity, ecosystem services, economy and/or society, are a major concern globally (Russell et al., 2017; Pauchard et al., 2018; Díaz et al., 2019; Stoett et al., 2019). There is growing evidence of adverse effects of IAS on ecosystem function (Schindler et al., 2015; Vilà and Hulme, 2017), ecosystem services (such as crop production, timber provision, seafood and recreation) and to economies and human health (Schindler et al., 2015; Martinou and Roy, 2018).

Invasive alien species can have direct negative impacts on human health through disease transmission, for example certain mosquito species (Moore and Mitchell, 1997), or through having highly allergenic pollen as is the case with some plants (Samson et al., 2017; Lazzaro et al., 2018). There are also examples of poisonous or venomous marine IAS causing direct health impacts, e.g., the venomous striped eel catfish *Plotosus lineatus* was responsible for 10% of the marine organism-related injuries experienced by fishermen off the coast of Israel (Gweta et al., 2008). Additionally, IAS can have indirect health impacts, for example, loss of agricultural production and food security, or increased traffic accidents (Schindler et al., 2015). Economically, costs of direct impacts and management of IAS to agriculture, forestry and fisheries were estimated at €12.5 billion in Europe in 2009, but this was considered a conservative estimate (Kettunen et al., 2009). In Great Britain, the cost to the economy incurred by IAS was estimated at £1.7 billion in 2010 (Williams et al., 2010).

Predicting the arrival of IAS and using this information to prioritize preventative action is therefore often seen as critical for informing the biosecurity and management of such species (Shine et al., 2010; Caffrey et al., 2014; Roy et al., 2015; Booy et al., 2017; Carboneras et al., 2018), with the ultimate goal of reducing the risk and impacts of IAS. Such prioritized lists of potential IAS provide an important tool to guide monitoring and inform early-warning detection systems, preventative action and biosecurity, as well as focusing the communication of risk to all stakeholders, including the public. Pathway action plans, which consider the ways IAS are transported around the world (Hulme et al., 2008), look to mitigate the risk of introduction through different pathways (Convention on Biological Diversity [CBD], 2014; Harrower et al., 2018), and are one approach to managing biological invasions informed by prioritized lists (Key and Moore, 2019).

Here, we present the outcomes of a horizon scanning study using an expert-elicitation approach (Roy et al., 2020), previously used in Great Britain (Roy et al., 2014), Europe (Roy et al., 2019a) and the United Kingdom Overseas Territories (Roy et al., 2019b). We build on a previous study in which a priority list of IAS with the potential to threaten <u>biodiversity and ecosystems</u> (Peyton et al., 2019) was derived for Cyprus through expert elicitation (Roy et al., 2020). We extend this approach to predict marine, terrestrial, and freshwater IAS which have the potential to threaten <u>human health and economies</u> for the island of Cyprus, including the Sovereign Base Areas of Akrotiri and Dhekelia.

## MATERIALS AND METHODS

### Study Area

Cyprus, located in the eastern Mediterranean, is the third largest island in the region and is bordered by Asia to the north and east, Europe to the west, and Africa to the south. The Mediterranean basin is renowned for being a biodiversity hotspot (Myers et al., 2000), and Cyprus has a high level of endemism across different taxonomic groups (Sparrow and John, 2016). Cyprus hosts a diverse range of habitats, from winter snow-capped mountains, conifer forest (containing species such as the endemic cedar *Cedrus brevifolia*), and coastal cliffs, to saltmarsh, riverine and agricultural plains. Other members of the European Union are the most important trading partner of Cyprus, with goods imported primarily from Greece, United Kingdom, Italy, and Germany

(Ministry of Energy, Commerce, Industry, and Tourism, 2014). In addition to strong trade links across Europe, it is estimated that over €2.23 billion revenue was generated from tourism for the period of January to September 2019 (Statistical Service of the Republic of Cyprus, 2019). Potatoes, wine, citrus are among products exported from Cyprus and are important both economically and culturally. These key trade and tourism activities are important when considering potential pathways of introduction for IAS.

## Selection of Experts

The experts involved in this horizon scanning study represented a range of disciplines with experience in biological invasions, human health and social economics (see **Supplementary Information 1** for the full list of participants). Forty-five experts contributed to the listing and initial scoring of the species. Most of the experts had more than 5 years' experience of working on IAS but two early career researchers studying biological invasions and conservation also contributed. All the thematic group leaders had previously participated in at least one horizon scanning study. Twenty-four of the 45 experts that contributed to the species listing in the current workshop had also contributed to a previous horizon scanning study on Cyprus (Peyton et al., 2019). The number of experts within each group varied from eight to thirteen. The plant species (terrestrial and freshwater) were scored by eight people, freshwater animals (invertebrates and fish) by seven people, terrestrial invertebrates by nine people, terrestrial vertebrates by eight people and marine species (invertebrates, vertebrates, and primary producers) by 13 people. Two experts from the terrestrial invertebrates group also worked within the plants group but only scored species for the terrestrial invertebrate group. Mosquitoes were included within the freshwater animals group. Thirty-nine of the 45 experts were present at the workshop.

To ensure clarity, the approach was clearly outlined through a guidance document (**Supplementary Information 2**) circulated six weeks before the workshop and through a presentation at the beginning of the workshop.

## Data Sources

Consultation on proposed IAS was undertaken between experts through e-mail discussions in advance of the workshop and through the workshop breakout groups. The long-list of IAS derived from the 2017 horizon scan of Peyton et al. (2019) for IAS to impact Cypriot biodiversity and ecosystem services was used as a starting point from which the thematic groups further updated, modified and developed the lists through consultation of relevant databases (e.g., CABI compendium and horizon scanning tool, GBIF, GRIIS, CyDAS) and other sources including peer-reviewed and gray literature of IAS with known invasion history around the world. Additionally, IAS of note from a recent study prioritizing IAS for the UKOTs were also considered during this initial selection (Roy et al., 2019b).

## Excluded IAS

Thirty-eight IAS from the Peyton et al. (2019) biodiversity and ecosystem list of 225 IAS were not considered relevant to the process outlined here: four plants, four freshwater animals, eight terrestrial invertebrates, seven terrestrial vertebrates, 13 marine animals and two marine plants. For the plant IAS that were removed, several were described for Cyprus subsequent to the 2017 workshop, although they may have arrived and established in Cyprus prior to 2017, e.g., *Heliotropium currasavicum* (Charilaou, 2018) and small-leaf spiderwort *Tradescantia fluminensis* (Spitale and Papatheodoulou, 2019). The four freshwater IAS (two mosquitofish fish *Gambusia* spp.), Nile tilapia *Oreochromis niloticus*, and two crustaceans: Louisiana crayfish *Procambarus clarkii* (Department of Environment, 2019; Ueda, 2020) and the tadpole shrimp *Triops cancriformis* (Tziortzis et al., 2014) were not considered because they were already established in Cyprus. Terrestrial invertebrates that were not considered, were omitted because there was recently published evidence of their presence on Cyprus, e.g., the three ants, the fire ant *Solenopsis geminata*, the pharoah ant *Monomorium pharaonis* and *Pheidole indica* (Salata et al., 2017). Terrestrial vertebrates were either not considered because they were established, e.g., brown rat *Rattus norvegicus* (Psaroulaki et al., 2006), or not relevant because of the absence of active pathways, e.g., Canadian beaver *Castor canadensis* and American mink *Neovison vison*. Wild boar *Sus scrofa* was added to the list as there had been past (1990s) releases for hunting in Cyprus, but populations were subsequently eradicated (Hadjisterkotis and Heise-Pavlov, 2006). The marine IAS list was considerably reduced as: (a) three IAS were reported from the island since 2017 (killer algae *Caulerpa taxifolia* var. *distichophylla*, the bryozoan *Amathia verticillata* and common moon crab *Matuta victor*); (b) one IAS (white crust tunicate *Didemnum perlucidum*) is cryptogenic (a species that cannot be reliably demonstrated as being either introduced or native, Carlton, 1996) and hence removed; and, (c), for the remaining eleven IAS the likelihood of arrival (mainly through shipping) and establishment was re-evaluated as low, and hence removed.

## Scoring IAS

Experts were asked to score each potential IAS within their thematic group for their separate likelihoods of: (i) arrival, (ii) establishment, (iii) magnitude of the potential negative impact on human health or economies. Quantification of the impact score on human health and economy were performed using a scoring scheme modified from the SEICAT system (Bacher et al., 2018) as shown in **Table 1**. Only primary impacts were considered; for example, should a person be absent from work because they were ill from a mosquito-borne infection, this would only be considered within human health impacts, but not economic impact.

We scored likelihood of arrival, establishment and impact (either human health or economic) for each IAS on a 5-point scale (1 = low likelihood; 5 = high likelihood) such that the maximum score, the product of the three scores, possible was 125. IAS scored were present on both the human health and economy lists with scores given for each impact category. For all the IAS included within the priority lists, we documented the pathways using the Convention on Biological Diversity (CBD) Level II (subcategory) nomenclature

**TABLE 1 |** Magnitude of impacts of invasive alien species on human health and economy adapted from Bacher et al. (2018).

| Score of impact | Magnitude of impact | Impact on human health | Impact on Economy |
|---|---|---|---|
| 1 | Minimal | No deleterious impacts or local, short-term reversible effects to few individuals | No deleterious impacts reported (not being confused with "data deficient") |
| 2 | Minor | Local, short-term reversible effects to larger groups of people | Negative effect on agriculture such that the alien taxon makes it difficult for individuals to participate in their normal activities, e.g., via income loss, higher effort or expenses to participate in activities. Activities are still carried out, i.e., the number of people participating in that activity remains the same |
| 3 | Moderate | Local, but irreversible effects on small groups of people or reversible effects on larger groups of people | Negative effects leading to changes in activities, i.e., the number of people participating decreases, but the activity is still carried out |
| 4 | Major | Local, significant irreversible effects at the regional scale or reversible effects over large areas | Local disappearance of the activity from all or part of the area invaded. Likely to be reversible within a decade after removal or control of the alien taxon. The disappearance refers to the typical spatial scale over which practices in the region are characterized |
| 5 | Massive | Widespread, severe, long-term, irreversible health effects over large areas | Local disappearance of the activity from all or part of the area invaded. Likely to be permanent and irreversible for at least a decade after removal of the alien taxon, due to fundamental structural changes of conditions |

*It is important to note that the scores agreed by the experts were for ranking purposes only and do not represent a comprehensive impact assessment. Magnitude of impact is based on a 5 point scale (minimal, minor, moderate, major, and massive) to achieve an appropriate balance between accuracy and resolution. 1 (Minimal) = small inconsequential changes; 0–10% of decline in species population, habitat or function affected or 0–10% impact on human health or economy. 2 (Minor) = changes in size, quality or function of some consequence; 10–25% of species population, habitat or function affected or 10–25% impact on human health or economy. 3 (Moderate) = considerable, important changes in size, quality or function; 25–50% of species population, habitat or function affected or 25–50% impact on human health or economy. 4 (Major) = large, highly significant changes in size, quality or function; 50–75% of species population, habitat or function affected or 50–75% impact on human health or economy. 5 (Massive) = loss of all, or almost all, of a species, function or habitat; 75–100% of species population, habitat or function affected or 75–100% impact on human health or economy.*

(Convention on Biological Diversity, 2014; Harrower et al., 2018), by which they are considered most likely to arrive. The temporal scope for the predictions, was of IAS likely to arrive in the next 10 years.

The geographic scope of the search for potential IAS was global but with the following restrictions. IAS were only considered:

- (i) If currently absent from Cyprus. Farmed animals such as goats *Capra hircus* were considered to be already established in the wild and, therefore, the potential for feral invasive populations was not considered here.
- (ii) If there was documented invasion histories illustrating undesirable impacts in previously invaded regions.
- (iii) If pathways of introduction of the IAS are active, that is:
  - (a) The IAS are traded within Cyprus or are present in areas that have strong trade or travel connections with Cyprus, and there is a recognized potential pathway of introduction.
  - (b) The IAS are present in captivity including in gardens, zoological parks, private collections, pet shops, aquaculture facilities or greenhouses.

## Ranking the Species by Consensus

The workshop (27–29 November 2019) considered the potential human health and economic impacts of a list of IAS following the methods outlined in Peyton et al. (2019) based on Roy et al. (2019b). In order to reduce potential bias that can occur with any expert-elicitation process (Sutherland and Burgman, 2015), we followed the ten guiding principles outlined in Roy et al. (2020). The IAS identified and scored by the experts within the thematic groups were compiled to produce a long list which was ordered on the basis of the scores given for each IAS. All the experts met in plenary to discuss the IAS and rank them within bands to provide a prioritized list. The overall scores a species received were only used as a guide to help inform the expert-elicitation process. Categorization of species into different bands allowed for greater resolution of prioritization which can then be linked to priority of management or awareness raising. The overall scores a species received were used a guide to help inform the expert-elicitation process.

# RESULTS

A total of 325 IAS were compiled into a long-list for consideration during the human health and economic impacts workshop. These 325 consisted of 89 plants, 37 freshwater animals, 61 terrestrial invertebrates, 93 terrestrial vertebrates and 45 marine species. Two prioritized IAS lists were derived: human health and economy.

The group, in plenary, reached a consensus on the ranking of 20 IAS predicted to have the potential for human health impacts in bands of 1–10 and 11–20 (**Table 2**). In contrast, 50 IAS with the potential for economic impacts was agreed through consensus in bands of 1–10, 11–20, and 21–50 (**Table 3**). The difference in list length reflects the higher number of

IAS considered a significant risk to economies compared to the number of IAS considered a human health threat. **Supplementary Information 3** gives the full list of 325 IAS reviewed during the workshop.

Ten freshwater animals, five of which were mosquitoes (yellow fever mosquito *Aedes aegypti*, Asian tiger mosquito *Ae. albopictus*, *Ae. flavopictus*, Asian bush mosquito *Ae. japonicus* and southern house mosquito *Culex quinquefasciatus*) comprised half of the species in the human health list. Five plants, four marine species and a terrestrial vertebrate constituted the remaining species in the human health top 20 list. There were no terrestrial invertebrates present within the human health top 20 list (**Figure 1**).

Within the ranked economic impact list, the numbers of IAS within each thematic group were more evenly divided, with five plant species, five freshwater animal species, four terrestrial invertebrate species, four terrestrial vertebrate species, and two marine species represented (**Figure 1**). The IAS ranked from 21 to 50 within the list of IAS constituting a potential threat to economies within Cyprus included 13 invasive alien plant species, six marine IAS, five terrestrial invertebrates and terrestrial vertebrates and a single freshwater animal (**Table 3**).

Ten of the IAS were considered a potential threat to both human health and economies. These ten IAS comprised five species of mosquito (*Ae. aegypti*, *Ae. albopictus*, *Ae. flavopictus*, *Ae. japonicus* and *C. quinquefasciatus*), three plant IAS (ragweed *Ambrosia artemisiifolia*, Cape ivy *Delairea odorata* and whitetop weed *Parthenium hysterophorus*) and two marine IAS (white stinger *Macrorhynchia philippina* and *P. lineatus*).

Twenty-five CBD Level II (subcategories) were identified for the top 20 IAS for human health and 23 pathways identified for the top 20 IAS for economy [**Figure 2**; all CBD Level I and II (subcategory) pathway names are given in italics]. The CBD Level II pathways, *Contaminant on plants*, *pet/aquarium/terrarium species (including live food for such species)*, *hitchhikers in or on aeroplanes*, *hitchhikers in or on ship/boats and vehicles* were the main introduction pathways that arose across both the list of IAS with potential human health and economic impacts.

For plants and freshwater animals, 14 separate introduction pathways were identified, for terrestrial animals seven were identified, five for terrestrial vertebrates and six for marine IAS (**Figure 3**). Marine, freshwater animals, terrestrial invertebrates and plants were considered more likely to be introduced via *Transport pathways*, both as contaminants or stowaways, whereas terrestrial vertebrates were considered more likely to be introduced through *Release* or *Escape* pathways. For marine IAS, *Corridor – interconnected waterways/basins/seas*, namely the Suez Canal, was noted as an important pathway.

## DISCUSSION

Prioritizing IAS that are currently absent within a region but could arrive, is an important component of IAS management, with clear ecological and economic benefits (Caffrey et al., 2014; Roy et al., 2015; Booy et al., 2017). The lists of IAS predicted to arrive, establish, and have adverse effects on human health and/or economies derived through this horizon scanning study complement the list derived in 2017 for IAS predicted to impact biodiversity and ecosystems (Peyton et al., 2019). The 325 IAS identified span a diverse range of taxa, habitats and ecosystems.

### High Scoring IAS

The list of IAS predicted to have human health impacts was dominated by mosquitoes. Mosquitoes are considered to be the most important vectors of disease (Romi et al., 2018). The invasion of the Asian tiger mosquito *Ae. albopictus*, a competent vector of disease, in the Mediterranean is facilitated by climate change (Roiz et al., 2011). Ryan et al. (2019) show shifts in *Aedes*-borne virus distributions toward the poles under changing climate as habitat suitability changes for both *Ae. aegypti* and *Ae. albopictus. Ae. albopictus* has caused outbreaks of chikungunya fever in Italy (Rezza et al., 2007; Riccardo et al., 2019). France, Croatia and Spain have reported autochthonous (i.e., locally acquired) cases of dengue fever linked to established *Ae. albopictus* populations (Succo et al., 2016; ECDC, 2019) and the risk of introduction of *Ae. albopictus* to Cyprus is a major concern. In addition to the risk of disease transmission, mosquitoes can also be considered a nuisance and can affect human well-being. They can deter visitors from recreational spaces, which in turn causes adverse economic impacts (Medlock and Vaux, 2015; Martinou et al., 2020). Recognizing the paucity of knowledge on invasive diseases (Roy et al., 2017), we excluded pathogens and other disease causing agents other than those transmitted by invasive alien vectors, such as mosquitoes. However, it was noted that the ongoing spread of the plant pathogenic bacterium *Xylella fastidiosa* in the Mediterranean region was seen as of major concern and a threat for the economy of Cyprus. Bosso et al. (2016) show that although climate change is unlikely to increase the climatic suitability range of *X. fastidiosa* in the Mediterranean, it strongly supports phytosanitary measures around the spread of this bacterium as there are many countries with prevailing suitable conditions, including Cyprus. The bacterium causes serious diseases in a wide range of plants, including olive trees, and is transmitted by various different Hemiptera species. Although it is a European and Mediterranean Plant Protection Organization (EPPO) quarantine organism, and measures are in place, its arrival on Cyprus would have be detrimental to the economy (Saponari et al., 2019).

### IAS Policy

Regulation (EU) No 1143/2014 on the prevention and management of the introduction and spread of invasive alien species (the 'IAS Regulation') requires European Union Member States to identify and prioritize pathways of unintentional introduction and spread of IAS of Union concern. Ranked lists are also valuable for the development of action plans to tackle priority pathways of introduction and spread. Five IAS of Union concern occurred within the two top 20 lists: water-hyacinth *Eichornia crassipes; P. hysterophorus; P. lineatus;* raccoon *Procyon*

**TABLE 2 |** Invasive alien species (IAS) considered to have high likelihood of arrival, establishment and human health impacts within Cyprus and ranked within two bands: top 1-10 IAS and 11-20 IAS.

| Rank | Species | Common name | Thematic group | Pathways | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1–10 | *Aedes albopictus* | Tiger mosquito | Freshwater animals | Air | Ship | Veh | Con Plant | | | |
| 1–10 | *Plotosus lineatus** | Striped eel catfish | Marine | Water | Nat | Pet | Res | | | |
| 1–10 | *Parthenium hysterophorus* | Whitetop weed | Plants | Lug | Seed | Mach | THM | | | |
| 1–10 | *Culex quinquefasciatus* | Southern house mosquito | Freshwater animals | Ship | Air | | | | | |
| 1–10 | *Ambrosia artemisiifolia* | Common or annual ragweed | Plants | Other Transport | Lug | Nat | Seed | THM | Veh | Mach |
| 1–10 | *Macrorhynchia philippina** | White stinger | Marine | Hull | Nat | | | | | |
| 1–10 | *Procyon lotor* | Raccoon | Terrestrial vertebrates | BZA | Other Escape | Pet | | | | |
| 1–10 | *Aedes aegypti* | Yellow fever mosquito | Freshwater animals | Air | Ship | Veh | Con Plant | | | |
| 1–10 | *Aedes flavopictus* | A mosquito | Freshwater animals | Air | Ship | Veh | Con Plant | | | |
| 1–10 | *Aedes japonicus* | East Asian bush mosquito, rock pool mosquito | Freshwater animals | Air | Ship | Veh | Con Plant | | | |
| 11–20 | *Broussonetia papyrifera* | Paper mulberry | Plants | Orn | For | Nat | EC | | | |
| 11–20 | *Synanceia verrucosa** | Reef stonefish | Marine | Water | | | | | | |
| 11–20 | *Pomacea canaliculata* | Golden apple snail | Freshwater animals | R | Aq | Pet | Bait | Con Plant | THM | Ang |
| 11–20 | *Pomacea maculata* | Giant apple snail | Freshwater animals | R | Aq | Pet | Bait | Con Plant | THM | Ang |
| 11–20 | *Sinanodonta woodiana* | Chinese giant mussel | Freshwater animals | Food | | | | | | |
| 11–20 | *Phyllorhiza punctata** | Spotted jellyfish | Marine | Hull | Ballast | Water | Nat | | | |
| 11–20 | *Datura wrightii* | Sacred datura | Plants | Seed | | | | | | |
| 11–20 | *Dreissena rostriformis bugensis* | Quagga mussel | Freshwater animals | Ballast | Hull | | | | | |
| 11–20 | *Delairea odorata* | Cape Ivy or German Ivy | Plants | Orn | CNM | | | | | |
| 11–20 | *Limnoperna fortunei* | Golden mussel | Freshwater animals | Ballast | Hull | | | | | |

*For each species the common name alongside the thematic group is given. Additionally the most likely pathways of arrival are also included. The pathway subcategory terminology follows Convention on Biological Diversity [CBD] (2014) and Harrower et al. (2018). Numbers in brackets alongside the pathway descriptions = occurrences within the table. EC, Erosion control (1); R, Release in nature for use (2); Ag, Agriculture (1); Aq, Aquaculture (2); BZA, Botanical garden/zoo/aquaria (1); Pet, Pet/aquarium/terrarium species (4); For, Forestry (1); Orn, Ornamental purpose other than horticulture (2); Res, Research and ex situ breeding (in facilities) (1); Other, Other escape from confinement (1); CNM, Contaminant nursery material (1); Bait, Contaminated bait (2); Food, Food contaminant (1); Con Plant, Contaminant on plants (excluding parasites and species transported by host and vector) (4); Seed, Seed contaminant (3); THM, Transportation of habitat material (2); Air, Hitchhikers in or on airplane (5); Ship, Hitchhikers in or on a ship/boat (5); Mach, machinery/equipment (2); Lug, People and their luggage/equipment (2); Ballast, Ship/boat ballast water (3); Hull, Ship/boat hull fouling (4); Veh, Vehicles (5); Other Transport, Other means of transport (1); Water, Interconnected waterways/basins/seas (3); Nat, Natural dispersal across borders of invasive alien species that have been introduced (5). Species marked with an asterisk (*) are marine species that the "waterway" pathway refers to introduction through the Suez Canal.*

**TABLE 3 |** Invasive alien species (IAS) considered to have high likelihood of arrival, establishment and economic impacts within Cyprus and ranked within three bands: top 1–10 IAS, 11–20 IAS, and 21–50 IAS.

| Rank | Species | Common name | Thematic group | Pathways | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 1–10 | *Daktulosphaira vitifoliae* | Grapevine phylloxera | Terrestrial invertebrates | CNM | Con Plant | | | | | |
| 1–10 | *Parthenium hysterophorus* | Whitetop weed | Plants | Lug | Seed | Mach | THM | | | |
| 1–10 | *Eichhornia crassipes* | Water hyacinth | Plants | Hort | Ang | Orn | | | | |
| 1–10 | *Aedes albopictus* | Tiger mosquito | Freshwater animals | Air | Veh | Con plant | Ship | | | |
| 1–10 | *Culex quinquefasciatus* | Southern house mosquito | Freshwater animals | Air | Ship | | | | | |
| 1–10 | *Ambrosia artemisiifolia* | Common or annual ragweed | Plants | Other Transport | Lug | Nat | Seed | THM | Veh | Mach |
| 1–10 | *Anoplophora chinensis* | Citrus longhorn beetle | Terrestrial invertebrates | TT | Con Plant | Container | Ship | | | |
| 1–10 | *Leptinotarsa decemlineata* | Colorado potato Beetle | Terrestrial invertebrates | CNM | Con Plant | THM | Container | Air | Ship | |
| 1–10 | *Plotosus lineatus** | Striped eel catfish | Marine | Water | Nat | Res | Pet | | | |
| 1–10 | *Sus scrofa* | Wild boar | Terrestrial vertebrates | H | | | | | | |
| 11–20 | *Psittacula krameri* | Ring-necked parakeet | Terrestrial vertebrates | Pet | | | | | | |
| 11–20 | *Pycnonotus jocosus* | Red-whiskered bulbul | Terrestrial vertebrates | Pet | Other Escape | | | | | |
| 11–20 | *Anoplophora glabripennis* | Asian longhorn beetle | Terrestrial invertebrates | TT | Con Plant | Container | Ship | | | |
| 11–20 | *Senecio inaequidens* | Narrow-leaved ragwort | Plants | Con Anim | Seed | Veh | Mach | | | |
| 11–20 | *Aedes aegypti* | Yellow fever mosquito | Freshwater animals | Air | Veh | Con plant | Ship | | | |
| 11–20 | *Aedes flavopictus* | A mosquito | Freshwater animals | Air | Veh | Con plant | Ship | | | |
| 11–20 | *Aedes japonicas* | East Asian bush mosquito, rock pool mosquito | Freshwater animals | Air | Veh | Con plant | Ship | | | |
| 11–20 | *Delairea odorata* | Cape Ivy or German Ivy | Plants | Orn | CNM | | | | | |
| 11–20 | *Callosciurus erythraeus* | Pallas's squirrel | Terrestrial vertebrates | Pet | Other Escape | Nat | BZA | | | |
| 11–20 | *Macrorhynchia philippina** | White stinger | Marine | Hull | Nat | | | | | |
| 21–50 | *Sphagneticola trilobata* | Wedelia | Plants | Hort | THM | L | Orn | Other Escape | | |
| 21–50 | *Penaeus aztecus* | Northern brown shrimp | Marine | Aq | | | | | | |
| 21–50 | *Procyon lotor* | Raccoon | Terrestrial vertebrates | BZA | Other Escape | Pet | | | | |
| 21–50 | *Prosopis juliflora* | Prosopis | Plants | For | Hort | L | Orn | | | |
| 21–50 | *Salvinia molesta* | Giant salvinia | Plants | Pet | BZA | Orn | Ang | Water | CNM | |
| 21–50 | *Decapterus russelli** | Indian scad | Marine | Water | Nat | | | | | |
| 21–50 | *Phyllorhiza punctata** | Spotted Jellyfish | Marine | Hull | Ballast | Water | Nat | | | |
| 21–50 | *Myiopsitta monachus* | Monk parakeet | Terrestrial vertebrates | Pet | | | | | | |
| 21–50 | *Rattus exulans* | Pacific rat | Terrestrial vertebrates | Ship | | | | | | |
| 21–50 | *Myriophyllum aquaticum* | Brazilian water milfoil | Plants | Pet | Ang | Orn | | | | |
| 21–50 | *Pistia stratiotes* | Water cabbage | Plants | Hort | Pet | Orn | L | | | |
| 21–50 | *Verbesina encelioides* | Golden crownbeard | Plants | Mach | Veh | Seed | Con Anim | | | |
| 21–50 | *Araujia sericifera* | Bladderflower | Plants | Orn | BZA | Mach | Lug | Veh | | |
| 21–50 | *Tamarix ramosissima* | Salt cedar or pink tamarisk | Plants | EC | L | Orn | | | | |
| 21–50 | *Synanceia verrucosa** | Reef stonefish | Marine | Water | | | | | | |
| 21–50 | *Cotylorhiza erythraea** | Jellyfish | Marine | Water | | | | | | |
| 21–50 | *Marivagia stellata** | Jellyfish | Marine | Water | | | | | | |
| 21–50 | *Phenacoccus peruvianus* | Bougainvillea mealybug | Terrestrial invertebrates | Con Plant | | | | | | |
| 21–50 | *Dreissena rostriformis bugensis* | Quagga mussel | Freshwater animals | Nat | | | | | | |
| 21–50 | *Mustela putorius furo* | Ferret | Terrestrial vertebrates | Other Escape | BC | H | | | | |

*(Continued)*

**TABLE 3 |** Continued

| Rank | Species | Common name | Thematic group | Pathways | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 21–50 | *Myriophyllum heterophyllum* | American water-milfoil | Plants | Ang | Orn | | | | | |
| 21–50 | *Ambrosia confertiflora* | Weakleaf bur ragweed | Plants | Seed | Con Plant | | | | | |
| 21–50 | *Ambrosia psilostachya* | Perennial ragweed | Plants | Seed | Con Plant | | | | | |
| 21–50 | *Datura wrightii* | Sacred datura | Plants | Seed | | | | | | |
| 21–50 | *Solanum sisymbriifolium* | Sticky nightshade | Plants | Seed | Con Plant | | | | | |
| 21–50 | *Vespa velutina* | Asian hornet | Terrestrial invertebrates | Hort | TT | Nat | | | | |
| 21–50 | *Wasmannia auropunctata* | Little fire ant | Terrestrial invertebrates | Container | Ship | Org | Nat | | | |
| 21–50 | *Halyomorpha halys* | Brown marmorated stink bug | Terrestrial invertebrates | Lug | Ship | Container | Veh | Mach | Food | Air |
| 21–50 | *Pycnonotus cafer* | Red-vented bulbul | Terrestrial vertebrates | Other Escape | Pet | | | | | |
| 21–50 | *Aethina tumida* | Small bee hive beetle | Terrestrial invertebrates | Container | Air | Ship | | | | |

*For each species the common name alongside the thematic group is given. Additionally the most likely pathways of arrival are also included. The pathway subcategory terminology follows Convention on Biological Diversity [CBD] (2014) and Harrower et al. (2018). Numbers in brackets alongside the pathway descriptions = occurrences within the table. BC, Biological Control (1); EC, Erosion control (1); H, Hunting (2); L, Landscape/flora/fauna improvement in the wild (4); Aq, Aquaculture (1); BZA, Botanical garden/zoo/aquaria (4); Pet, Pet/aquarium/terrarium species (10); For = Forestry (1); Hort, Horticulture (6); Orn, Ornamental purpose other than horticulture (10); Res, Research and ex situ breeding (in facilities) (1); Other, Other escape from confinement (6); CNM, Contaminant nursery material (4); Food, Food contaminant (including of live food) (1); Con Anim, Contaminant on animals (except parasites) (2); Con Plant, Contaminant on plants (12); Seed, Seed contaminant (8); TT, Timber trade (3); THM, Transportation of habitat material (4); Ang, Angling/fishing equipment (4); Container, Container/bulk (6); Air, Hitchhikers in or on airplane (8); Ship, Hitchhikers in or on a ship/boat (12); Mach, machinery/equipment (6); Lug, People and their luggage/equipment (4); Org, Organic packing material, in particular wood packaging (1); Ballast, Ship/boat ballast water (1); Hull, Ship/boat hull fouling (2); Veh, Vehicles (9); Other transport, Other means of transport; Water, Interconnected waterways/basins/seas (7); Nat, Natural dispersal across borders of invasive alien species that have been introduced (9). Species marked with an asterisk (*) are marine species that the "waterway" pathway refers to introduction through the Suez Canal.*

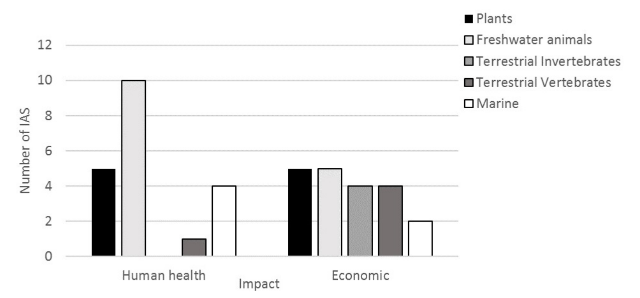

**FIGURE 1 |** Number of top 20 invasive alien species predicted to arrive, establish and have human health and/or economic impacts within Cyprus, across the five thematic groups; plant species (terrestrial and freshwater), freshwater animals (fish and invertebrates), terrestrial invertebrates, terrestrial vertebrates and marine species (primary producers, invertebrates and vertebrates).

*lotor* and Asian hornet *Vespa velutina*. There is one EPPO A1 species citrus longhorn beetle *Anoplophora glabripennis* (A1 species are absent from the EPPO region) and three EPPO A2 species *Eichhornia crassipes*, grapevine phylloxera *Daktulosphaira vitifoliae*, and Colorado potato beetle *Leptinotarsa decemlineata* (A2 species are locally present in the EPPO region) on our list. Cyprus also has a protected zone status for *D. vitifoliae*, *L. decemlineata* and the bark beetle *Ips sexdentatus* under the EU Plant Health Law [Regulation (EU) 2016/2031 & (EU) 2019/2072]. *Ips sexdentatus* was present on the longer list of IAS that were reviewed, but with moderate scores for chance of arrival and establishment (**Supplementary Information 3**), and hence not present within our ranked lists. *Daktulosphaira vitifoliae* and *L. decemlineata* occur on our priority list for economic impact. As such, measures are needed to avoid the introduction of these pests (e.g., restrictions on movement of commodities, surveys) and to ensure their eradication if found present. We anticipate that the lists of IAS identified through this horizon scanning will have relevance for Cyprus but also more widely across the region. Indeed, the inclusion of experts with expertise in policy and roles within the Cypriot government departments was seen as critical to ensure relevance of the expert-elicitation process. The Department of the Environment within the Cyprus Government outlines activities in relation to EU Commitments through Regulations and Directives including the IAS Regulation and the Habitats Directive in their Strategic Plan[1]. The need to raise awareness and inform different stakeholders through the establishment of programs and voluntary agreements are seen as critical for the implementation of relevant environmental actions and measures.

## Awareness Raising Including Case Studies for Five IAS

Five species, one from each of the thematic groups to provide representative examples for a range of taxa and environments, were selected from the top 20 human health and economic impact

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[1] http://www.moa.gov.cy/moa/environment/environmentnew.nsf/index_en/index_en?OpenDocument

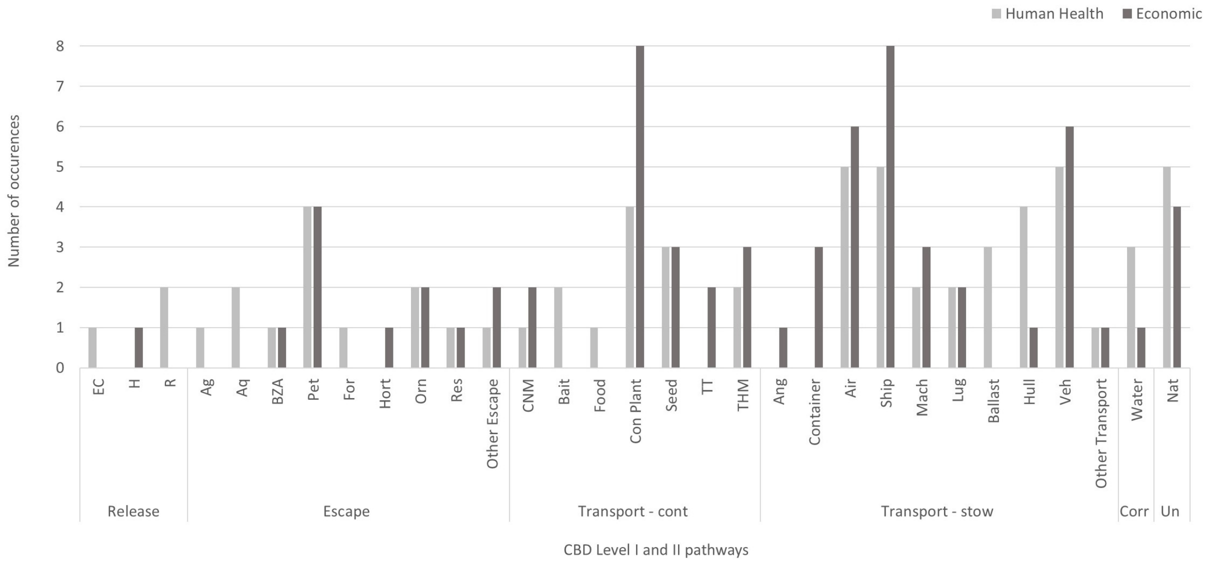

**FIGURE 2 |** Number of occurrences of CBD Level I and II (subcategory) pathways of arrival (Convention on Biological Diversity, 2014; Harrower et al., 2018) for the top 20 invasive alien species predicted to arrive, establish and have human health and/or economic impacts within Cyprus. CBD Level I pathways are given first, followed by CBD Level II pathways. *Release in nature (Release): EC*, *Erosion control; H*, *Hunting, R*, *Release in nature for use. Escape from confinement (Escape): Ag*, *Agriculture (including Biofuel feedstocks); Aq*, *Aquaculture; BZA*, *Botanical garden/zoo/aquaria; Pet*, *Pet/aquarium/terrarium species; For*, *Forestry; Hort*, *Horticulture; Orn*, *Ornamental purpose other than horticulture; Res*, *Research and ex situ breeding (in facilities); Other Escape*, *Other escape from confinement. Transport – contaminant (Transport – cont): CNM*, *Contaminant nursery material; Bait*, *Contaminated bait; Food*, *Food contaminant; Con Plant*, *Contaminant on plants; Seed – Seed contaminant; TT, Timber Trade; THM*, *Transportation of habitat material. Transport – stowaway (Transport – stow): Ang*, *Angling/fishing equipment; Container*, *Container/bulk; Air*, *Hitchhikers on airplane; Ship*, *Hitchhikers on a ship/boat; Mach*, *machinery/equipment; Lug*, *People and their luggage/equipment; Ballast*, *Ship/boat ballast water; Hull*, *Ship/boat hull fouling; Veh*, *Vehicles; Other Transport*, *Other means of transport. Corridor: Water*, *Interconnected waterways. Unaided: Nat*, *Natural dispersal across borders of invasive alien species that have been introduced.*

lists, for further discussion in the paper. We highlight where developing communication campaigns around their pathways of introduction could raise awareness of the threat these IAS pose to human health and economies across Cyprus. Raising awareness of the impacts of IAS is, and will continue to be, an important part of the management of the introduction, spread and impact of species that cause negative impacts (Booy et al., 2017). When communicating information on IAS, it is important to use clear messaging from the project onset and throughout the duration of programs (Davis et al., 2018). Campaigns such as the "Check, Clean, Dry," designed to communicate information and so decrease the spread of freshwater IAS have been widely implemented (Defra, 2010). Public perception of management options can be counter to the requirement to control IAS (Hine et al., 2015; Novoa et al., 2017; Crowley et al., 2019; Shackleton et al., 2019), and so it is critical to include stakeholders, including the public, in the development of communication campaigns, to develop shared understanding of the challenges posed by IAS. There are a number of Europe-wide initiatives including the COST Action Alien CSI[2] which will be informative for the development of communication campaigns to raise awareness about the IAS identified through this study.

Increased awareness would be beneficial for informing prevention and early-warning strategies across all IAS, however it is likely that campaigns targeted at specific IAS or, indeed, specific relevant sectors and stakeholders will be most effective (Davis et al., 2018). Here we provide representative examples of the IAS prioritized within the top 20 in one or both of the lists (human health and economic impacts), highlighting the breadth of taxa, environments and introduction pathways (**Figure 4**). CBD Level I and II (subcategory) pathways (Convention on Biological Diversity, 2014; Harrower et al., 2018) are used throughout in italics when describing pathways of introduction.

## *Parthenium hysterophorus* Whitetop Weed

*Parthenium hysterophorus*, a plant originally from Mexico, Central and South America (ISSG, 2010), was ranked in the top 20 in both the human health and economic impacts lists. *Parthenium hysterophorus*, an IAS of Union concern, has had large impacts on human health where it causes breathing difficulties and allergenic reactions in humans (Patel, 2011). It can kill cattle and contaminate meat and milk, reducing the quality (Lakshmi and Srinivas, 2007), and so also has economic impacts (McConnachie et al., 2011). Notably it is present in Israel which has similar climatic conditions to Cyprus. At the time of the workshop, there were 28 direct flights per week between Cyprus and Israel. This IAS was predicted to arrive through *luggage/equipment* (in particular tourism), as a *seed contaminant*, on *machinery/equipment* and through *transportation of habitat material (soil, vegetation, wood etc.)*;

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[2] https://alien-csi.eu/

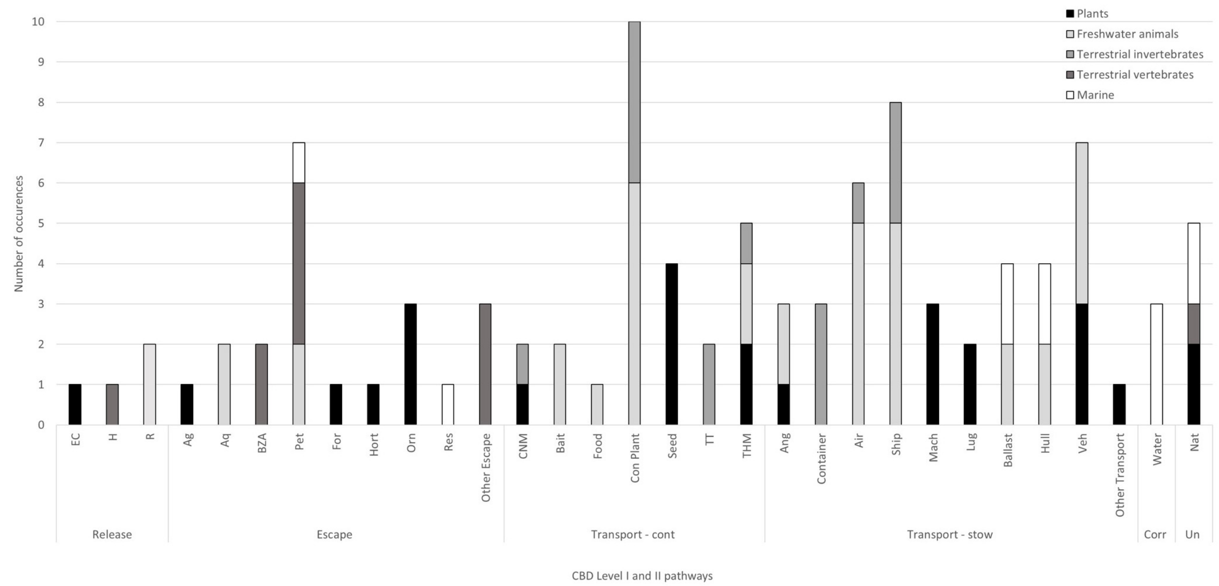

**FIGURE 3 |** Number of occurrences of CBD Level I and II (subcategory) pathways of arrival (Convention on Biological Diversity [CBD], 2014; Harrower et al., 2018) for the top 20 invasive alien species predicted to arrive, establish and have human health and/or economic impacts within Cyprus, across five thematic groups; plant species (terrestrial and freshwater), freshwater animals (fish and invertebrates), terrestrial invertebrates, terrestrial vertebrates and marine species (primary producers, invertebrates and vertebrates). CBD Level I pathways are given first, followed by CBD Level II pathways. Where an IAS had both human health and economic impacts, the pathway information was only given once. *Release in naure (Release): EC, Erosion control; H, Hunting, R, Release in nature for use (other than above). Escape from confinement (Escape): Ag, Agriculture (including Biofuel feedstocks); Aq, Aquaculture; BZA, Botanical garden/zoo/aquaria; Pet, Pet/aquarium/terrarium species; For, Forestry; Hort, Horticulture; Orn, Ornamental purpose other than horticulture; Res, Research and ex situ breeding (in facilities); Other Escape, Other escape from confinement. Transport – contaminant (Transport – cont): CNM, Contaminant nursery material; Bait, Contaminated bait; Food, Food contaminant; Con Plant, Contaminant on plants; Seed, Seed contaminant; TT, Timber Trade; THM, Transportation of habitat material. Transport – stowaway (Transport – stow): Ang, Angling/fishing equipment; Container, Container/bulk; Air, Hitchhikers on airplane; Ship, Hitchhikers on a ship/boat; Mach, machinery/equipment; Lug, People and their luggage/equipment; Ballast, Ship/boat ballast water; Hull, Ship/boat hull fouling; Veh, Vehicles; Other Transport, Other means of transport. Corridor (Corr): Water, Interconnected waterways. Unaided (Un): Nat, Natural dispersal across borders of invasive alien species that have been introduced.*

consequently raising awareness for these pathways would be valuable. We recommend developing collaborative campaigns with key industry partners, such as horticultural organizations, to increase biosecurity awareness around ornamental plants and seed contaminants, applying the European Code of Conduct on Horticulture and IAS (EPPO, 2009). The European Code of Conduct, aimed toward the tourism and industry sectors, gives five recommendations for reducing the risk of IAS arrival (Scalera, 2017).

## *Aedes aegypti* Yellow Fever Mosquito, *Ae. albopictus* Asian Tiger Mosquito, *Ae. flavopictus*, *Ae. japonicus* Asian Bush Mosquito and *Culex quinquefasciatus* Southern House Mosquito

Five mosquito IAS were included within the top 20 lists of IAS with the potential to adversely affect human health and economies. *Aedes aegypti* is native to Asia, *Ae. albopictus* is native to south east Asia, *Ae. flavopictus* is native to north east Asia, *Ae. japonicus* native to eastern Asia. *Culex quinquefasciatus* has uncertain origins with both Africa and Asia being possible (Fonseca et al., 2006). All these mosquito IAS are capable of reducing tourism through nuisance biting but, more seriously, can be vectors of human disease such as dengue, yellow fever, chikungunya, and Zika (Smith et al., 2016). These IAS were identified predominantly to arrive as *hitchhikers in or on airplanes* and *hitchhikers in or on ships/boats*, in *vehicles* and for the *Aedes* mosquitoes through *contaminant on plants* pathways as this species lay their eggs on plant stems e.g., *Aedes albopictus* and lucky bamboo *Dracaena sanderiana* (Hofhuis et al., 2008). On contact with water, either during transit, or on arrival at the destination, the eggs develop into larvae and ultimately hatch into adult mosquitoes. These plants are predominantly introduced to countries via nurseries. Mosquito awareness campaigns, as well as following the guidance outlined in Martinou et al. (2020) for wetland management, could focus on these pathways supported through checks and signposting at airports and ports of arrival such as those carried out in New Zealand (Young, 2003), as well as within the horticulture industry.

## *Daktulosphaira vitifoliae* Grapevine Phylloxera

*Daktulosphaira vitifoliae*, a small insect in the Order Hemiptera, originally from North America, was agreed to be of highest concern from the perspective of economic impacts in the context of Cyprus, and is regulated in Plant Health Regulation (EE) 2016/2031. Cyprus is one of the few countries that uses traditional European vine root stock for growing grapes (Myrianthousis, 1980), whereas in most parts of Europe, due to the presence

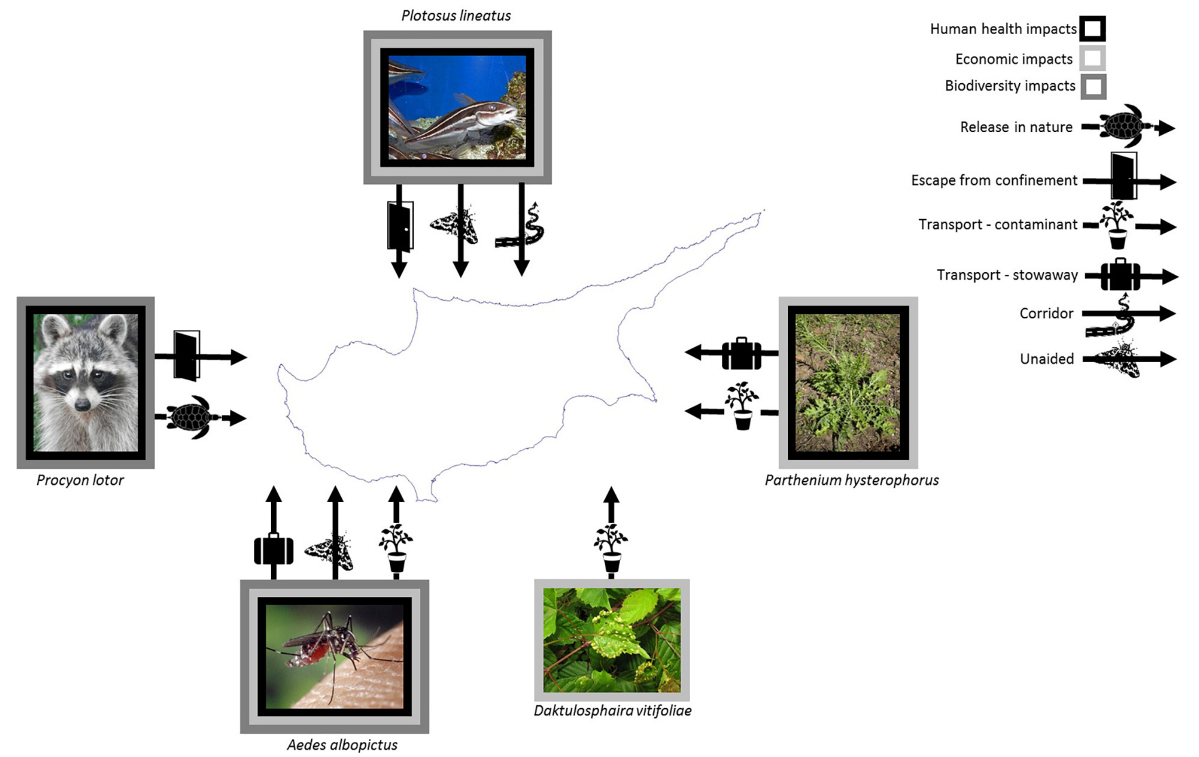

**FIGURE 4 |** Examples of invasive alien species considered likely to arrive, establish and adversely affect human health (black border) and/or economies (light gray border) within Cyprus. Species listed in Peyton et al. (2019) as having a negative impact on biodiversity and ecosystems (dark gray border) are also highlighted. *Procyon lotor* and *Plotosus lineatus* were listed within the top twenty of the biodiversity and ecosystem list. *Aedes albopictus* was scored but unranked in the biodiversity and ecosystem list. The CBD Level I pathways of introduction considered to be of importance for these representative species are depicted by symbols on arrows; *Release in nature*, *Escape from confinement, Transport – contaminant*, *Transport – Stowaway*, *Corridor* and *Unaided* (Convention on Biological Diversity [CBD], 2014, Harrower et al., 2018). Image credits: Map of Cyprus: ©d-maps.com accessed on 23/05/2020 from https://d-maps.com/pays.php?num_pay=187&lang=en. *Aedes albopictus*: © CDC – This media comes from the Centers for Disease Control and Prevention's Public Health Image Library (PHIL). Contributor: James Gathany. *Procyon lotor:* Racoon © Ryan Hodnett (https://commons.wikimedia.org/wiki/File:Common_Raccoon_(Procyon_lotor)_-_Guelph,_Ontario.jpg), https://creativecommons.org/licenses/by-sa/4.0/legalcode. *Plotosus lineatus:* Striped eel catfish © Stan Shebs (https://commons.wikimedia.org/wiki/File:Plotosus_lineatus_1.jpg), "Plotosus lineatus 1", https://creativecommons.org/licenses/by-sa/3.0/legalcode. *Parthenium hysterophorus*: Whitetop weed © Ethel Aardvark (https://commons.wikimedia.org/wiki/File:Parthenium_hysterophorus_plant_with_flowers.jpg), "Parthenium hysterophorus plant with flowers", https://creativecommons.org/licenses/by/3.0/legalcode. *Daktulosphaira vitifoliae:* Grape phylloxera © Beatriz Moisset (https://commons.wikimedia.org/wiki/File:Daktulosphaira_vitifoliae.jpg), https://creativecommons.org/licenses/by-sa/4.0/legalcode.

and subsequent damage caused by *D. vitifoliae* in the late 19th century, American root stock is used (Granett et al., 1996). If this IAS arrived into Cyprus, there would be devastating effects, both culturally and economically to the wine production of the country. As such, it was ranked number one in the list of IAS anticipated to have a negative economic impact. Alongside strict biosecurity protocols, efforts campaigning for awareness around this species should focus on *Transport – contaminant pathways* (such as *contaminant nursery material* and *contaminant on plants*). As with *P. hysterophorus* and for the *Aedes* mosquitoes, working closely with the horticultural industry, as well as with the agricultural industry, would support this objective.

## *Procyon lotor* Raccoon

*Procyon lotor* is listed as an IAS of Union concern, and was included within the top 20 list of species with the potential to affect human health and within the top 50 for affecting economies. This species was also listed within the top 20 IAS to arrive, establish and impact biodiversity and ecosystem services (Peyton et al., 2019). *Procyon lotor*, originally from Central and North America, is found throughout Europe in the wild having escaped or been deliberately released from collections and is spreading in the Mediterranean (García et al., 2012; Mori et al., 2015; Lassnig et al., 2020). They were deliberately released for fur farming and hunting in Germany and the former USSR in the 1920s and 1930s (Aliev and Sanderson, 1966; Lutz, 1984). *Procyon lotor* is a versatile predator and can vector wildlife diseases and zoonosis, including rabies and raccoon roundworm *Baylisascaris procyonis* (Beltrán-Beck et al., 2012). *Procyon lotor* is an IAS identified as being traded in the pet trade. In terms of arrival to Cyprus, inclusion in the IAS of Union concern, Article 7 of the EU Regulation 1143/2014 means that restrictions for import, movement and trade have been in place since being listed in 2016. It is worth noting that, although trading the IAS is illegal, private owners who kept *P. lotor* as a companion animal before it was added as an IAS of Union concern are allowed to keep them under confinement. A risk of unintentional escape or intentional release is still possible, however, from private keepers or zoos, and such a case was documented before 2016 in the Akrotiri area in Cyprus and the animal was removed from the wild by the Game and Fauna Service. As such, *P. lotor* is predicted as most likely to arrive as an escape from confinement through the *botanical garden/zoos and aquaria (excluding domestic aquaria)*, the *pet/aquarium/terrarium species (including live food for such species)* and *other escape from confinement* pathways. Campaigns co-designed with the pet trade would support reducing the risk of escape or release.

### *Plotosus lineatus* Striped Eel Catfish

*Plotosus lineatus*, native in the Red Sea, was identified as having the potential to impact both human health and economies; notably it had also previously been identified as a potential threat to biodiversity and ecosystems. *Plotosus lineatus* produces a venomous hemolytic neurotoxin and can cause serious injury associated with infections and severe clinical manifestations as well as impacting economies through tourism and fisheries declines. It has been found along the Israel (Golani, 2002; Galil, 2007) and Turkish coasts (Doğdu et al., 2016) and is considered to be one of the 100 "Worst Invasives" in the Mediterranean sea (Streftaris and Zenetos, 2006). This IAS entered the Mediterranean through the Lessepsian migration route via the Suez Canal, a major source of many of the invasive alien marine species in the Mediterranean. A full risk assessment of the species (Galanidi et al., 2019) led to its inclusion in the list of IAS of Union concern (EU, 2014). This IAS was predicted to arrive in Cyprus marine area through *natural dispersal*, through *interconnected waterways/seas/basins*, *pet/aquarium/terrarium species (including live food for such species)* and *research and ex situ breeding (in facilities)*. As with *P. lotor*, inclusion on the IAS of Union concern means that this species is banned from being placed in the market, transported, kept or bred in contained holdings but can be kept for its natural life in the domestic environment if already purchased. In addition, this species could be kept within laboratories within the EU for research. A permit would be required under Article 8 of the EU Regulation 1143/2014 for research purposes. *Escape from confinement* through both these pathways are considered possible and hence included. With the exception of northern brown shrimp *Penaeus aztecus*, all marine IAS identified were of Indo-Pacific origin which are predicted to arrive through the pathway *Corridor* (Convention on Biological Diversity, 2014; Harrower et al., 2018), which in the case of the Mediterranean refers to the Suez Canal. The Suez Canal, just under 400 nautical miles south of Cyprus, provides a gateway for major shipping routes to the Red Sea, with over 18,000 vessels carrying more than 980 M tons of cargo through the canal annually (Suez Canal Authority, 2020). The creation and subsequent widening of the Suez Canal has resulted in the increasing transfer of marine species between the Red Sea and the Mediterranean Sea, with large ecological and economic impacts and there have been calls to use the brine output from planned desalination plants along the canal to create an effective salinity barrier to halt these invasions (Galil et al., 2017).

There are many challenges associated with managing established IAS in the marine environment (Russell et al., 2017). The feasibility of eradicating marine IAS is generally low (Booy et al., 2017), therefore early reporting of new IAS is critical to inform mitigation strategies (Zenetos et al., 2019), and public awareness and education campaigns are an important part of the management of marine IAS (Giakoumi et al., 2019).

## CONCLUSION

Horizon scanning to prioritize species with the potential to have negative impacts on human health or economies is an important first step in IAS decision-making and will be invaluable in informing targeted surveillance and enabling management contingency planning (Shine et al., 2010; Caffrey et al., 2014; Roy et al., 2015). Prioritized lists of IAS not yet present within a region can support biosecurity teams in implementing surveillance for early warning systems (Reaser et al., 2020) at borders, such as ports and airports, and at key hubs, such as garden centers and pet shops. Such lists are also useful for developing action plans to tackle important pathways of introduction and spread, a key component of which is the drafting of targeted communication and awareness campaigns for the public. It is critical that risk communication is developed collaboratively to ensure maximum engagement from relevant stakeholders and communities. Collaborations among all stakeholders, ensuring shared goals and understanding between citizen scientists, policy makers and researchers, is critical to informing the development of IAS decision support tools and ultimately supporting the management of biological invasions (Vanderhoeven et al., 2015; Groom et al., 2019).

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## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

HR, JP, and AM conceived the idea for this extension to the horizon scanning approach including economic impacts alongside human health impacts. HR, JP, AM, TA, NC, PK, ETr, and WR contributed to refining the study design. TA, NC, PK, AM, JP, ETr, and WR led the thematic groups. All the authors contributed to the compilation of information and the expert elicitation workshop, reviewed and approved the submitted version. JP, SR, and HR led the database development and produced the summary statistics. JP and HR led the drafting of the manuscript.

## FUNDING

This work was funded by the Defra Darwin Initiative Plus (reference DarwinPlus088 Addressing drivers of change in Lake Akrotiri, Cyprus) and supported through the Natural Environment Research Council award number NE/R016429/1 as part of the UK-SCAPE programme delivering National Capability.

## ACKNOWLEDGMENTS

We would like to thank the Defra Darwin Initiative Plus and NERC UK-SCAPE Programme. We would also like to thank the Akrotiri Environmental Education Centre for their ongoing support and for hosting this workshop. The plant team would also like to thank Ralf Hand for his provision of the Flora of Cyprus, which proved an invaluable tool in working through the plant lists. Finally, we thank the reviewers and the journal editor for the very useful comments they provided.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.566281/full#supplementary-material

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**Conflict of Interest:** PK and DK were employed by the company Marine and Environmental Research (MER) Lab Ltd., MG was employed by the company Ustun Energy Engineering LLC, and AP was employed by the company I.A.CO Environmental & Water Consultants.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 08 January 2021
doi: 10.3389/fevo.2020.625137

# Non-native Species Surrounding Protected Areas Influence the Community of Non-native Species Within Them

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Protected areas (PAs) are a key element of global conservation strategies aiming to protect habitats and species from various threats such as non-natives species (NNS) with negative ecological impacts. Yet little is known about the mechanisms by which PAs are colonized by NNS, and more specifically the role of colonizing events from surrounding areas. Here, we compared terrestrial and freshwater non-native plants and animals recorded in Norwegian PAs and in 5-km belts around them, using the database of the Norwegian Biodiversity Information Centre Species Map Service. Our analysis included 1,602 NNS and 671 PAs. We found that NNS were recorded in only 23% of the PAs, despite the fact that 90% of the 5-km belts were colonized by at least one NNS. A Zero-inflated negative binomial regression model showed that the number of NNS in the 5-km belts was a strong explanatory variable of the NNS richness inside PAs. Other significant variables included the surface area of the PA, mean human population density in the PA, main type of habitat and accessibility of PAs. We also observed similarity in the species in and around the PAs, with, on average, two thirds of the NNS present in a specific PA also present in its 5-km belt. Furthermore, NNS were recorded in PAs on average 4.5 years after being recorded in the 0–5 km belts, suggesting a dynamic of rapid colonization from the belts to the PAs. Invasive NNS represented 12% of NNS in the belts but 40% in the PAs. This difference was related to the higher abundance of invasive NNS in the belts. Our results highlight the necessity of expanding the focus of NNS management in PAs beyond their boundaries, in particular to prevent incursions of NNS with high negative ecological impact.

**Keywords: protected areas, non-native species, alien species, protected area boundaries, invasive species, species distribution**

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***Specialty section:***
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *02 November 2020*
***Accepted:*** *09 December 2020*
***Published:*** *08 January 2021*

***Citation:***
*Holenstein K, Simonson WD, Smith KG, Blackburn TM and Charpentier A (2021) Non-native Species Surrounding Protected Areas Influence the Community of Non-native Species Within Them. Front. Ecol. Evol. 8:625137. doi: 10.3389/fevo.2020.625137*

# INTRODUCTION

Protected areas (PAs) are key target elements of global biodiversity conservation strategies. In 2010, 150 governmental leaders committed, through the Aichi Target 11 in the Convention on Biological Diversity, to improve the status of biodiversity by setting 17% of the global terrestrial area under protection by 2020 (CBD, 2020). The main purposes of PAs are to maintain natural ecosystem functioning, prevent habitat degradation due to human activities (Rodrigues et al., 2004), conserve biodiversity (Worboys, 2015) and protect nature from various threats (Mathur et al., 2015) such as acting as natural filters against invasive non-native species (Foxcroft et al., 2011).

According to IUCN, a non-native species (NNS) is a species introduced outside its natural past or present distribution (IUCN, 2016). During the last two centuries the number of introduced NNS species has increased substantially worldwide with no sign of saturation (Seebens et al., 2017a). Their spread is a consequence of increased human mobility, and the expansion and globalization of trade between countries and continents (Nunes et al., 2015; Chapman et al., 2017; Seebens et al., 2018; Ward et al., 2020). Although the ecological impacts of most NNS are either negligible or unknown (Jarić and Cvijanović, 2012; Seebens et al., 2018; Blackburn et al., 2019), some non-natives are invasive, or potentially invasive: i.e., they have negative impacts on the recipient species and ecosystem (IUCN, 2016; Blackburn et al., 2019). Biological invasions are one of the leading causes of global biodiversity loss (Intergovernmental science-policy platform on biodiversity ecosystem services, 2019) and are one of the principal drivers of recent species extinctions (Clavero and García-Berthou, 2005; Bellard et al., 2016; Blackburn et al., 2019).

Numerous guidelines and technical tools have been developed to assist in the management of invasive NNS in PAs (e.g., de Pooter et al., 2007; Monaco and Genovesi, 2014). These manuals generally advocate the early detection and eradication of all NNS, including those that have not been proven to be invasive, as an implementation of a precautionary approach that considers all NNS to be potentially invasive (McNeely et al., 2001; Monaco and Genovesi, 2014). Beyond the threat to biodiversity posed by invasive species, all NNS represent a human footprint on natural environments. NNS introduced by humans are considered undesirable in PAs, the purpose of which is to preserve nature in as pristine a state as possible (Hettinger, 2001). The presence of NNS also potentially contributes to increasing homogenization of native biological communities (McKinney and Lockwood, 1999; Lambdon et al., 2008; Kortz and Magurran, 2019).

Previous studies have shown that NNS richness patterns within PAs are linked to anthropogenic factors such as road networks and human population density inside PAs (Spear et al., 2013; Dimitrakopoulos et al., 2017; Gallardo et al., 2017; Moustakas et al., 2018). Other properties of the PAs, such as their surface area and protection status, also influence NNS richness (Gallardo et al., 2017; Liu et al., 2020). Furthermore, NNS presence in PAs is also driven by the properties of the surrounding areas, including human land use, human population density and road density (Foxcroft et al., 2011; Spear et al., 2013). These results suggest that, even if long-distance dispersal can be important for the expansion of NNS, especially in the early stages (Ramakrishnan et al., 2010), short-distance dispersal represents a significant contribution to their colonization dynamics. One of the few documented examples was published recently by Liu et al. (2020), based on the global alien distributions of 894 animal species: they found that 89–99% of PAs had an established population of at least one of these species within 10–100 km of their boundaries, but the majority of PAs were not colonized by any of them. Nevertheless, little is known about the influence of the NNS pool present in close proximity to PAs on the NNS communities within them (but for an example see Meiners and Pickett, 2013).

Here, we analyze the composition of terrestrial and freshwater non-native plants and animals present in Norwegian PAs, and in belts of 0–5, 5–10, and 10–20 km around them, to assess the extent to which the community of NNS in areas immediately surrounding PAs relates to NNS within PAs. We selected Norway due to the availability of an extensive database on NNS from the Norwegian Biodiversity Information Centre (NBIC) and the Global Biodiversity Information Facility Norway (GBIF Norway). We hypothesized that the presence of NNS in PAs should mainly be a result of colonization from surrounding areas. NNS in close proximity to PAs should thus influence the community of NNS present in PAs qualitatively, quantitatively and temporally. We expected to find:

1. A high proportion of NNS present in a PA are also present in its surroundings (qualitative similarity). The NNS in a PA will have taxonomic and ecological similarities to the pool of NNS in its surroundings. However, since invasive NNS are expected to have a higher colonization potential than non-invasive NNS, invasives should be present in higher proportions inside PAs than outside in comparison to other NNS.
2. The total number of NNS present inside a PA is a positive function of the richness of NNS in its surroundings (quantitative influence). In addition, the most abundant species in the surroundings of PAs are more likely to be present within the PAs.
3. NNS are recorded in the areas surrounding PAs earlier than inside the PAs (temporal sequence).

# METHODS

## Data on Non-native Species

We downloaded NNS data from the NBIC Species Map Service (https://www.artskart.artsdatabanken.no, 10/04/2020. Data from: List supplementary material. Downloaded through the Species Map service). This database is provided by various contributors including research institutes, environmental agencies and NGOs. Biodiversity data from online databases are potentially biased, for example by accessibility of sites, lack of coverage of geographic and environmental variation that cover species distributions (Hortal et al., 2007), or by taxonomy, such as societal preferences in citizen science projects (Troudet et al., 2017). However, we consider the Norwegian database as one of the most robust that is available, as it contains an extensive collection and evaluation of NNS from a wide range of taxa and across the country (Sandvik et al., 2019; Tsiamis et al., 2019).

We selected terrestrial and freshwater NNS records of the Kingdom "Animalia" and "Plantae" with an accuracy of <= 100 m. For this purpose, we retained only those species with the following habitat categories assigned by Norwegian Biodiversity Information Center (NBIC, https://www.biodiversity.no): terrestrial, limnic/terrestrial, limnic/marine habitats. We filtered for records from the year 1950 to the present. After selection, our NNS database included a total of 350,286 records of 1,602 species representing 21 different taxonomic classes. 14.9% of the NNS were animals and 85.1% were plants.

In order to consider potential ecological impacts caused by NNS, we used the ecological risk assessment conducted by the Norwegian Biodiversity Information Centre, in which each NNS is assigned to one of the following categories:

- "Severe impact" (SE): NNS with actual or potential ecologically harmful impact and the potential to become established across large areas;
- "High impact" (HI): NNS with either a moderate ability to spread but which cause at least a medium ecological effect, or have a minor ecological effect but have a high invasion potential;
- "Potentially high impact" (PH): NNS with either a high ecological effect and low invasion potential or high invasion potential without known ecological effect;
- "Low impact" (LO): NNS with no substantial impact upon Norwegian nature
- "Not known impact" (NK): NNS with no known impact;
- "Not risk assessed" (NR): NNS not yet risk assessed.

NNS belonging to "Severe impact" and "High impact" categories are included in the Norwegian Black List 2012 of Alien Species. In total, 60% of the NNS included in the analysis were risk assessed, while 40% were not.

## Data on Protected Areas

We extracted the shape files and information on the designation year and surface area of Norwegian PAs from the World Data Base on Protected Areas (WDPA, UNEP-WCMC and IUCN, 2019). The WDPA contains 3,143 registered Norwegian PAs of which 2,178 PAs are terrestrial and cover 54,749 km² of the land area of Norway (http://protectedplanet.net, accessed March 2020). We selected for analysis PAs with status "designated" and categorized as "terrestrial," excluding "marine," and "coastal" PAs. There are also PAs that are not assigned to any management categories (i.e., category marked as not assigned, not reported, not applicable); these PAs were excluded.

Protected areas of the WDPA are categorized in different International Union for Conservation of Nature (IUCN) categories, which range from category I (strictly protected or large, unmodified or slightly modified areas) to VI (protected areas with sustainable use of natural resources) whilst further PAs that are not assigned, not reported and not applicable (IUCN, https://www.iucn.org). For our study we selected PAs in category I, II (national parks) and IV (habitat/species management areas) with a surface area >= 1 km². Since our analysis investigated NNS in PAs and belt zones up to a distance of 20 km around the PAs (see below), we also excluded PAs whose belt zones crossed the political borders with Sweden, Finland and Russia.

Applying these filters resulted in 671 PAs in our analysis: 623 PAs of IUCN category I (average surface area = 7.8 km²), 18 PAs of IUCN category II (average surface area = 1,064.9 km²) and 30 PAs of IUCN category IV (average surface area = 142.3 km²). All PAs were designated between 1959 and 2017 and had areas ranging between 1 and 3,444.8 km² (average 42.2 km²). They covered 28,314.9 km², which is 49.5% of the total terrestrial protected area of Norway.

## Belt Zones Around Protected Areas

We mapped belt zones of 0–5, 5–10, and 10–20 km circumjacent to PAs using QGIS (http://qgis.osgeo.org, version 3.4.2-Madeira) (**Figure 1**). All PAs and belt zones were entirely within Norway. Where the belt zone of a PA included part or all of another PA, the intersecting area was not excluded from the belt, such that belts should not be considered as indicators of the state of protection. Our analysis focused on the belt of 0–5 km (henceforth referred to as 5-km belt) to investigate whether the composition of NNS communities within PAs was influenced by NNS in the immediate vicinity of PAs. The surface area of this belt naturally varied with the size of the PA, with a range 99.1–2,218.2 km² (average 167.7 km²).

## Statistical Analysis

All analyses were performed using the statistical analysis tool R [R Core Team (2019), https://www.R-project.org, version 4.2.0]. We extracted NNS records for all the PAs and their belts, deriving from this a list of NNS for each PA and its surrounding belt. To test qualitative similarity, we used tests across all PAs and belts (i.e., overall comparisons considering independently the records made in a PA and in 5-km belts). The temporal sequence analysis was based on data where the NNS was present in the PA and the associated belts using a pairwise comparison. To test for quantitative influence, we used a mixture of tests considering data in PAs and their associated belts as independent (tests on abundance) or as paired for the other analysis (NNS present in PAs and associated 5-km belts and modeling NNS richness).

### Qualitative Similarity

#### *Taxonomy and Ecological Impact*

We compared the proportions of taxonomic classes and ecological impact categories of NNS between the PAs and belts using Pearson's chi-squared tests.

#### *Most Frequent NNS*

To identify the most frequent NNS in the PAs, we selected NNS that were present in at least ten PAs. We compared them with the same number of NNS that were most frequent in the 5-km belts.

### Quantitative Influence

#### *NNS Abundance*

We defined the abundance of a species in a PA or a belt as the number of records of this species. The mean abundance of a

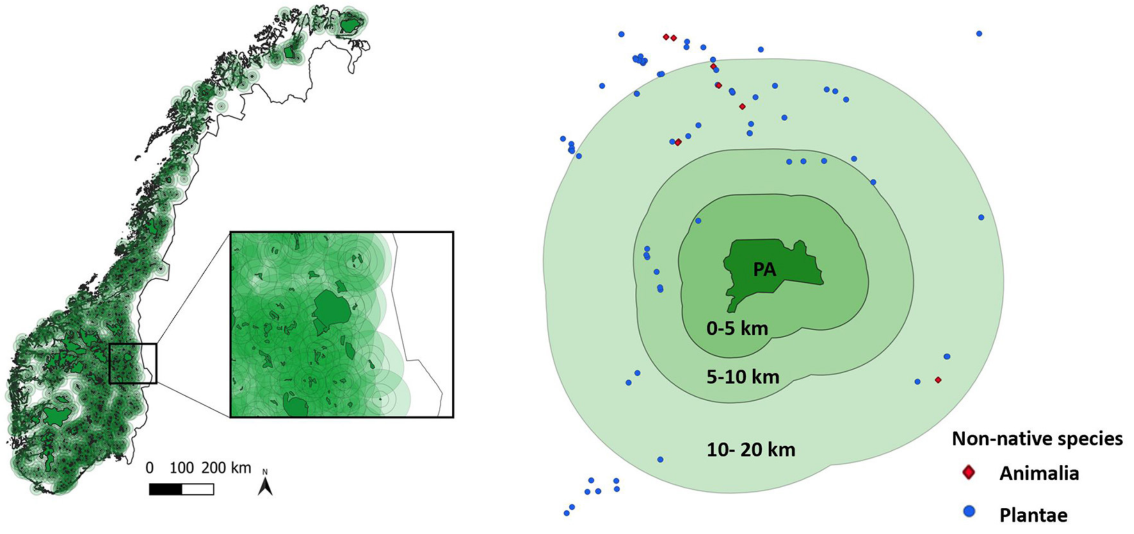

**FIGURE 1 |** Left: Map of Norway with protected areas (PAs) and belt zones, with an example of part of the network (detail shown in inset). Right: An example (Møysalen National Park) showing the area of the PA, the three belts of 0–5, 5–10, and 10–20 km distance from the PA boundary, and the locations of records of non-native animal and plant species.

species is therefore the number of records divided by the number of PAs or belts where it was present.

For NNS present in both the PAs and the 5-km belts, we tested if there was a correlation between their mean abundance in the PAs and the belt using a Spearman's rank correlation (rho).

To test whether the NNS present in the PAs are among the most abundant in the 5-km belts, we compared the mean abundance of NNS present in both the PAs and the belts with the mean abundance of NNS present only in the belts using a Wilcoxon Rank Sum Test.

To test whether NNS of the impact categories "Severe impact" and "High impact" (black listed NNS) were more abundant in the 5-km belts than NNS of less severe impact categories (non-black listed NNS), we compared the mean abundance of these two groups of NNS in the 5-km belts using a Wilcoxon Rank Sum Test.

### *NNS Present in PAs and Associated 5-km Belts*

To investigate the hypothesis that the presence of NNS in PAs is mainly a result of colonizing events from surrounding areas, we calculated, for each NNS present in the 5-km belts, the proportion of times it was present in both the belt and its associated PA, and the proportion of times it was present only in the 5-km belt but not in its associated PA. We then calculated the mean of these proportions for all the NNS present in the 5-km belts.

We applied the same approach for the NNS present in the PAs. We calculated the proportion of time they were present in both the PA and its associated 5-km belt, and the proportion of time they were present only in the PA but not in its associated 5-km belt. We then calculated the mean of these proportions for all the NNS present in the PAs.

### *Modeling NNS Richness*

We selected five explanatory variables to model NNS richness in PAs, comprising two biotic variables (the most abundant land cover in the PAs and NNS richness in the 5-km belts); two anthropogenic variables (mean human population density of the region in which the PA is located and their accessibility), and PA surface area. Land cover was obtained from Copernicus Land Monitoring Service using information Label 1 (CLC, 2018). Label 1 information consists of five categories: "Artificial surfaces", "Agricultural areas", "Forest" and semi natural areas", "Wetlands" and "Water bodies". We extracted the land cover of each PA in QGIS and calculated the percentage of the most abundant land cover category in each PA.

NNS richness in each of the PAs and their associated 5-km belt zones was extracted from the NNS lists. The mean accessibility of PAs, calculated as the mean travel time from within PAs to the nearest city with a population >50,000 inhabitants, was extracted from Nelson (2008), a map integrating transportation networks and agglomeration index (a measure of urban concentration) and was downloaded from the European Commission (https://forobs.jrc.ec.europa.eu). Mean human population density was obtained from WorldPop (2018). The surface areas of the PAs were filtered from the World Database of Protected Areas (WDPA, https://protectedplanet.net). We assessed the relationships between predictor variables using Spearman's Rank correlation. All predictors were retained for the analysis since they had little correlation among them (**Supplementary Figure 1**).

We applied a Zero-inflated Negative Binomial regression model with Poisson distribution (ZINB, Lawal, 2012) to test if the NNS richness in PAs is a result of the NNS richness in the associated 5-km belts, anthropogenic and PA properties. We assumed that if NNS have the opportunity to colonize PAs their richness inside is between 0 or higher and therefore is a count process (Gallardo et al., 2017). On the other hand, for PAs that were uncolonized by NNS, we assumed this was due to missing vectors, distance, or the PA not having suitable habitat (Gallardo et al., 2017). The only outcome in this case is zero. The ZINB model consists of two parts: The first part is the negative binomial regression model, which explains the relationship between conditional variance and conditional mean compared to the Poisson distribution model. The second part, the binary distribution model, captures the excess of zero values that exceed the predicted zeros by the negative binomial distribution. We used the package "pscl" to run the ZINB (Achim et al., 2008; Jackman, 2020).

### Temporal Sequence

#### *Year of First Record in PAs and Associated Belts*

To test whether NNS were recorded earlier in the surrounding belt than inside PAs, we extracted the years of first record for each NNS in the PAs and the 0–5, 5–10, and 10–20 km belt zones. We selected only NNS present in PAs. For each NNS we looked at the PA and the associated belts. We compared the years of first record in PAs and their three associated belts using a Kruskal-Wallis and Dunn's test for pairwise comparison with the "fdr" adjustment method.

# RESULTS

We analyzed 671 Norwegian PAs, of which only 22.8% were colonized by any NNS. In contrast, at least one NNS was present in 89.5% of the 5-km belts. The total number of NNS records was 8,641 in PAs, and 156,736 in the 5-km belts, which represents 2.4 and 44.7%, respectively, of all the Norwegian NNS records included in the analysis. The remaining records were in the 5–10 km belts and 10–20 km belts or outside of them. The number of NNS was between 0 and 53 in PAs (mean = 0.87, SD = 3.68) and 0 and 440 (mean = 23.3, SD = 50.62) in 5-km belts. Of the 1,602 NNS in our analysis, 196 were present in the PAs, and 1,123 in the 5-km belts. All bar one of the 196 NNS present in the PAs (99.5%) were among the NNS present in the 5-km belts, the exception being the plant, *Leucanthemum maximum*. The number of NNS present in PAs also varied between IUCN categories (category I: mean ± SD = 0.68 ± 2.85; category II: 1.27 ± 2.35; category IV: 4.53 ± 11.03).

## Qualitative Similarity

### Taxonomy

More than 75% of the NNS in both the PAs and the 5-km belts were plants, although the proportion of plants was lower in PAs than in 5-km belts (**Figure 2A**). Five plant classes were present in the PAs vs. eight in the 5-km belts (**Figure 2B**). Eudicots (e.g., broadleaf trees *Acer pseudoplatanus* and *Sambucus racemosa*) represented the highest proportion in both the PAs and the 5-km belts but the proportion was significantly lower in the PAs than in the 5-km belts (**Figure 2B**). The inverse relationship was observed for Pinopsida (e.g., coniferous trees *Picea stichensis* and *Abies alba*), with a higher proportion of Pinopsida present in PAs. Non-native animal species represented 22% and 13% of the NNS in PAs and 5-km belts, respectively. Six animal classes were present in the PAs and 8 in the 5-km belts, of which Insecta (e.g., the beetles *Acrotrichis insularis* and *Cartodere nodifer*) showed the highest proportion in PAs and 5-km belts, followed by Aves (e.g., the Canada goose *Branta canadensis* and the Mandarin duck *Aix galericulata*), with a significant higher proportion of Aves in PAs (**Figure 2B**).

### Ecological Impact

NNS listed in the 2012 Norwegian Black List comprised ∼ 40% of the NNS in PAs, with 28.5% classified as species with "Severe impact" (SE) and 11.3% with "High impact" (HI) (**Figure 2C**). In contrast, 12% in the 5-km belts were listed in the Norwegian Black List, with 6.7% "SE" and 5.3% "HI," this difference being significant ($X^2 = 90$, df = 1, $p < 0.05$). Fifty-seven percent of the NNS in the Black List that were present in the 5-km belt were also present in the PAs, compared to only around 12% of the non-listed NNS ($X^2 = 165.19$, df = 1, $p < 0.001$).

### Most Frequent NNS

Nine NNS were present in at least 10 PAs. The most frequent being the Canada goose (*Branta canadensis)*, which was present in 34/671 PAs (5%) (**Figure 3**). Of the top 9 NNS, six were plants and three were animals, one plant and one animal being aquatic. The three animals were chordates (*B. canadensis, Neovison vison* and *Salvelius fontinalis*). *B. canadensis* was also among the top 9 NNS present in the 5-km belts, but at a much higher proportion, colonizing 28% of them (**Figure 3**). In the 5-km belts, the most frequent NNS was the Garden lupin (*Lupinus polyphyllus),* which was present in 437/671 (65%) of the belts and was also among the top 9 NNS in PAs. Seven of the top 9 NNS present in PAs and seven of the top 9 NNS present in the 5-km belts were in the Norwegian Black List of Alien Species 2012.

## Quantitative Influence

### NNS Abundance

The mean abundance of NNS present in PAs was significantly positively correlated with that of the 5-km belts (Spearman's rank correlation rho: $S = 598{,}446$, $p < 0.001$, rho = 0.52).

NNS present in both the 5-km belts and the PAs were significantly more abundant in the 5-km belts than the NNS present only in the 5-km belts (mean abundance in the belts: 8.51 and 2.13 records per NNS, respectively, Wilcoxon Rank Sum Test: $W = 34{,}914$, $p < 0.001$). In the 5-km belts, the abundance of black-listed NNS was significantly higher than the other NNS (mean abundance in belts: 9.48 and 2.38 records per NNS, respectively, Wilcoxon Rank Sum Test: $W = 26{,}002$, $p < 0.001$).

### NNS Present in the PAs and Their Associated 5-Km Belts

Of the pool of NNS present in the associated 5-km belt of a PA, only 1% on average were also present inside the PA they surround. In contrast, on average 63% of NNS present in a PA were also present in its associated 5-km belt, while the remaining

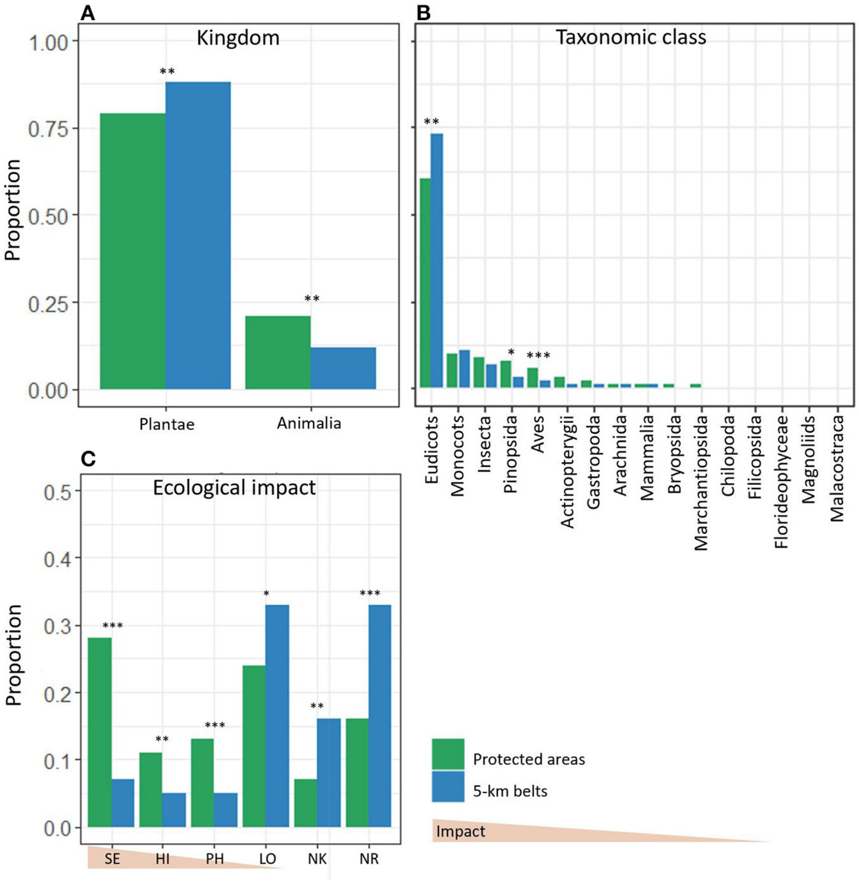

**FIGURE 2 |** Proportions of non-native species in protected areas and 5-km belts represented by **(A)** Kingdom, **(B)** Taxonomic classes, **(C)** Ecological Impact. The ecological impact was assessed by the Norwegian Biodiversity Information Center (NBIC, https://www.biodiversity.no) (SE, Severe impact; HI, High impact; PH, Potentially high impact; LO, Low impact; NK, not known impact; NR, Not risk assessed). Significance of the Pearson $X^2$-test: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

37% of NNS present were only in the PAs and not in the associated 5-km belts.

### Modeling NNS Richness

The results of the Zero-Inflated Negative Binomial regression show a significant positive relationship between NNS richness in PAs and richness in the associated 5-km belts (**Table 1**, **Figure 4**). NNS richness in the 5-km belts was also the only significant variable in the zero part of the model (i.e., modeling PAs free of NNS), being lower when surrounding PAs with no recorded NNS.

The most abundant land cover in the majority of PAs was "Forest and semi natural areas" (525 PAs, 78.6%) followed by "Wetlands" (99 PAs, 14.8%) and "Waterbodies" (42 PAs, 6.3%) (**Figure 4**). Agricultural area was the most abundant land cover of only two PAs. The count part of the ZINB model shows that the number of NNS in PAs was highest where water bodies were the most abundant land cover (**Table 1**). The number of NNS in PAs also significantly increased with increasing mean human population density in the PAs and the surface area of PAs, and was negatively correlated with travel time to large cities (**Table 1**, **Figure 4**).

## Temporal Sequence

### Year of First Records in PAs and Associated Belts

Overall, NNS were recorded later in PAs than in any of the three associated belts, with the difference on average being 4.5 years (0–5 km), 6 years (5–10 km), and 5.5 years (10–20 km) (**Figure 5**). The average years of first records in the three belts were not significantly different. Of the NNS present in both the PA and the associated 5-km belt, 59.4% were recorded earlier in the belt, 17.5% in the same year and 23.1% earlier in the PAs. This overall pattern of delayed records in the PAs was observed for 5 of the 11 taxonomic classes (**Figure 6**). Of the top 9 NNS in PAs, six were recorded significantly earlier in the PAs than in at least one of the belts (Kruskal-Wallis-Test: $X^2 = 62.21$, df = 3, $p < 0.001$) (**Supplementary Figure 2**).

## DISCUSSION

Our study provides an extensive nationwide analysis of how the NNS community in the vicinity of PAs influences the NNS community inside PAs. Using data on 1,602 non-native terrestrial

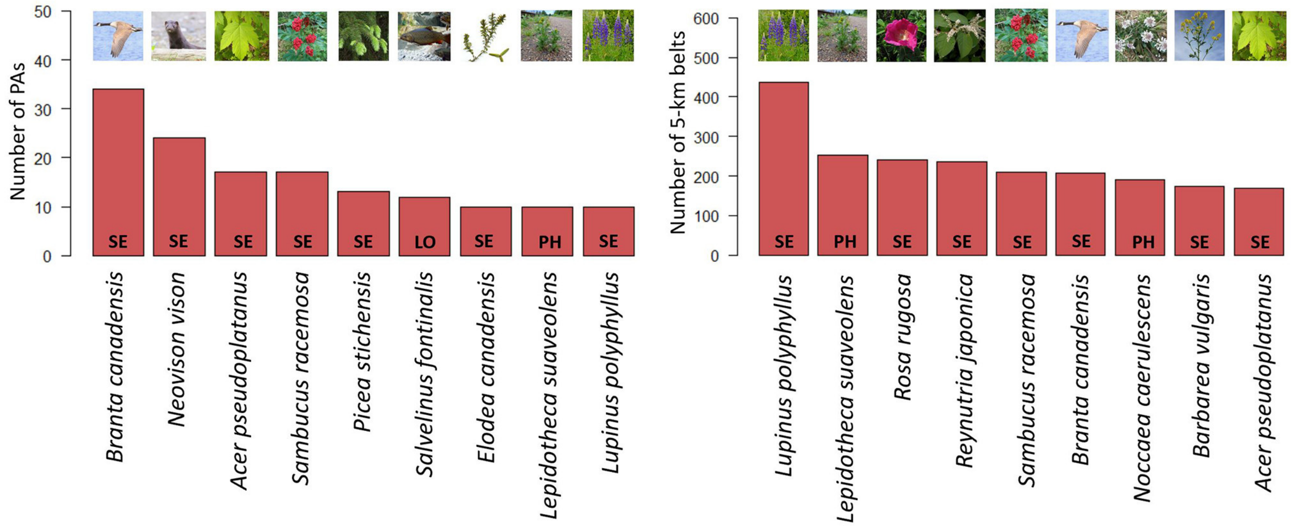

**FIGURE 3 |** The nine most frequent NNS in PAs (left) and 5-km belts (right). Ecological impact classification assessed by the Norwegian Biodiversity Information Centre (NBIC, https://www.biodiversity.no) shown inside the bar: SE, "Severe Impact;" PH, "Potentially High Impact;" and LO, "Low Impact;" on ecology. (Credit pictures: *B. canadensis* & *N. vison*: T.M. Blackburn*; A. pseudoplatanus*: Willow, CC BY-SA 2.5; *S. racemosa*: Opioła Jerzy, CC BY 2.5; *P. stichensis*: Rosser1954, CC BY-SA 4.0; *S. fontinalis*: marrabbio2, CC BY-SA 3.0; *E. canadensis*: Christian Fischer, CC BY-SA 3.0; *L. sauveolens*: AfroBrazilian, CC BY-SA 3.0; *L. polyphyllus*: Andreas Eichler, CC BY-SA 4.0; *R. rugosa*: Vihljun, public domain; *R. japonica*: Andrea Moro, CC BY-SA 4.0; *B. vulagris*: Stefan.lefnaer, CC BY-SA 4.0; *N. caerulescens*: Konrad Lackerbeck, CC BY-SA 2.5).

**TABLE 1 |** Results from the Zero-Inflated Negative Binomial regression model (ZINB) between non-native species (NNS) richness in protected areas (PAs) and mean accessibility to PAs, mean human population density in the PAs, NNS richness in 5-km belts, land cover type (Agriculture, Forest and semi natural areas, Water bodies, Wetlands) in the PAs and surface area of the PAs.

| Factors | Estimate | SE | CI (5/95%) | *z*-value | *p*-value |
|---|---|---|---|---|---|
| **Count model coefficients (Poisson with log link)** | | | | | |
| Intercept | 0.1669 | 0.3713 | −0.4440/0.7778 | 0.449 | ns |
| Mean accessibility | −0.0015 | 0.0007 | −0.0027/−0.0003 | −2.123 | * |
| Mean human population density | 0.5103 | 0.0712 | 0.3932/0.6275 | 7.164 | *** |
| NNS richness belt 5 km | 0.0029 | 0.0004 | 0.0021/0.0034 | 6.018 | *** |
| Landcover PA: Forest and semi natural areas | 0.5195 | 0.3759 | −0.0988/1.1378 | 1.382 | ns |
| Landcover PA: water bodies | 1.4486 | 0.3735 | 0.8342/2.0631 | 3.878 | *** |
| Landcover PA: wetlands | −0.3208 | 0.5259 | −0.1859/0.0544 | −0.610 | ns |
| Surface area | 0.0006 | 0.0001 | 0.0005/0.0008 | 6.541 | *** |
| **Zero-inflated model coefficients (binomial with log link)** | | | | | |
| Intercept | −11.474 | 905.1471 | −1500.3084/1477.3605 | −0.013 | ns |
| Mean accessibility | 0.0017 | 0.0012 | −0.003/0.0037 | 1.431 | ns |
| Mean human population density | −2.5744 | 1.5697 | −5.1563/0.0075 | −1.640 | ns |
| NNS richness belt 5 km | −0.0081 | 0.0038 | −0.0143/−0.0019 | −2.159 | * |
| Landcover PA: Forest and semi natural areas | 12.7044 | 905.1470 | −1476.1300/1501.5387 | 0.014 | ns |
| Landcover PA: water bodies | 11.3893 | 905.1470 | −1477.4451/1500.2237 | 0.013 | ns |
| Landcover PA: wetlands | 12.2484 | 905.1472 | −1476.5862/1501.0830 | 0.014 | ns |
| Surface area | −0.0007 | 0.0004 | −0.0014/0.0000 | −1.576 | ns |

*Log-likelihood: −736.8 on 16 DF.*
*671 PAs were considered.*
****significant at $p < 0.001$; *significant at $p < 0.05$; ns: not significant.*

and freshwater animals and plants of Norway, we showed that 77% of the PAs included in our analysis were free from any of them. This result is in accordance with a previous study on a global scale, which found more than 90% of PAs free from any of 894 non-native animals (Liu et al., 2020). The absence of NNS in PAs is often attributed to their remoteness, which keeps them far from areas where many NNS are introduced: the introduction of NNS is often associated with trading and

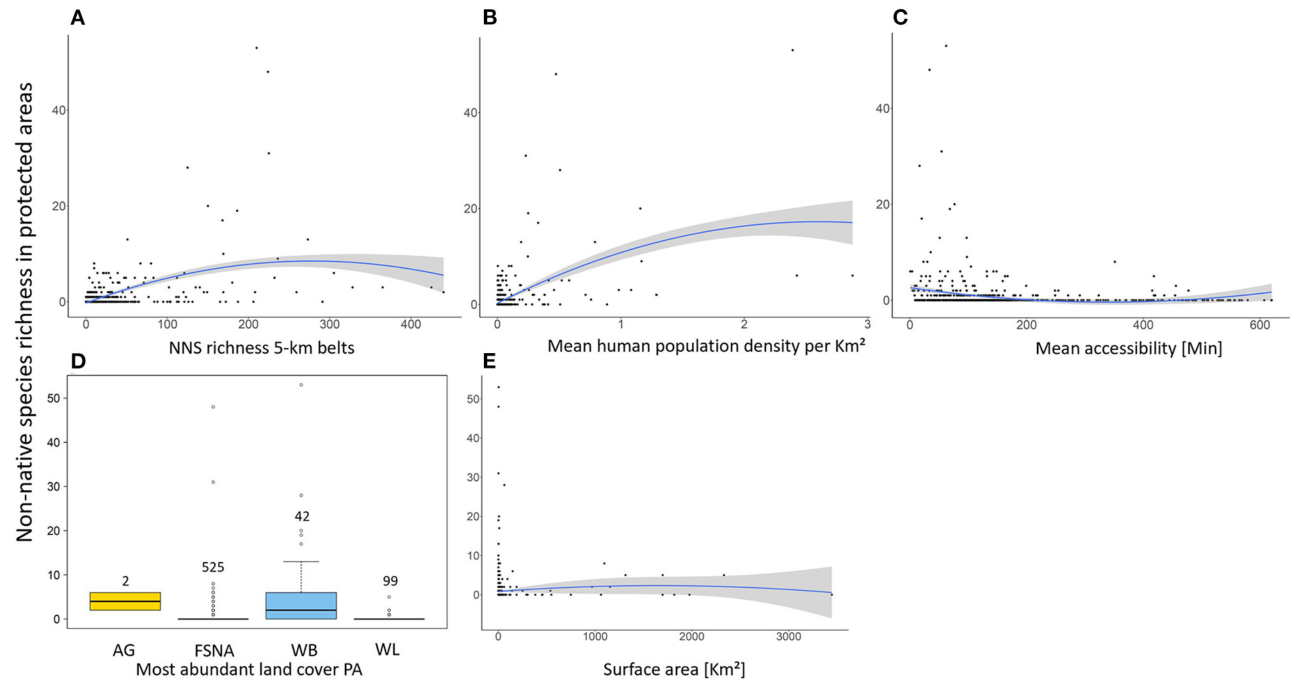

**FIGURE 4 |** Response of Non-native species (NNS) richness in protected areas (PAs) to: **(A)** NNS richness in 5 km-belts, **(B)** Mean human population density in the PAs, **(C)** Mean accessibility of PAs, **(D)** Most abundant land cover in the PA (AG, Agricultural areas; FSNA, Forest and semi natural areas; WB, Water bodies; WL, Wetlands) and **(E)** Surface area of the PA. Solid blue line and shaded area represent the mean and standard error of NNS richness, fitted by GAM.

transport activities between cities and countries (Banks et al., 2015; Nunes et al., 2015; Seebens et al., 2017b; Seebens, 2019) and NNS further spread by vectors such as roads, streams or intended and unintended human transportation (Leuven et al., 2009; Nunes et al., 2015; Brancatelli and Zalba, 2018; Ward et al., 2020). However, in our study, the low NNS richness in the 5-km belts surrounding PAs was the only variable explaining variation in the presence or absence of NNS in PAs (i.e., the zero part of the ZINB regression). This suggests that low colonization and propagule pressure in close proximity seems to be a better explanatory factor for the absence of NNS in PAs than their accessibility. For PAs occupied by NNS, their NNS richness was again significantly related to NNS richness in the surrounding 5-km belts, the accessibility of PAs having a lower effect (i.e., the count part of the ZINB regression). These results again support our hypothesis of a quantitative effect of the pool of NNS in areas close to PAs on the richness of NNS within the PAs. Nevertheless, three other factors also influenced the richness of NNS in PAs: their surface area, the human population density inside them and the main type of habitat they contain. PAs in which water bodies were the most abundant habitat had the highest NNS richness, highlighting lakes and rivers as corridors for the colonization of both limnic (Leuven et al., 2009) and terrestrial NNS (Malíková and Prach, 2010; Francis et al., 2019).

The temporal analysis carried out in our study revealed that NNS were recorded earlier in the immediate surroundings of PAs than within them. On average, NNS were recorded in the PAs 4.5 years after being recorded in the 0–5 km belts. We also measured a delay in the first records of NNS in the PAs for five of the eleven taxonomic classes of NNS and six of the nine most frequent NNS found in PAs. This spatio-temporal sequence of occurrence confirms that PAs are not prime locations for

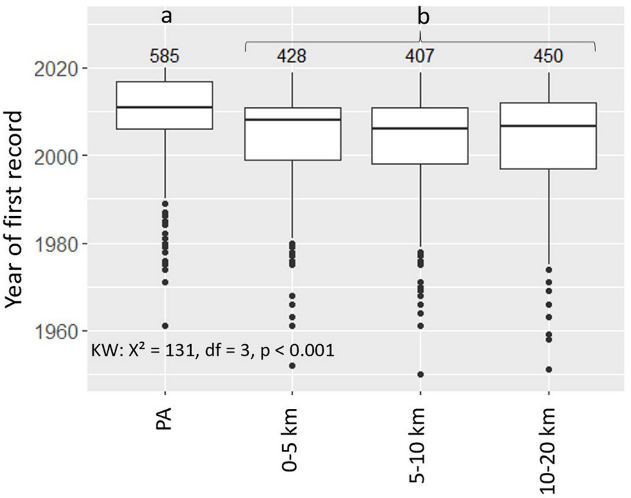

**FIGURE 5 |** Year of first records in protected areas and their associated belts 0–5, 5–10, and 10–20 km for the 196 non-native species recorded within protected areas. We selected only non-native species present in protected areas. For each non-native species, we compared protected areas and their associated belts. The numbers above the boxes represent the numbers of first records of the non-native species included in the analysis. Small letters (a, b) indicate elements that are significantly different from each other according to a Dunn's test for pairwise comparison following a significant Kruskal-Wallis Test (KW).

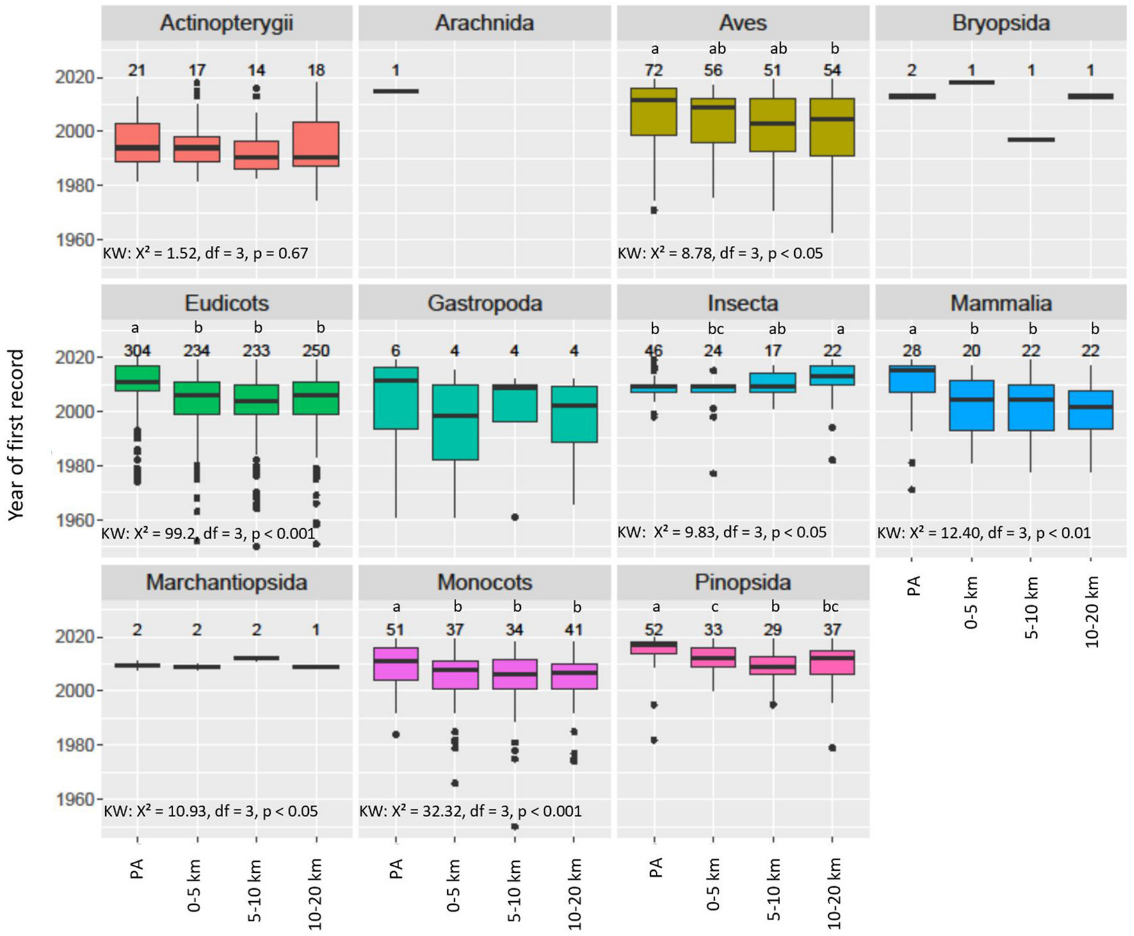

**FIGURE 6 |** Boxplot NNS species taxonomic classes present in PAs: The year of first record in PAs and within a distance of 0–5, 5–10, and 10–20 km from the PA (associated belts). The numbers above the boxes represent the numbers of first records of the non-native species. Small letters (a, b, c) indicate elements that are significantly different from each other according to Dunn's test with "fdr" adjustment, following a significant Kruskal-Wallis Test (KW).

the introduction of NNS and further suggests the important role of colonizing events from within a few kilometers of their boundaries in the processes involved in the spread of NNS in PAs. These results also suggest an invasion debt, i.e., the time lag between the introduction of a non-native species into a region and its potentially negative ecological consequences (Rouget et al., 2016). For example, ornamental plants already introduced for horticultural purposes, but not yet naturalized (i.e., not yet established as persistent wild populations outside of cultivation), represent a risk of invasion in the future that could be exacerbated by climate change (Haeuser et al., 2018). Once naturalized, the time it takes for an invasive species to reach remote PAs, potentially containing many threatened native species, may be another element of this debt. Garden lupin (*L. polyphyllus)*, for example, considered a severely impacting NNS, which was most common in the 0–5 km belts, but much less common in PAs, should require special consideration in their management. This pattern is also supported by the qualitative similarity that we observed within and around PAs, with, on average, two thirds of the NNS present in a specific PA also present in its associated 5-km belt. Nonetheless, previous studies have shown that successful colonization of new environments by NNS varies from species to species depending on environmental conditions and species characteristics (Sakai, 2001; Gallien and Carboni, 2017). Differences in environmental conditions inside and outside PAs, as already shown by Mas (2005), could explain differences in species frequency inside and around PAs. For instance, the Garden lupin (*L. polyphyllus*) the most frequent NNS in the 5-km belts, is an ornamental plant which is common in Norwegian gardens from where it escaped from cultivation (Fermstad, 2010). Another example of differences in environmental conditions are reflected by the fact that the proportions of NNS of two classes, Aves and Pinopsida, were higher inside PAs than in their surroundings. Ten of the 12 non-native birds were Anseriformes (ducks, geese and swans), thus dependent on aquatic habitats, such as the Canada goose (*B. canadensis),* which is the most frequent NNS in the PAs. The Canada goose utilizes open and grassy habitats and nearby lakes and other water bodies, feeding on aquatic plants and animals amongst other food (Jansson et al., 2008). Concerning the conifers (class of *Pinopsida*), suitable habitats comprise forest and semi natural areas, which was the most abundant land cover type in the majority of the PAs in our study. Non-native waterfowl and conifers may thus find more suitable habitat in PAs than around them, as many PAs, unlike belts, have probably been delineated to include high conservation value habitats such as water bodies and forests.

Our analyses show that invasive NNS (i.e., listed on the Norwegian, 2012 blacklist) are over-represented in Norwegian PAs compared to non-invasives. Invasive NNS accounted for 12% of the NNS in the 5-km belts but 40% in the PAs. Furthermore, 57% of invasive NNS present in 5-km belts are also present inside PAs. This high colonization success of invasive NNS in PAs may be explained by their high abundance outside PAs and by having characteristics that permit their fast colonization and spread. In the belt, an invasive NNS was, on average, four times as abundant as a non-invasive NNS (with species abundance measured as the number of records). Several studies have already demonstrated the crucial role of propagule pressure, and especially the number of new immigrants, on the colonization success of NNS (Cassey et al., 2018; Alzate et al., 2020). The higher abundance of invasive NNS in the belts could thus result in a higher propagule pressure inside PAs, and a subsequent higher probability of establishment of invasive NNS in PAs. Four NNS - *R. rugosa*, *R. japonica*, *N. caerulescens* and *B. vulgaris* – were all among the top 9 NNS in 5-km belts but not among the top 9 NNS in PAs. These are clear candidates for future colonization of PAs. This information is of relevance for managers of PAs to remain vigilant to future non-native colonizers.

In conclusion, our study strongly emphasizes the role of colonizing events from the surroundings of PAs in shaping NNS communities inside PAs. Both the abundance and the composition of the NNS communities around PAs influence NNS within PAs. Moreover, our study also reveals differences which are highly relevant for the conservation of PAs, such as the over-representation of invasive NNS within PAs. For all these reasons, we strongly suggest expanding the focus of NNS management within PAs to beyond PA boundaries as recommended by Monaco and Genovesi (2014). Considering the significance of the impact of invasive NNS in PAs (Hulme et al., 2014), efforts in monitoring and controlling invasive NNS are required from the PA management authorities, but also surrounding landowners. Similar advice has already been provided for PAs surrounded by high human population densities (Spear et al., 2013; Liu et al., 2020) - our study generalizes and reinforces it. The focus on NNS in the vicinity of PAs is of relevance for future conservation strategies, especially to prevent incursions of NNS with severe ecological impacts.

## DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found at: https://artskart.artsdatabanken.no and https://www.protectedplanet.net.

## AUTHOR CONTRIBUTIONS

KH did the analysis. KH and AC wrote the first draft of the manuscript. All authors commented, approved the manuscript, and conceived the study.

## FUNDING

KH has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 766417.

## ACKNOWLEDGMENTS

We thank the editors of Frontiers in Ecology and Evolution for this Special Issue. Further, we would like to thank two reviewers for their supportive and constructive comments on the manuscript. We also thank the Norwegian Biodiversity Information Centre (NBIC) for providing their database on alien species. The opinions given herein belong solely to the authors and do not represent the views or policies of IUCN.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.625137/full#supplementary-material

### List Data Providers:

Agder naturmuseum ARC, Arkeologisk Museum UiS, BioFokus, Ecofact, Ento Consulting, Faun Naturforvaltning AS, GBIF-noder utenfor Norge, JBJordal, MFU, MiljÃ,direktoratet, MiljÃ,lÃ|re.no, Molltax, Multiconsult, Naturhistorisk Museum – UiO, Naturrestaurering AS, Norges miljÃ,- og biovitenskapelige universitet, botanisk forening, Norsk entomologisk forening, Norsk institutt for naturforskning, Norsk institutt for vannforskning, Norsk Ornitologisk Forening, Norsk zoologisk forening, NTNU-Vitenskapsmuseet, RÃ¥dgivende Biologer AS, Svalbardflora.net, Sweco Norge AS, TromsÃ, museum – Universitetsmuseet, Universitetsmuseet i Bergen, UiB.

**Supplementary Figure 1 |** Spearman rank correlation index of non-native species (NNS) richness in protected areas (PAs) and the four continuous explanatory variables: Mean accessibility of PAs, surface area of PAs, NNS richness in 5-km belts and mean human population density in PAs.

**Supplementary Figure 2 |** Years of first record of NNS in PAs and within a distance of 0–5, 5–10, and 10–20 km from the PA (belt zones). The numbers above the boxplot indicate the numbers of PAs and associated belts in which the NNS were present. Small letters (a,b) indicate elements that are significantly differentiated from each other according to Dunn's Test with "fdr" adjustment following a significant Kruskal-Wallis Test (KW).

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor declared a past co-authorship with one of the authors, TB.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 22 January 2021
doi: 10.3389/fevo.2020.619861

# Effects of Soil Nutrient Heterogeneity on the Growth and Invasion Success of Alien Plants: A Multi-Species Study

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Spatial heterogeneity in soil nutrient availability can influence performance of invasive plant species under competition-free environments. However, little was known about whether invasive plants perform better under heterogeneous than under homogeneous soil nutrient conditions in competition with native plant communities. We conducted a multi-species greenhouse experiment to test the effect of soil nutrient heterogeneity on the growth and invasion success of alien plants in a native plant community. We grew ten alien invasive plant species that are common in China under a homogeneous or heterogeneous environment alone or together with a community consisting of six native plant species from China. Compared with the homogeneous soil condition, the heterogeneous soil condition significantly increased aboveground biomass of the invasive plants. However, soil nutrient heterogeneity did not affect the relative abundance of the invasive species, as measured by the ratio of aboveground biomass of the invasive species to total aboveground biomass of the whole community. There were no significant interactive effects of soil nutrient heterogeneity and competition from the native community on aboveground biomass of the invasive plants and also no significant effects of soil nutrient heterogeneity on its relative abundance. Our results indicate that soil nutrient heterogeneity has a positive effect on the growth of invasive plants in general, but do not support the idea that soil nutrient heterogeneity favors the invasion success of exotic plant species in native plant communities.

**Keywords: biological invasion, environmental heterogeneity, invasibility, invasiveness, multi-species**

***Edited by:***
*Joana Raquel Vicente,*
*University of Porto, Portugal*

***Reviewed by:***
*Jian Liu,*
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***Specialty section:***
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *21 October 2020*
***Accepted:*** *28 December 2020*
***Published:*** *22 January 2021*

***Citation:***
*Gao F-L, He Q-S, Zhang Y-D, Hou J-H and Yu F-H (2021) Effects of Soil Nutrient Heterogeneity on the Growth and Invasion Success of Alien Plants: A Multi-Species Study. Front. Ecol. Evol. 8:619861. doi: 10.3389/fevo.2020.619861*

## INTRODUCTION

Soil nutrients are generally spatially heterogeneously distributed in nature, and such soil nutrient heterogeneity occurs at different scales relevant to plant growth and distribution (Jackson and Caldwell, 1993a; Stein et al., 2014; Brezina et al., 2019). Soil nutrient heterogeneity may affect plant population dynamics, community structure and ecosystem function (Day et al., 2003a,b; Wijesinghe et al., 2005; Gazol et al., 2013; Tamme et al., 2016; Xi et al., 2017) as it can modulate intra- and interspecific competition owing to the different responses of plant species to nutrient heterogeneity (Mommer et al., 2011, 2012; Roiloa et al., 2014; Tsunoda et al., 2014; Xue et al., 2018). Alien plant invasions can directly reduce the diversity of native plant communities due to their greater competitive advantages compared with native ones (Vilà et al., 2011; Zhang et al., 2019). Soil nutrient heterogeneity, particularly at fine scales, may influence the invasion success of alien plants by shifting the competitive balance between native plants and invaders (Chen et al., 2017; Liu et al., 2017).

Plant species frequently perform better in environments with a heterogeneous than with a homogenous soil nutrient supply, even though the total amount of nutrients are the same in the two environments (Cahill et al., 2010; Zhou et al., 2012; Liu et al., 2020). This is because plants have a foraging response and can capture more resources from resource-rich patches in heterogeneous environments (Robinson et al., 1999; James et al., 2009; Gao et al., 2012). Invasive exotic non-clonal plant species typically have a stronger root-foraging ability than non-invasive species or natives (Rajaniemi and Reynolds, 2004; Drenovsky et al., 2008; Keser et al., 2015). Alternatively, some invasive clonal plants have a higher ability of selectively placing nutrient-acquisition organs in high-resource patches and translocating more resources between interconnected ramets than native clonal plants, which benefit their ramets in nutrient-poor patches and thus promote the performance of the whole clone (Keser et al., 2014; Wang et al., 2017; Chen et al., 2019). Since invasive plants can benefit more from environmental heterogeneity than natives (Wang et al., 2017; Chen et al., 2019), we hypothesized that environmental heterogeneity can increase the competitive ability of invasive species more than that of native species so that it can promote the invasion success of exotic plants in native plant communities.

Although soil nutrient heterogeneity has the potential to promote the growth of invasive plants, most previous studies testing the heterogeneity effects on the invasion success consisted of only two species, i.e., one target species of invasive plants and one species of competing native plants (Chen et al., 2017; Liang et al., 2020). In addition, experiments on invasive plants with an assembled community were conducted mostly in a homogenous environment (Kennedy et al., 2002; Heckman and Carr, 2016). Thus, little is known about whether soil nutrient heterogeneity affects the invasion success of exotic plant species in native communities consisting of multiple plant species.

To assess the effects of soil nutrient heterogeneity and competition from the native community on the growth and invasion success of alien plant species, we conducted a greenhouse experiment using ten invasive plant species that are common in southeast China and a synthetic community that consisted of six native plant species. We grew the ten invasive plants alone (without competition) or with a synthetic community (with competition) in a homogenous or heterogeneous environment. Specifically, we addressed the following two questions. (1) Does soil nutrient heterogeneity generally increase the growth of invasive species in competition with the native plant community, as measured by aboveground biomass of the invasive species? (2) Does soil nutrient heterogeneity generally promote the invasion success of invasive plant species in the native plant community, as measured by the ratio of aboveground biomass of the invasive species to that of the whole community (native and invasive plants together)?

# MATERIALS AND METHODS

## Plant Species and Cultivation

We used ten alien invasive plant species in China (**Table 1**). Ramets of *A. philoxeroides*, *W. trilobata*, and *H. vulgaris* were collected from five locations spaced at least 500 m apart to increase the likelihood of sampling ramets from different genets, i.e., genotypes. Then, they were propagated vegetatively in a greenhouse in Taizhou University, Taizhou, China, for at least 1 year before use. Seeds of *S. canadensis* and the six non-clonal species were collected from 3 to 5 populations spaced at least 1.5 km apart in Taizhou. Seeds of six native plant species were collected in Taizhou (**Table 1**) and used to construct native plant communities. We chose these six native species as they are widely distributed in China and also co-occur with the invasive species used in the experiment.

On May 18, 2019, seeds of the native species and the alien invasive species were sown separately in 13 trays (20 × 12 × 5 cm) filled with a mixture of equal amounts of peat, vermiculite and sand. On May 25, 2019, we planted 90 one-node stem fragments of each of *A. philoxeroides*, *W. trilobata*, and *H. vulgaris* in three plastic containers (71 × 45.5 × 18 cm) filled with the same soil mixture. A total of 32 similarly sized individuals of each alien invasive species and 160 similarly sized individuals of each native species were selected for use in our experiment.

## Experimental Design

Each of the ten invasive species was subjected to two soil nutrient treatments (homogeneous or heterogeneous) crossed with two competition treatments (native community present or absent), with four replicates. For the heterogeneous treatment, each pot (24 cm in diameter and 20 cm in height) was divided into four equal quadrants, two of which were filled with a high nutrient soil and the other two with a low nutrient soil, arranged in a checkerboard pattern. For the homogeneous treatments, the four quadrants of the pot were each filled with an equal mixture of the low and the high nutrient soils. The high and the low nutrient soils were an equal mixture of peat, sand and vermiculite with 7.2 and 0.8 g $L^{-1}$ slow-release fertilizer (14:14:14 N:P:K, Osmocote Exact Standard 3–4 M; Scotts, Marysville, Ohio, USA), respectively. There were no physical barriers between the quadrants, so the plant roots could grow across different quadrants.

For the treatment without competition, two plants of an invasive species were grown in the center of a pot, and no plants of native species were grown in the pot (**Figure 1**). For the treatment with competition, two plants of an invasive species were grown in the center of a pot, and two plants of each of the six native species (a total of 12 plants) were grown in the pot (**Figure 1**). The 12 plants of the native species were randomly assigned to the 12 planting positions along the four border lines of the four quadrants with three positions along each line (**Figure 1**). There were a total of 160 pots (10 invasive species × 2 soil treatments × 2 competition treatments × 4 replicates). The pots were randomly arranged on a bench in a greenhouse at Taizhou University.

**TABLE 1 |** Information on the ten alien invasive plant species (A) and the six native plant species (B) used in this experiment.

| Species | Family | Life form | Clonality | Collection site |
|---|---|---|---|---|
| **(A) Alien invasive species** | | | | |
| *Ageratum conyzoides* L. | Asteraceae | Annual | No | Taizhou city |
| *Alternanthera philoxeroides* (Mart.) Griseb. | Amaranthaceae | Perennial | Yes | Taizhou city |
| *Bidens frondosa* L. | Asteraceae | Annual | No | Taizhou city |
| *Bidens pilosa* L. | Asteraceae | Annual | No | Taizhou city |
| *Celosia argentea* L. | Amaranthaceae | Annual | No | Taizhou city |
| *Erigeron annuus* (L.) Cronq. | Asteraceae | Annual | No | Taizhou city |
| *Hydrocotyle vulgaris* L. | Umbelliferae | Perennial | Yes | Taizhou city |
| *Sesbania cannabina* (Retz.) Poir. | Fabaceae | Annual | No | Taizhou city |
| *Solidago canadensis* L. | Asteraceae | Perennial | Yes | Taizhou city |
| *Sphagneticola trilobata* (L.) Pruski | Asteraceae | Perennial | Yes | Guangzhou city |
| **(B) Native species** | | | | |
| *Achyranthes bidentata* Blume. | Amaranthaceae | Perennial | No | Taizhou city |
| *Artemisia argyi* Lévl. et Van. | Asteraceae | Perennial | No | Taizhou city |
| *Arthraxon hispidus* (Trin.) Makino | Poaceae | Perennial | No | Taizhou city |
| *Bellis perennis* L. | Asteraceae | Perennial | No | Taizhou city |
| *Patrinia scabiosaefolia* Fisch. ex Trev. | Valerianaceae | Perennial | No | Taizhou city |
| *Plantago asiatica* L. | Plantagonaceae | Perennial | No | Taizhou city |

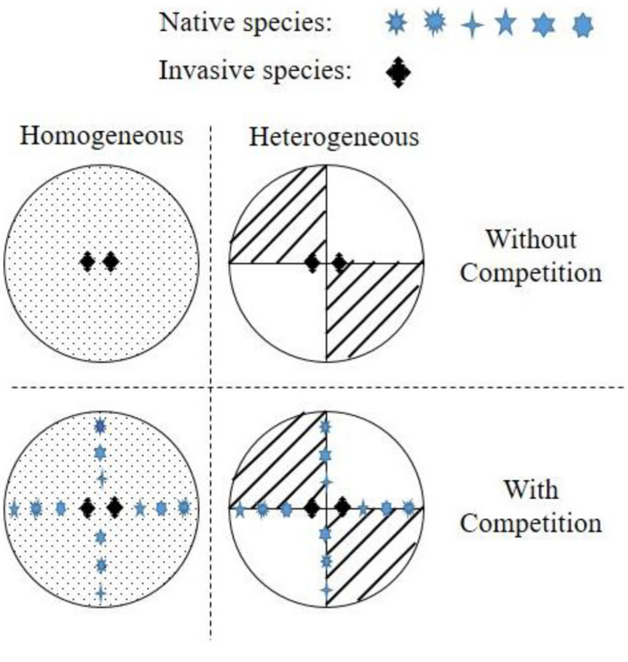

**FIGURE 1 |** Schematic representation of the experimental design. Two plants of each ten invasive species were grown alone in the center of a pot under soil homogeneous condition or were grown together with 12 native plants (two plants of each of six native species) under heterogeneous soil environment. The total amount of soil nutrients in a pot was the same in all the treatments. Black filled pattern represents invasive species and blue filled different patterns indicate six native species.

The experiment started on June 19, 2019, ended on August 13, 2019, and lasted for 52 days. The mean temperature in the greenhouse was 27.3°C, and mean relative humidity was 80.1% during the experiment. The light intensity inside the greenhouse was ∼70% of the natural light outside the greenhouse.

## Harvest and Measurements

We measured initial height of each invasive plant in each pot at the beginning of the experiment. At the end of the experiment, we harvested aboveground part of the invasive species for the treatment without competition and the aboveground part of the invasive species and of each of the native species for the treatment with competition in each pot. All the plant materials were dried at 70°C in ovens for 72 h and weighed to obtain aboveground biomass. Total aboveground biomass per pot was the sum of aboveground biomass of the invasive species and that of the six native species in a pot. The relative abundance of the invasive species in a pot was calculated by dividing aboveground biomass of the invasive species in the pot by total aboveground biomass of all the species in pot (Parepa et al., 2013).

## Data Analysis

Since we were preferentially interested in the generality of the effect of soil nutrient heterogeneity on the growth and invasion success of exotic plant species, we analyzed all ten invasive species jointly. Aboveground biomass and the relative abundance of the alien species were analyzed with a linear mixed model using the *lme* function in the R package *nlme* (Pinheiro et al., 2016). In this model, we included competition with native species (with or without), soil nutrient heterogeneity (heterogeneous or homogeneous), and their interactions as fixed terms. We accounted for differences in the initial size of the exotic alien species by including initial height as a covariate in the model. We accounted for variation among the different species by including species as random terms. To improve the normality of residuals, we tried different transformations and achieved the best residual

**TABLE 2 |** Results of linear mixed effect models to test the effects of soil nutrient heterogeneity and competition on (A) aboveground biomass and (B) the relative abundance of invasive plant species in plant communities.

| | (A) Aboveground biomass | | | (B) Relative abundance | | |
|---|---|---|---|---|---|---|
| **Effect** | **df** | **F** | ***P*** | **df** | **F** | ***P*** |
| Initial height | 1,145 | 29.35 | **<0.0001** | 1.67 | 1.97 | 0.1647 |
| Heterogeneity (H) | 1,145 | 3.98 | **0.0479** | 1.67 | 0.70 | 0.4061 |
| Competition (C) | 1,145 | 453.37 | **<0.0001** | | | |
| H × C | 1,145 | 0.05 | 0.8320 | | | |

*Species was included as a random effect. Values are in bold when P < 0.05.*

distributions with a square root transformation of aboveground biomass and the relative abundance of exotic alien species. Since the homoscedasticity assumption was violated, we also included variance structures that modeled different variances per species in the models using the "*varIdent*" function in the R package *nlme* (Zuur et al., 2009; Pinheiro et al., 2016).

We were also interested in the effect of soil nutrient heterogeneity on aboveground biomass, the Shannon–Wiener diversity index ($H'$) and evenness of the native community. $H'$ was calculated as $-\sum p_i \ln p_i\ (i = 1, 2, \ldots, S)$, where $S$ is number of species in a community, and $p_i$ is aboveground biomass of species $i$ divided by total biomass of all species in the community (Kent and Coker, 1992). Evenness ($J$) was derived as $J = H'/H'_{\max} = H'/\ln S$ (Kent and Coker, 1992). These data were also analyzed with a liner mixed model using the package *nlme* (Pinheiro et al., 2016). In these models, soil nutrient heterogeneity was acted as fixed terms and species as random terms. To improve the normality of residuals, we tried different transformations and achieved the best residual distributions with a natural-log transformation for aboveground biomass of the native community and with the square root transformation for $H'$ and $J$. To account for the heterogeneity of variance, we used the "*varIdent*" variance structure implemented in the *nlme* function to allow for different variances for each combination of species and soil nutrient heterogeneity treatment. All the analyses were implemented in R 3.6.1 (R Core Team, 2019).

## RESULTS

Soil nutrient heterogeneity significantly increased aboveground biomass of invasive species (**Table 2**, **Figure 2**), but had no significant effect on the relative abundance (**Table 2**, **Figure 3**), suggesting that it promote the growth but not the invasive succession of invasive species in native plant communities. Not surprisingly, competition from the native communities decreased aboveground biomass of invasive species (**Table 2**, **Figure 2**). There was no interactive effect of soil nutrient heterogeneity and competition from the native community on aboveground biomass of invasive species (**Table 2**). Soil nutrient heterogeneity did not significantly affect aboveground biomass, but marginally significantly increased species diversity and evenness of the native community (**Figure 4**).

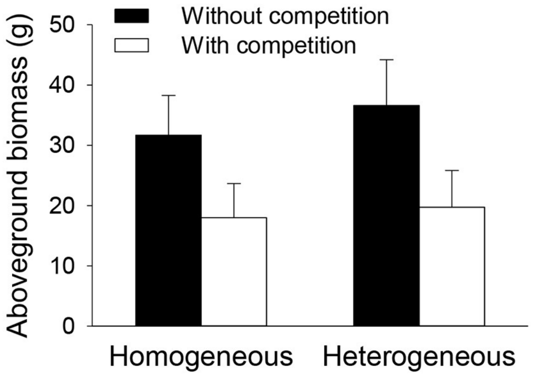

**FIGURE 2 |** Aboveground biomass (mean + SE) across the ten invasive plant species in the homogeneous or heterogeneous soil nutrient treatment with or without competition from the native community.

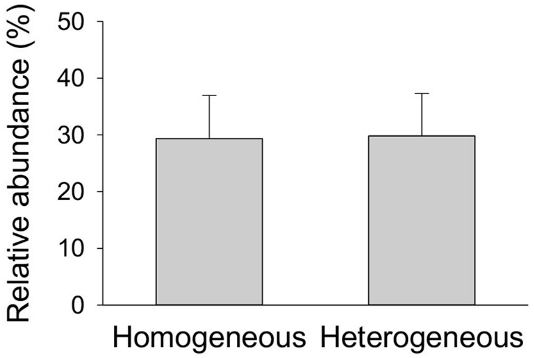

**FIGURE 3 |** Mean relative abundance (mean + SE) across the ten invasive species in the homogeneous and heterogeneous soil nutrient treatments.

## DISCUSSION

Spatial heterogeneity of environmental factors are common in nature (Jackson and Caldwell, 1993b; Alpert and Mooney, 1996; Liu et al., 2003; Liang et al., 2007; Gao et al., 2021), and may influence exotic plant invasions (Keser et al., 2015; Chen et al., 2017; Wang et al., 2017; Liang et al., 2020). However, previous studies testing effects of soil heterogeneity on invasive

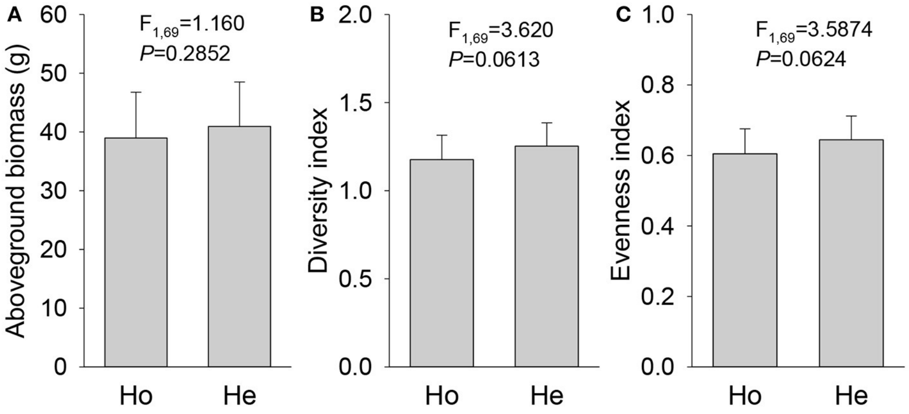

**FIGURE 4 | (A)** Aboveground biomass, **(B)** species diversity, and **(C)** species evenness of the native community under the homogeneous (Ho) and heterogeneous (He) soil nutrient treatment.

plants were conducted mostly under competition-free conditions (Keser et al., 2014, 2015; Dong et al., 2015; Wang et al., 2017), and its effects on the invasion success of exotic plant has not been adequately addressed (Liang et al., 2020). Our results suggest that, although soil heterogeneity increased the performance of invasive plant species in the presence of native plant communities, it did not increase the final invasion success of exotic plant species.

We found that biomass of invasive plant species was generally greater in heterogeneous than in homogeneous soil nutrient conditions (**Table 2**; **Figure 2**). This result is in line with a recent study showing that biomass of the invasive plant *A. philoxeroides* was significantly higher in heterogeneous nutrient treatment than in the homogeneous nutrient treatment, and such an effect did not depend on whether the invasive plant was grown alone or with the native plant *A. sessilis* (Liang et al., 2020). One potential mechanism is that plants usually capture more nutrients in nutrient-rich patches in heterogeneous environments, and thus promote the performance by selectively proliferating roots or concentrating other resource-acquiring organs in nutrient-rich patches (Robinson et al., 1999; Zhou et al., 2012; Gao et al., 2014; Roiloa et al., 2014). The heterogeneity-mediated increase in plant performance suggests that soil nutrient heterogeneity has the potential to improve the invasiveness of alien plant species.

However, we found that soil nutrient heterogeneity had no effect on the invasion succession of exotic plants (**Table 2**; **Figure 3**), suggesting that heterogeneous soil condition did not significantly shift the competitive balance between alien plants and natives toward the invaders. This is not consistent with previous studies showing that the competitive effects of the invasive species on some native species was greater in heterogeneous than homogeneous soils (Chen et al., 2017; Liang et al., 2020). This discrepancy might be attributed to the differences in the diversity of native competitors (Stachowicz et al., 1999; Kennedy et al., 2002), as previous studies demonstrated that native biodiversity can suppress the success of plant invasion owing to increased resource use, i.e., complementarity of resource use between species results in lower levels of available resources at high diversity (Kennedy et al., 2002; Fargione and Tilman, 2005). The native communities in our experiment, consisting of six different native species, have more species diversity than the previous studies. Thus, the effects of soil nutrient heterogeneity on the competitive ability of invasive species may be more complex and unpredictable for the native community with diverse native species.

One caveat is that the effect of soil nutrient heterogeneity on the invasion success of exotic plant may depend on the scale of soil spatial nutrient heterogeneity considered. In our study, the patch scale of soil heterogeneity may be too fine to induce a significant effect on the invasion success of exotic plants. Thus, experiments involving larger scales of soil nutrient heterogeneity should be considered in future studies. Also, the interaction between native species diversity and soil nutrient heterogeneity should also be considered to fully understand the effect of soil nutrient heterogeneity on exotic plant invasions.

We conclude that soil nutrient heterogeneity has a positive effect on the growth of invasive plants in general, but do not support the idea that soil nutrient heterogeneity favors the invasion success of exotic plant species in native plant communities. However, we cannot exclude the possibilities that soil nutrient heterogeneity plays a roles in exotic plant invasions under other scales of soil heterogeneity and different levels of native plant diversity. Further studies should be conducted to test these new hypotheses.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

F-LG and F-HY designed the study and analyzed the data. Q-SH, Y-DZ, and J-HH performed the research and collected the data. F-LG drafted the manuscript. F-HY revised the manuscript.

## FUNDING

This study was supported by the Ten-Thousand Talent Program of Zhejiang Province (2018R52016), the Joint Fund of Zhejiang Provincial Natural Science Foundation (LTZ20C030001), and a Startup Project for Doctor's Scientific Research of Binzhou University (2019Y35).

## ACKNOWLEDGMENTS

We thank Prof. Yanjie Liu for help with the data analysis using R and two reviewers for their comments.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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MINI REVIEW
published: 28 January 2021
doi: 10.3389/fevo.2021.631338

# Monitoring the Spread of Water Hyacinth (*Pontederia crassipes*): Challenges and Future Developments

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**Specialty section:**
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

**Received:** *19 November 2020*
**Accepted:** *04 January 2021*
**Published:** *28 January 2021*

**Citation:**
*Datta A, Maharaj S, Prabhu GN, Bhowmik D, Marino A, Akbari V, Rupavatharam S, Sujeetha JARP, Anantrao GG, Poduvattil VK, Kumar S and Kleczkowski A (2021) Monitoring the Spread of Water Hyacinth (Pontederia crassipes): Challenges and Future Developments. Front. Ecol. Evol. 9:631338. doi: 10.3389/fevo.2021.631338*

Water hyacinth (*Pontederia crassipes,* also referred to as *Eichhornia crassipes*) is one of the most invasive weed species in the world, causing significant adverse economic and ecological impacts, particularly in tropical and sub-tropical regions. Large scale real-time monitoring of areas of chronic infestation is critical to formulate effective control strategies for this fast spreading weed species. Assessment of revenue generation potential of the harvested water hyacinth biomass also requires enhanced understanding to estimate the biomass yield potential for a given water body. Modern remote sensing technologies can greatly enhance our capacity to understand, monitor, and estimate water hyacinth infestation within inland as well as coastal freshwater bodies. Readily available satellite imagery with high spectral, temporal, and spatial resolution, along with conventional and modern machine learning techniques for automated image analysis, can enable discrimination of water hyacinth infestation from other floating or submerged vegetation. Remote sensing can potentially be complemented with an array of other technology-based methods, including aerial surveys, ground-level sensors, and citizen science, to provide comprehensive, timely, and accurate monitoring. This review discusses the latest developments in the use of remote sensing and other technologies to monitor water hyacinth infestation, and proposes a novel, multi-modal approach that combines the strengths of the different methods.

**Keywords: remote sensing, synthetic aperture radar, ground sensor network, unmanned aerial vehicle, citizen science, machine learning, aquatic weeds, wetlands**

## INTRODUCTION

Originating from the Amazon Basin, water hyacinth (*Pontederia crassipes*) has spread to more than 80 countries over the past century (Jafari, 2010). This monocotyledonous macrophyte reproduces asexually using stolons and sexually by seeds (Havel et al., 2015), with a rapid reproductive capacity enabling it to double its biomass in 6–14 days under conducive growth conditions (Keller and Lodge, 2009). Researchers have estimated that over 8 months, 10 water hyacinth plants can reproduce into 655,360 plants, covering approximately half a hectare

(Gunnarsson and Petersen, 2007). It is thus not surprising that water hyacinth has been listed among the world's worst weeds (Riches, 2001). A comparative assessment of invasive weed species in China (Bai et al., 2013) introduced two indices using a scale of 1–4: "impact index," representing social, economic, and ecological impacts; and "spread index," representing rate of spread. Water hyacinth was assessed as having impact index 4 and spread index 3, highlighting its enormous adverse environmental impact. The weed reduces species diversity by reducing penetration of sunlight (Huang et al., 2008), affecting turbidity and dissolved oxygen (Chukwuka and Uka, 2007), depleting nutrients (Brendonck et al., 2003), and disturbing the food-web (Coetzee et al., 2014; Mironga et al., 2014). The thick floating weed mats harbor pathogenic micro-organisms, pests, and insect larvae, promoting diseases like schistosomiasis, dengue, chikungunya, and malaria (Muyodi, 2000). The mats challenge boat traffic by obstructing waterways and damaging propellers, and hamper fishing activity because casting of nets becomes impossible (European Environment Agency, 2000). Trends in urbanization and increased eutrophication of inland and coastal waterbodies imply that these problems will only grow worse in future (Williams et al., 2005).

Effectively tackling this menace requires accurate and timely monitoring of potential water hyacinth habitats within aquatic ecosystems (Shekede et al., 2008). Monitoring is necessary for estimating the size of an infestation, providing data for use in developing strategies for management and control (Dube et al., 2017). Traditionally, water hyacinth infestation monitoring has relied on field surveys with limited spatial coverage, using methods that are time and labor intensive (Ritchie et al., 2003). This limited the amount of data that can be collected, leading to poor understanding of factors affecting the emergence and spread of water hyacinth in different geographies. During the last decade, increasing availability of open sources of satellite data has created new possibilities for low-cost, large scale monitoring of water bodies (Turner et al., 2013). Satellites can provide spatial snapshots, with a short time interval, of areas known for water hyacinth infestation, particularly valuable for inaccessible and vulnerable ecologies or areas of significant commercial interests. However, challenges remain in developing effective automated methods for accurate detection of the presence of water hyacinth in satellite images and discriminating it from other aquatic vegetation that may be present. Potential solutions include using powerful machine learning algorithms that can handle large datasets, and the complementary use of data collected using other methods such as aerial surveys, in-water sensor devices, and technology-assisted surveillance by local people (citizen science).

We describe some of the ways in which water hyacinth is currently managed and explain how these can be made more effective through improved monitoring. Historically, water hyacinth has been treated as a pest requiring eradication or strict control, but there are also novel initiatives to use it as a resource for economic exploitation; improvements in monitoring have benefits for both approaches. We then review a range of technological methods that can be applied and end by proposing a novel, multi-modal approach.

## BENEFITS OF IMPROVED MONITORING FOR INFESTATION CONTROL

Management practices for water hyacinth infestation have primarily focused on eradication through physical, biological or chemical means, with modest success (Wilson et al., 2007). Mechanical removal of water hyacinth mats is the most common approach, particularly in navigation channels (Toft et al., 2003). Over the last few decades, the insect *Neochetina eichhorniae* and a suite of other species have been widely used as biocontrol agents in many parts of the world (Center et al., 2002; Hill and Coetzee, 2017). When combined with other plant stress factors, biocontrol has been found to be effective (Reddy et al., 2019). Use of herbicides in coordination with biocontrol has showed considerable success in maintaining the weed within acceptable levels (Tipping et al., 2017). Improvements in monitoring capability will make it possible to compare the efficacy of various control measures at a larger scale and within different geographic and climatic contexts, providing data that can be used to inform the choice of the most appropriate control method when an infestation is detected. Improved monitoring will also make it possible to detect new patches of infestation at an earlier stage, when they can be more easily and cheaply suppressed.

## BENEFITS OF IMPROVED MONITORING FOR EXPLOITATION OF HARVESTED WATER HYACINTH BIOMASS

Efficient utilization of harvested water hyacinth biomass for the production of fuels (biogas, bioethanol, or biohydrogen) and other value-added products will significantly mitigate the nuisance caused by the weed. Researchers have demonstrated bioethanol production potential from the hemicellulose and cellulose rich biomass (Okewale et al., 2016). Several value-added products, including cellulose, xanthogenate, levulinic acid, shikimic acid, biopolymer, biobutanol, composites, biofertilizers, fish feed, superabsorbent polymer, and xylitol have been demonstrated. With only minimal treatment, the biomass can be used as substrate for mushroom cultivation (Kumar et al., 2014; Prabhu, 2016) or for making handicrafts and other products.

Despite this known potential, none of these ideas has yet seen widespread adoption. To develop a financially viable proposal for a large scale processing unit, it is necessary to have data about the expected biomass quantity and time (to optimize scale of processing and assess viability), seasonal variation of the biomass (to schedule operations and plan storage requirements), and site-specific details such as remoteness of the location and proximity to transport routes and markets. Improved monitoring through remote sensing will be able to precisely measure the acreage of water hyacinth mats as well as their seasonal and temporal quantity variations. This will help with quantifying and forecasting biomass availability for commercial planning. There is potential in realizing this opportunity for improving livelihoods in impoverished communities.

# TECHNOLOGY-BASED METHODS OF MONITORING WATER HYACINTH

## Remote Sensing

Satellite remote sensing data has potential for effective and low-cost short interval monitoring of the temporal and spatial distribution of water hyacinth infestation at a large scale. The availability, frequency and coverage of satellite remote sensing data have increased considerably during the last years, in particular due to the European space agency (ESA)'s Copernicus program with Sentinel-1 and Sentinel-2. Currently, this potential is largely unexploited, due in part to the limited training of aquatic scientists and hydrologists in using remote sensing (Nagendra et al., 2013). **Table 1** presents a list of currently available open-access satellite-based sensor systems that can be used for monitoring water hyacinth. Remote sensing datasets may come from optical systems or from synthetic aperture radar (SAR). Optical images are typically well-suited for monitoring water hyacinth, because of their high spatiotemporal resolution, wide spatial coverage and broad spectrum. However, they are severely affected by cloud cover and meteorological conditions, and they are dependent on solar illumination. The data can be supplemented with data from SAR sensors which, in general, are unaffected by day-night, clouds and weather conditions. These two types of instruments may supplement each other in operational systems.

The primary focus of efforts using optical datasets has been to discriminate between hyacinth mats and algal blooms or other aquatic macrophytes. With improved spectral and spatial resolution sensors, the 10 m/pixel ground sampling distance (GSD) of Sentinel-2 MSI (multispectral instrument) has significantly enhanced research capability to detect and estimate water hyacinth infestation and coverage. Submerged macrophytes are clearly distinguished by their lower absolute reflectance in the near infrared (NIR), while other narrow hyperspectral channels are used to discriminate species on the basis of leaf optical properties and other biophysical or biochemical properties (Vidhya et al., 2014, Cheruiyot et al., 2014). Additionally, using remote sensing, critical water quality parameters, such as chlorophyll-a, turbidity and phosphorus concentration can be estimated (primarily through physics-based approaches) with high accuracy (Weghorst, 2008; Yao et al., 2010; Chawira et al., 2013; Kibena et al., 2013; Majozi et al., 2014).

Unlike optical datasets, SAR images have the benefit of being unaffected by cloud cover. Silva et al. (2010) showed the utility of SAR in monitoring of aquatic macrophytes, even during challenging weather conditions. The difference in dielectric constant and roughness between surface water and vegetation allows SAR to discriminate between dry and flooded vegetation (Evans et al., 2010). The lack of penetration of microwaves into water minimizes the error in signal capturing due to presence of submerged vegetation. The intensity of the radar backscatter being directly influenced by surface roughness, volumetric scattering, wavelength information and polarization makes it possible to develop vegetation-specific signatures (Robertson et al., 2015).

## Machine Learning Algorithms for Classifying Water Hyacinth in Remote Sensing Data

Machine learning algorithms have potential to significantly improve classification accuracy when identifying water hyacinth within satellite acquired imagery. For examples, the inaccuracy of pixel-based (Zhang and Foody, 1998) can be circumvented using algorithms that can extract expert knowledge derived from secondary data, and statistical tools such as Maximum Likelihood Classifier (Xie et al., 2008).

Atmospheric correction is another area where machine learning can contribute. Traditionally, algorithms for detecting chlorophyll a in MERIS spectrometer data relied on the water-leaving reflectance (Gitelson et al., 2009). However, common atmospheric correction software failed to resolve the shape of

**TABLE 1 |** Salient features of open access satellite-based sensor systems that can potentially be used for monitoring water hyacinth infestation.

| Satellite | Sensor type | Spatial resolution | Temporal resolution | No. of bands | Swath Width (km) |
|---|---|---|---|---|---|
| Sentinel-1 | SAR | 5–10 m<br>mode-dependent | 6/12 days | 2 | 250<br>mode-dependent |
| Sentinel-2 | Optical | 10–60 m | 5 days | 10 | 290 |
| MERIS | Optical | 0.3–1.2 km | 2 days | 15 | 1,150 |
| Oceansat-2 | Optical | 300 m | 2–3 days | 15 | 1,420 |
| LANDSAT 1–7 | Optical | 30 m | 16 days | 4 | 185 |
| LANDSAT 8 | Optical | 30 m | 16 days | 5 | 185 |
| ASTER | Optical | 15–90 m | 16 days | 14 | 60 |
| ALOS AVNIR 2 | Optical | 10 m | 14 days | 4 | 70 (at nadir) |
| NISAR | SAR | 3–10 m<br>mode-dependent | 12 days | Polarimetric<br>(single, dual, compact, quad) | >240 |

*Some of this information was taken from the following sources: (Shanthi et al., 2013; Oyama et al., 2015; Villa et al., 2015; Guerschman et al., 2016; Dube et al., 2017; Malthus, 2017; Veloso et al., 2017; Binding et al., 2018).*

the water-leaving reflectance accurately, particularly in the red-NIR MERIS bands for eutrophic waters (Guanter et al., 2010). An Artificial Neural Network approach for atmospheric corrections for Case 2 Regional Coast Color (C2RCC) was developed for MERIS (Doerffer and Schiller, 2008). C2RCC included a 5-component bio-optical model, as well as a coastal aerosol model aimed at expanding MERIS and Sentinel capabilities to coastal and inland waters (Brockmann et al., 2016). The radiative transfer code derived from the simulation of a satellite signal is based on successive orders of scattering approximations and it intends to simulate reflection observed for a typical water surface using a coupled atmosphere-surface system (Martins et al., 2017). POLYMER is used for spectral optimization using polynomials to model separate spectral influence from atmosphere and sunlight (Steinmetz et al., 2011). POLYMER decomposes the total signal after Rayleigh correction into a water reflectance spectrum, a spectrally smooth function for the atmosphere, and everything else which is "non-water." The iCOR atmospheric correction is a completely image-based processor which uses sun and sensor geometry, aerosol optical depth, ozone, water vapor, and elevation to derive atmospheric parameters from pre-computed MODTRAN (MODerate resolution atmospheric TRANsmission)-5 Look-Up-Tables (De Keukelaere et al., 2018). These approaches greatly enhance the capacity to discriminate between cyanobacterial blooms, surface scum, and floating macrophyte such as water hyacinth.

Other machine learning algorithms that have been applied to remote sensing data include decision tree approaches, used in Song et al. (2012) to improve the accuracy of land cover classification in low-resolution images, random forest (Adelabu and Dube, 2014), and support vector machines (Mountrakis and Ogole, 2011).

## Aerial Surveys

Historically the identification of individual species was based on laborious and subjective interpretation of analog or digital aerial high-resolution photography (Husson et al., 2014). The availability of low-cost unmanned aerial vehicles (UAVs) equipped with high-quality digital cameras has resulted in a resurgence of such systems for environmental monitoring (Anker et al., 2014). Airborne optical monitoring can greatly enhance remote monitoring capabilities. The ability of aerial photography to acquire images under the clouds and with much higher resolution makes image interpretation easier compared to satellite data. Common systems in use are CASI (Compact Airborne Spectrographic Imager), MIVIS (Multispectral Infrared and Visible Imaging Spectrometer), HyMAP (airborne hyperspectral imaging sensor), AVIRIS (Airborne Visible/Infrared Imaging Spectrometer), and sensors deployed on UAVs. The high cost of hyperspectral UAV/camera systems is a barrier to their widespread use; however, cheaper multispectral systems have recently become available and are a promising alternative.

Challenges such as changing sun angles and variable wind speeds affect aerial image acquisition, therefore flight scheduling requires skill and site-specific knowledge (Hestir et al., 2008). Airborne sensors provide high spectral resolution and facilitate differentiation of macrophytes strategies (Giardino et al., 2015). Becker et al. (2007) explored various bands of hyperspectral scanner data to derive the optimal system parameters (e.g., resolution, number of bands) to enable classification of common wetland vegetation. Their study reported an optimal spatial resolution of 2 m with strategically located bands in the red-NIR region. Repeated airborne LIDAR acquisitions can be used to produce a high-resolution canopy digital elevation model and canopy height model of the water hyacinth. This can help to track water hyacinth growth and detect infestation at an early stage (Hopkinson et al., 2005).

## Ground-Level Sensors

Sensor devices of various kinds can be placed within water and used for detecting indicators of the presence of aquatic plants or the conditions conducive to their growth. Sensors may be used for spot measurements or placed on site long term to detect changing conditions. Maintenance of long-term installations presents various challenges, such as the risk of theft or damage to devices, or reduced effectiveness due to biological colonization. However, if these can be overcome, useful data can be gathered. For example, a spectro-radiometer can be used to detect aquatic plants using their reflectance spectra and discriminate between floating and submerged plants (Penuelas et al., 1993). This ground-level data can be usefully combined with other data to yield better information: for example, Wolf et al. (2013) investigated freshwater lakes in Germany using a submersible spectro-radiometer and suggested that the reflectance spectra of vegetation or sediments on and below the lake bottom were useful to control the atmospheric and water column deviations of remote sensing data from satellites.

Sensors may be combined with actuators and communication capabilities (Internet of Things) for real-time data gathering and early warning systems (Abdullah and Hagem, 2020) placed a Wi-Fi-enabled photon board and an ultrasonic sensor in an irrigational channel to provide an early warning system for detecting *Ceratophyllum* and *Eichhornia*. Water quality monitoring was performed using sensors for critical parameters like turbidity, temperature and dissolved oxygen while assessing the impact of herbicides used for control of water hyacinth in the Sacramento-San Joaquin delta (Tobias et al., 2019). Monitoring of phosphate concentration too is important as it is closely linked with water hyacinth infestation (Kobayashi et al., 2008; Datta et al., 2016). An IoT based sensor that monitors water quality in real-time was demonstrated by Manimegalai (2020). Vaseashta et al. (2020) developed a prototype from commercial-off-the-shelf sensors to monitor contaminants in underground and surface water. A detailed review of microfluidic-based sensors for monitoring water quality can be found in Jaywant and Arif (2019).

## Citizen Science

The traditional method of monitoring water hyacinth using manual field surveys can be greatly enhanced by the use of smartphones and mobile applications to enable quick and effective data collection. Widespread and growing cellular network penetration in countries across the world has enabled citizen science initiatives such as the Plantix mobile application (Wang et al., 2020), which is used by farmers in India for

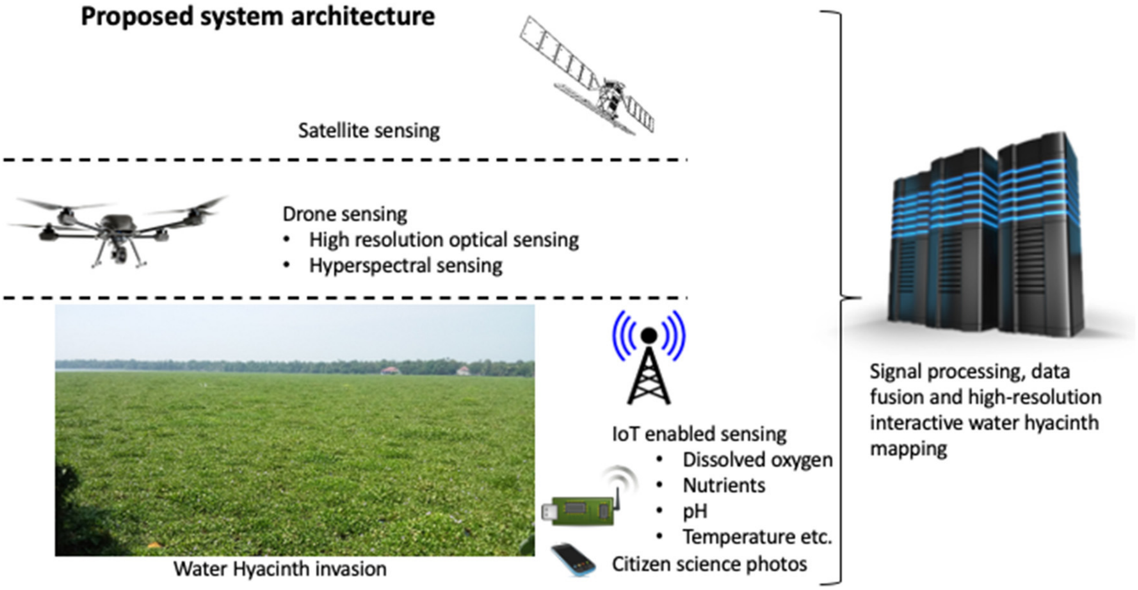

**FIGURE 1 |** Proposed system architecture for a multi-modal system for monitoring water hyacinth infestation.

quick reporting and diagnosis of agricultural pests and diseases found in their fields. Gervazoni et al. (2020) used citizen science to monitor spread of invasive *Iris pseudacorus* in Argentinian wetlands. There is potential to develop similar applications that can be provided to fishermen, farmers, irrigation workers and other users of waterbodies to report sightings of water hyacinth. Photographs augmented with timing and geolocation data can build a valuable repository of data that can be used for monitoring infestations and can serve as ground-truth data for the development of algorithms for automated detection of water hyacinth from remote sensing data.

## DISCUSSION AND PROPOSAL FOR A MULTI-MODAL APPROACH TO MONITORING WATER HYACINTH

We have seen that a wide variety of technological approaches for monitoring water hyacinth infestation are available, though the full potential of most of these is currently underexploited. Remote sensing has considerable advantages over other methods, as it is low in cost and can provide extensive spatial and temporal coverage, enabling ongoing surveillance and reaching inaccessible locations. Optical images can be used for their high resolution and broad coverage and can be supplemented with SAR data to provide datasets that are resilient to cloud coverage and poor weather conditions. Aerial surveys and citizen science can provide detailed, very high-resolution imagery that can be used to complement and ground-truth satellite data. Sensors placed within waterbodies can provide supplementary data and provide early warnings of infestations.

A comprehensive solution to the problem of monitoring water hyacinth must involve a combination of methods. Our team is working to design and test prototypes of a multi-modal system (**Figure 1**) which can be used to continuously monitor the presence of water hyacinth, using a data driven approach that merges environmental datasets obtained from: (i) SAR and optical imaging by European satellites, essential for understanding spatio-temporal variability of vegetation cover and distribution; (ii) monitoring of target sites using drone-mounted multispectral cameras, essential for collecting very high resolution data to ground truth satellite observations; (iii) continuous real time data from an Internet-of-Things enabled ground sensor network placed permanently in the water, collecting data indicative of water hyacinth presence, such as dissolved oxygen, nutrients, pH levels and temperature, and (iv) citizen science, using a mobile application to gather photographs, timestamps, geolocation data and other metadata about sightings of water hyacinth infestations. New algorithms will be developed, leveraging advances in signal processing, e.g., texture analysis and machine learning techniques, such as deep learning, along with multimodal data fusion strategies. We envisage a system which uses satellite and remote sensing data to detect if weed infestation is present, producing alerts that trigger a drone campaign to acquire more detailed information. The system will include a network of sensors that can sense water quality conditions conducive to water hyacinth growth and detect infestation at an early stage. If successful, this system will provide low-cost, comprehensive, timely, and accurate data for effective management of what many consider the world's worst aquatic weed.

## AUTHOR CONTRIBUTIONS

AD conceived the original idea for this paper and carried out most of the literature review. AD, SM, GP, DB, AM, VA, and SR contributed to the writing and preparation of figures. JS, GA, SK, and AK provided feedback on drafts. All authors approved the final submission and agree to be accountable for the content of the paper.

## FUNDING

This work was supported by the UKRI Global Challenges Research Fund through grant (FF\1920\1\37) from the Royal Academy of Engineering.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 05 February 2021
doi: 10.3389/fevo.2021.575599

# Using Genomics to Link Populations of an Invasive Species to Its Potential Sources

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The introduction and subsequent range expansion of the Northern snakehead (*Channa argus*: Channidae, Anabantiformes) is one of a growing number of problematic biological invasions in the United States. This harmful aquatic invasive species is a predatory freshwater fish native to northeastern Asia that, following deliberate introduction, has established itself in multiple water basins in the eastern United States, as well as expanding its range into the Midwest. Previous work assessed the population structure and estimated the long-term effective population sizes of the populations present in the United States, but the source of the initial introduction(s) to the U.S. remains unidentified. Building on earlier work, we used whole genome scans (2b-RAD genomic sequencing) to analyze single nucleotide polymorphisms (SNPs) from *C. argus* to screen the genomes of these invasive fish from United States waters and from three sites in their native range in China. We recovered 2,822 SNP loci from genomic DNA extracted from 164 fish sampled from the eastern United States and Arkansas (Mississippi River basin), plus 30 fish sampled from three regions of the Yangtze River basin in China ($n$ = 10 individuals per basin). Our results provide evidence supporting the Yangtze River basin in China, specifically the Bohu and/or Liangzi lakes, is a likely source of the *C. argus* introductions in multiple regions of the U.S., including the Lower Hudson River basin, Upper Hudson River basin and Philadelphia (Lower Delaware River basin). This information, in conjunction with additional sampling from the native range, will help to determine the source(s) of introduction for the other U.S. populations. Additionally, this work will provide valuable information for management to help prevent and manage future introductions into United States waterways, as well as aid in the development of more targeted strategies to regulate established populations and inhibit further spread.

**Keywords: population genomics, invasive species, RADseq, molecular ecology, Northern snakehead (*Channa argus*)**

***Edited by:***
*Ana Novoa,*
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***Specialty section:***
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

***Received:*** *23 June 2020*
***Accepted:*** *18 January 2021*
***Published:*** *05 February 2021*

***Citation:***
*Resh CA, Galaska MP,*
*Benesh KC, Gardner JPA, Wei K-J,*
*Yan R-J and Mahon AR (2021) Using*
*Genomics to Link Populations of an*
*Invasive Species to Its Potential*
*Sources. Front. Ecol. Evol. 9:575599.*
*doi: 10.3389/fevo.2021.575599*

## INTRODUCTION

Invasive species are usually environmentally harmful and economically expensive, yet deliberate and non-intentional introductions continue to occur at an increasing rate (Leung et al., 2002; Lodge et al., 2006; Pimentel, 2005). These invasions contribute to environmental change, loss of biodiversity, and threaten human health and the economy in many regions of the world

(Nuñez and Pauchard, 2009). In the United States alone, invasive species control costs are estimated to be over $100 billion annually (Pimentel, 2005). The cost of invasive species control increases as the abundance of a non-native species increases over time and once an invasive species has become established, eradication becomes extremely unlikely, and long-term management is required. Therefore, knowledge of population histories of invasive species is extremely important, particularly when early detection and rapid responses to invasions can still be effective (Early et al., 2016). Genomic biosurveillance, including genomics and other cutting edge molecular technologies such as whole genome scans, have advanced to levels where they are capable of rapidly informing management agencies and stakeholders about the invasive organisms in both their native and non-native habitats (e.g., Hamelin and Roe, 2019). In particular, the development of datasets from high throughput sequencing technologies that include genome-wide single nucleotide polymorphisms (SNPs) can provide fine scale, cost efficient, information about the invasion process (Cristescu, 2015; Hamelin and Roe, 2019).

The Northern Snakehead (*Channa argus*) is a harmful aquatic invasive fish with multiple established populations in the eastern United States and Arkansas (Resh et al., 2018; Fuller et al., 2020). The native range of the species is China, eastern Russia, and portions of North Korea, and it is primarily found in the Yangtze River drainage (Yan et al., 2018). *Channa argus* is a voracious predator, matures rapidly, and can withstand a wide range of environmental conditions, including surviving up to 4 days out of water (Orrell et al., 2005; Fuller et al., 2020). These characteristics, as well the fish's high fecundity and parental care exhibited by both parents for several weeks after fry hatch, have contributed to its ability to spread and establish populations throughout the United States since first being observed approximately 20 years ago (Fuller et al., 2020). Once a population of an invading species becomes established in a region, the logistics and costs of eradication become exponentially higher than at pre-establishment. Therefore, as well as it being imperative to understand the population dynamics of *C. argus* to prevent further spread within the United States, it is equally important to identify the source(s) of introduction prevent further introductions into the United States.

In our previous work, we identified five genetically distinct populations of *C. argus* present in the United States that were the result of at least two separate introductions (Wegleitner et al., 2016; Resh et al., 2018). However, the source or sources of the *C. argus* invasion(s) remain unknown. The addition of samples from three sites in the Yangtze River basin (Yan et al., 2018), part of the native range of *C. argus,* to our previous datasets provide an opportunity to build on this work and potentially discover the location of source populations of *C. argus* in the U.S. Identifying the sources of the invasions of non-native species helps to identify invasion routes and vectors, which will allow for more targeted management plans to be implemented that aim to prevent trade and reduce the risk of further introduction of this harmful aquatic invasive species (Harris et al., 2016). Additionally, knowledge of the invasive species' native environment provides information about factors that regulate its distribution and population, which in turn, will enable better predictions about potential expansion of the invasive species in its introduced range (Geller et al., 2010). Therefore, the goal of this study is to expand on our previous 2b-RAD sequencing data from fish collected from a portion of the native range of *C. argus*, to begin to determine the source(s) of the *C. argus* introduction(s) in the United States. The populations in the United States are admixed, so it is not possible to determine how many introductions have occurred, but previous studies provide evidence for at least two separate introductions (Wegleitner et al., 2016; Resh et al., 2018). As a result, we hypothesize that individuals from at least one of the introduction events originated from the Yangtze River basin in China. An understanding of source population information is important to manage existing populations and reduce the risk of future introductions of *C. argus* into the United States. This study presents a methodological advance in analyzing populations of invasive species using cutting edge genomic technology and provides a novel suite of data that can be directly used by management stakeholders. The resulting data from this study will aid in that goal because they will contribute to more effective predictions of potential expansion and the development of biological control options.

## MATERIALS AND METHODS

### Sample Collection and Preparation

Sequence data from Resh et al. (2018) were used for this study. Genomic DNA was extracted from the fin clips of *C. argus* from the eastern United States and Arkansas (Mississippi River basin) using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, United States), following manufacturer's protocols (**Figure 1**; full collection information in **Supplementary Table 1**). Additionally, fin clips were collected from 30 *C. argus* individuals from three lakes in the native range of *C. argus* that are part of the Yangtze River basin in China: Bohu Lake ($n = 10$), Liangzi Lake ($n = 10$), and Poyang Lake ($n = 10$) (**Figure 1**). Genomic DNA was extracted from the fin clips using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, United States), following manufacturer's protocols.

### 2b-RAD Data Collection

Genomic DNA was prepared based on the 2b-RAD protocol from Wang et al. (2012), with the restriction enzyme *Alf*I. A one quarter (1/4) reduction scheme using ligation adaptors (NC/NN) was chosen based on the approximate genome size of *C. argus* (616–861 Mb, Gregory, 2021), as well as to target approximately 2,500 SNP loci. Samples were dual barcoded with unique combinations and then sequenced to generate 50 bp single end reads at the Genomics and Cell Characterization Core (University of Oregon, OR, United States) on an Illumina Hi-Seq 4000 using v4 chemistry.

### Data Analyses

The raw Illumina reads were demultiplexed by sample, quality filtered, and the *AlfI* recognition sites were extracted using Dr. Eli

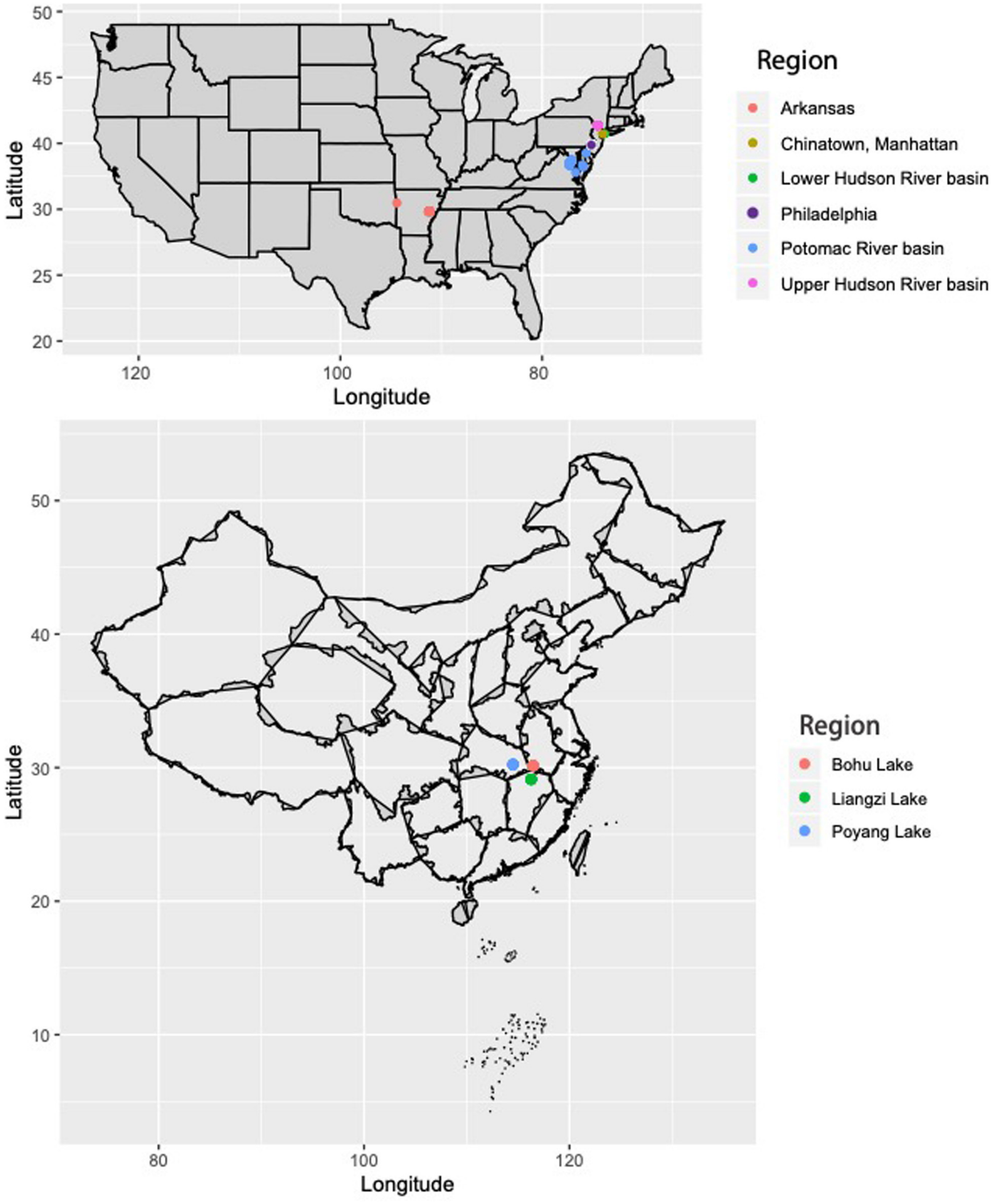

**FIGURE 1 |** Collection locations for *Channa argus* individuals in the United States and China. For detailed map of U.S. collections, see Resh et al. (2018) and **Supplementary Table 1**.

Meyer's scripts (Oregon State University)[1]. The software package Stacks v.2.41 created a custom *de novo* reference file using the pipeline *denovo_map.pl* within Stacks v2.41 to align the raw Illumina reads and assign to unique stacks (Catchen et al., 2011, 2013). Assignment of homozygotic loci was allowed to have a maximum variance of 1% and heterozygotic loci assignment required a minimum of 25% variance. Loci had to occur in 75% or more individuals within a sampling locality and be present in

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[1] http://github.com/Eli-Meyer

at least 2 localities to be processed. If these requirements were not met, then the loci were discarded prior to analyses.

Principal components analyses (PCAs) were performed by locality on the dataset using the Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences (ade4) v1.7-13 package (Dray and Dufour, 2007) in the R v3.6.1 statistical program (R Core Team, 2015) and the top principal components were compared. Discriminant Analysis of Principal Components (DAPC) in the Adegenet v2.1.1 package (Jombart and Ahmed, 2011) in R was used to analyze the SNP data to determine group (population) membership across localities (i.e., collection locations of each sample). Adegenet v2.1.1 conducts a series of PCAs on the dataset and then performs a Discriminant Analysis on all the retained principal components. The optimal number of clusters (*K*), which estimates the number of populations, is identified through Bayesian information criterion (BIC) likelihood values from retained principal components. Visualization of these analyses was performed in the Adegenet v2.1.1 package (Jombart and Ahmed, 2011).

Population structure and potential admixture were assessed using the Landscape and Ecological Associations (LEA) v1.8.1 package in R (Frichot and François, 2015). The number of ancestral populations, *K*, was estimated with the cross-entropy criterion and least squares estimates (Frichot and François, 2015).

Summary statistics were generated for the samples from the nine localities and genetic differentiation was analyzed using the HIERFSTAT v0.04-30 package in R (Goudet, 2005). Summary statistics included the private alleles at each locality, expected heterozygosity, observed heterozygosity, and the inbreeding coefficient ($F_{is}$), with the variance and standard error values for each statistic included. Additionally, Bartlett tests were conducted using the HIERFSTAT v0.04-30 package for each locality to determine if the expected and observed heterozygosities differed (Goudet, 2005). Pairwise genetic distances ($F_{st}$) were estimated and bootstrapping was performed over the pairwise $F_{st}$ values to generate 97% confidence intervals (Nei, 1987; Goudet, 2005).

Lastly, we calculated the migration rates as a proxy for how closely related introduced and native localities may have been, using the diveRsity v1.9.90 package in R (Keenan et al., 2013). DiveRsity calculates genetic diversity and differentiation statistics (Nm), as well as bootstrapped 95% confidence intervals, for pairwise locality comparisons and allows for calculation of directional migration levels among localities.

## RESULTS

In total, 52,409 single nucleotide polymorphic loci were recovered from 194 *C. argus* individuals. After quality filtering of the data and subsequent SNP calling, 2,822 independent SNP loci were retained in the final dataset.

The results of the principal components analysis (PCA) by locality indicate the genetic similarity between the native Bohu Lake and Liangzi Lake populations, and the introduced Philadelphia (Lower Delaware River basin) and Lower Hudson River basin populations (**Figure 2**). In contrast, the PCA (**Figures 2A,C**) identified the Poyang Lake population as being separate from the other two native Chinese populations, as well as the introduced U.S. populations. These results indicate that there is genetic dissimilarity between the Poyang Lake individuals and the fish of the other two native localities, despite the three native range sites being part of the same river basin. Additionally, Poyang Lake individuals were identified as being genetically differentiated from the introduced U.S. populations.

Results of the DAPC analyses indicated six geographically and genomically distinct clusters or populations of *C. argus* (*K* = 6, **Figure 3** and **Supplementary Figure 11**). Cluster 1 contained 10 individuals and consisted of 100% of the fish collected from the Poyang Lake. Cluster 2 contained 58 individuals, 98% (58 of 59) of the fish that were collected from the Upper Hudson River basin. Cluster 3 contained 18 individuals: 100% of the fish collected from Arkansas. Cluster 4 contained 22 individuals: 1.9% (1 of 54) of the fish collected from the Potomac River basin and 100% of the fish collected from Philadelphia. Cluster 5 contained 53 individuals: 98% of the fish collected from the Potomac River basin (53 of 54). Cluster 6 contained 34 individuals: 100% of the fish collected from Bohu Lake and Liangzi Lake, 1.7% (1 of 59) of the fish collected from the Upper Hudson River basin, 100% of the fish collected from the Lower Hudson River basin, and 100% of the fish from the Chinatown, Manhattan fish market.

The results of the admixture analyses in LEA also supported the existence of six populations (*K* = 6, **Figure 4** and **Supplementary Figure 2**). Each of the populations was partially admixed, although the relative amount of admixture varied among the populations. The fish from Bohu Lake and Liangzi Lake were statistically from the same population. These two lakes share ancestral genotypes with the fish from Poyang Lake, the Lower Hudson River basin, Chinatown Manhattan, Philadelphia, and Arkansas populations, as well as one individual in both the Upper Hudson River and Potomac River basins. In contrast, the main ancestral genotype of the rest of the fish from the Upper Hudson River and Potomac River is rare in the Bohu Lake and Liangzi Lake populations.

Summary statistics of genetic diversity and genetic distances between the putative *C. argus* populations (**Tables 1–3**) revealed that each population contained private alleles. The Poyang Lake population contained the most private alleles and the Upper Hudson River population the least (337 and 60, respectively).

The observed heterozygosity was lower than expected heterozygosity for the Potomac River basin ($H_o$: 0.112 and $H_e$: 0.120; $p = 0.044$), Arkansas ($H_o$: 0.063 and $H_e$: 0.065; $p = 0.003$), and Poyang Lake ($H_o$: 0.132 and $H_e$: 0.138; $p = 8.28\text{e}^{-8}$) populations. Observed heterozygosity was higher than expected heterozygosity for the Lower Hudson River basin population ($H_o$: 0.128 and $H_e$: 0.123; $p = 2.2\text{e}^{-16}$). The observed heterozygosity did not deviate from expected values for Bohu Lake ($H_o$: 0.106 and $H_e$: 0.123; $p = 0.386$), Upper Hudson River basin ($H_o$: 0.060 and $H_e$: 0.060; $p = 0.379$), and Philadelphia ($H_o$: 0.074 and $H_e$: 0.077; $p = 0.255$). Observed heterozygosity was significantly different than expected heterozygosity for Liangzi Lake ($H_o$: 0.107 and $H_e$: 0.107; $p = 3.49\text{e}^{-10}$) and the fishes that came from the Chinatown, Manhattan fish market ($H_o$: 0.120 and

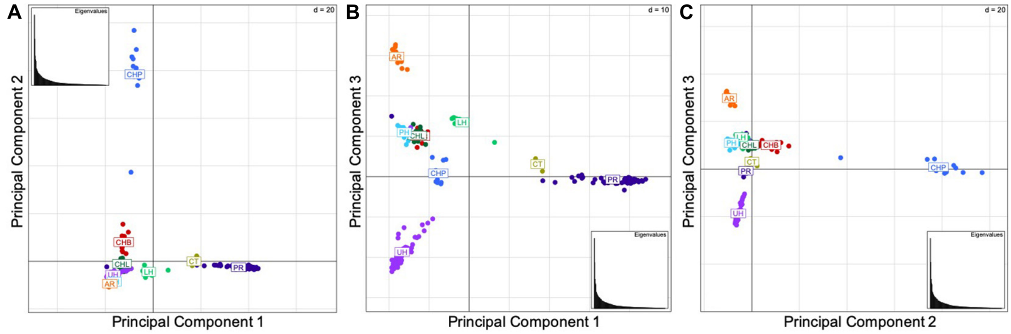

**FIGURE 2 | (A)** Components 1 and 2, **(B)** Components 1 and 3, **(C)** Components 2 and 3. Principal component analyses by locality. The abbreviations are as follows: CHB, Bohu Lake, China; CHL, Liangzi Lake, China; CHP, Poyang Lake, China; AR, Arkansas; CT, Chinatown, Manhattan; LH, Lower Hudson River basin; PH, Philadelphia; PR, Potomac River basin; and UH, Upper Hudson River basin. The three principal components explain 46.49% of the variation in the data set.

$H_e$: 0.122; $p = 2.2e^{-16}$). The inbreeding coefficient was positive for all putative populations except Liangzi Lake and the Upper and Lower Hudson River basins. Bohu Lake had the highest inbreeding coefficient at 0.1379. The two localities that had the smallest genetic distance (0.061) were Poyang Lake and Liangzi Lake within the native range of *C. argus*. In contrast, the largest pairwise genetic distance value occurred between Poyang Lake and the Upper Hudson River basin populations (0.224).

The relative directional migration rates between the localities are shown as a network (**Figures 5**, **6**). Each node represents a locality, and arrows indicate the direction of gene flow, with the relative strength of the flow indicated by the bootstrap support value, as well as the shading and thickness of each connecting line. For the first analysis (**Figure 5**) the three native lake localities in China were grouped together, and for second (**Figure 6**) the three native lake localities were analyzed separately. In both cases, there was evidence of gene flow between the native populations in China and the introduced Philadelphia and Lower Hudson River basin populations. The relative directional migration levels were relatively higher between the populations of Bohu Lake and Liangzi Lake vs. Philadelphia (Nm = 0.26). The Lower Hudson River basin vs. Liangzi Lake and Bohu Lake populations had Nm values of 0.31 and 0.27, respectively, showing evidence of gene flow between the localities. While these values do not represent migration between the sites or waterways, they are instead indicative of human-mediated transfer of fish and this information is still valuable because the data show how the fish were related to one another before the introductions occurred, thereby helping identify putative source populations.

## DISCUSSION

The main goal of this study was to use cutting edge technology in the form of whole genome scans to analyze genomic data from Northern snakehead individuals (*C. argus*) from the introduced populations in the United States, as well as a portion of their native range, to attempt to determine the source of the North American *C. argus* introductions. The genomic data generated in this study, with the inclusion of the new samples from the native range in China, support the presence of six genetically distinct populations of *C. argus* recovered from the United States and central China. While five of the U.S. populations are still extant, the Upper Hudson River basin population was successfully eradicated in 2008–2009 (Aquatic Nuisance Species [ANS] Task Force, 2014). The addition of genomic data from fishes collected from the new collection locations within the native range of *C. argus* may provide a number of benefits to management agencies, as well as to ecological and environmental research in the field.

Identification of source populations is crucial for effective management because information about source(s) provides insight into the invasion pathway(s) and mode(s) of introduction, which will aid in effective development of strategies to prohibit natural and human mediated transport in the introduced ranges (Collins et al., 2002; Casso et al., 2019). For instance, Austin et al. (2011) used a multi-locus genomic dataset from both the native and introduced ranges to determine the origin, mode, and tempo of the invasion of a scincid lizard (*Carlia*) that was introduced to Guam, the Northern Marianas, and Palau islands. Additionally, source information can aid in the effective development and implementation of biological control agents. For example, the predatory ladybird beetle, *Cryptolaemus montrouzieri*, native to Australia, is a widely used biological control agent that has been introduced to over 64 countries/territories to control over 16 pest species over the last century (Kairo, 2013). Li et al. (2019) showed that pronounced genetic differentiation has occurred between the sampled populations from both native and introduced ranges of *C. montrouzieri*, which may impact the efficiency and invasion potential of this important biological control agent. This source information aids in the discovery of cryptic species in biological control agent populations, which is important for minimizing unpredicted non-target effects so as to maximize biological control efficiency, as well as providing potential new biological control agents (Paterson et al., 2016; Smith et al., 2017).

The addition of genomic data from the native range of an invasive species is beneficial for ecological and evolutionary studies because it allows researchers to compare the invasive species' response to its native and introduced environments and determine invasion success (Hierro et al., 2005; Bock et al., 2015;

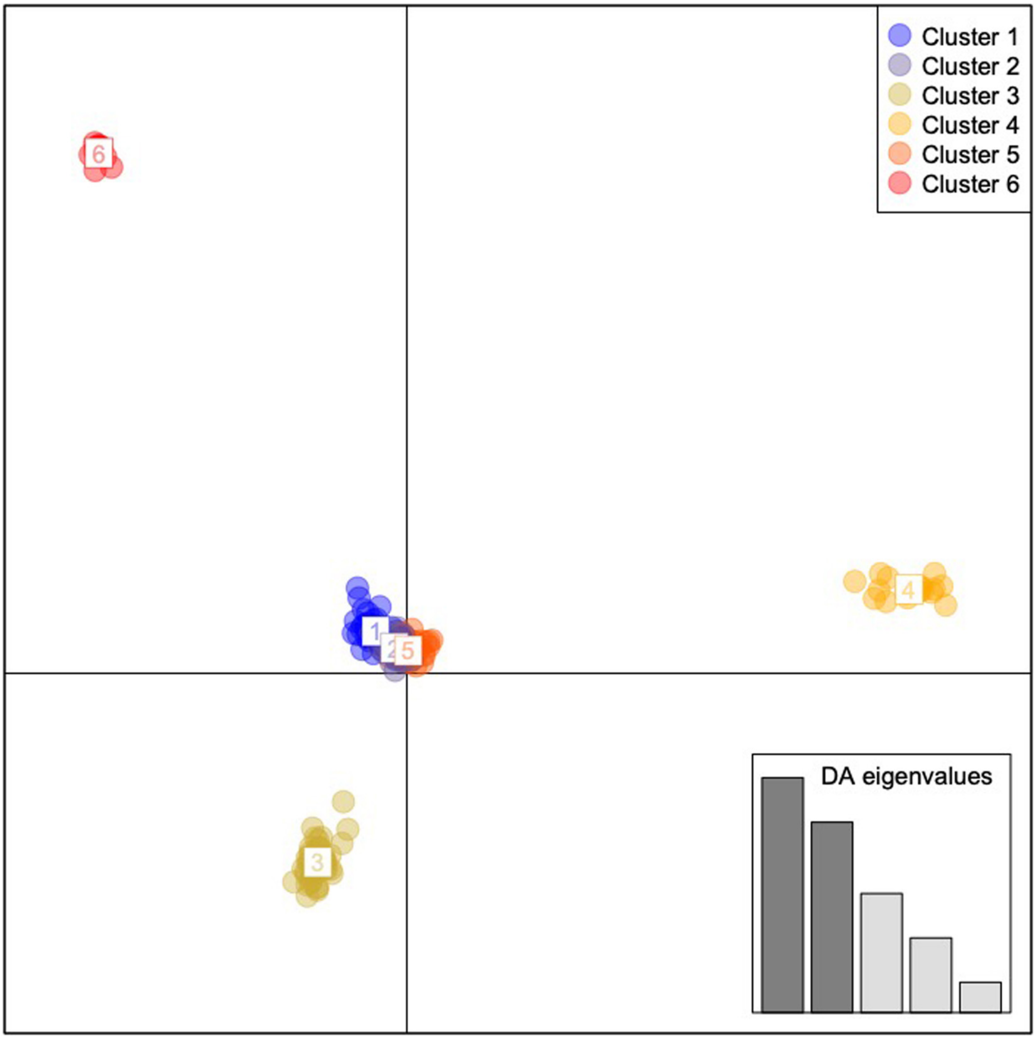

**FIGURE 3 |** Discriminant Analysis of Principal Components for *Channa argus* single nucleotide polymorphism data. Cluster 1: all of the fish collected from the Bohu and Liangzi Lakes in China, 1.7% (1 of 59) of the fish collected from the Upper Hudson River basin, all of the fish collected from the Lower Hudson River basin, and all of the fish from the Chinatown, Manhattan fish market. Cluster 2: 1.9% (1 of 54) of the fish collected from the Potomac River basin and all of the fish collected from Philadelphia. Cluster 3: 98% of the fish collected from the Potomac River basin (53 of 54). Cluster 4: all of the fish collected from Arkansas. Cluster 5: 98% (58 of 59) of the fish that were collected from the Upper Hudson River basin. Cluster 6: All individuals sampled from Poyang Lake, China.

Martin et al., 2016). For example, Tepolt and Palumbi (2015) provided evidence that local adaptation in the native range of the European green crab (*Carcinus maenas*) may have facilitated the spread of its invasion through multiple introductions in North America. Invasive species' adaptations can be better understood with the addition of source population information, which will greatly improve predictions of invasion risk and development of effective management strategies (Lodge et al., 2006; Tepolt, 2014). Future studies should also consider using the cost efficient and advanced genomic SNP data to investigate loci under selection that would allow us to better understand the genetic basis of adaptation and invasion success.

The likely sources of the introduced *C. argus* in Philadelphia, the Lower Hudson River basin, and Upper Hudson River basin are the Bohu and/or Liangzi lakes, part of the Yangtze River basin in central China. This was supported by our analyses that found significant genetic similarity among the fish of the native Bohu and Liangzi lakes populations and the introduced Philadelphia, Lower and Upper Hudson River basin populations. In contrast, the Potomac River basin and Arkansas populations share less genetic similarity with the Bohu and Liangzi lakes populations, and did not cluster together in any analyses. However, that does not eliminate the possibility of those Chinese lakes being the source of those introductions, as well, they are simply not supported by the current dataset. *Channa argus* is a freshwater fish, so after introduction, the individuals likely experienced reproductive isolation, which led to genetic divergence, and thus could account for the genetic structure recovered in those two introduced populations.

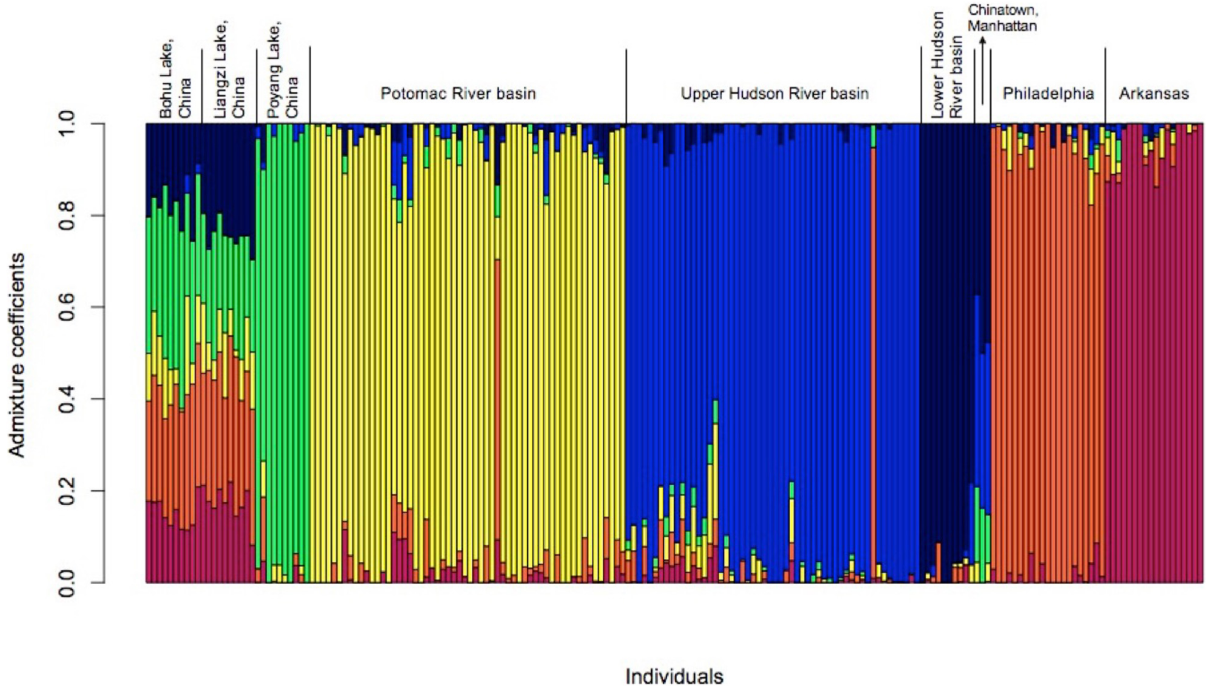

**FIGURE 4 |** Admixture for *C. argus* populations ($k = 6$) in the United States when compared to three native range populations from central China.

**TABLE 1 |** Summary statistics for single nucleotide polymorphism locus variation at each collection site.

| Putative population | Private alleles | $H_o$ | $H_t$ | $D_{st}$ | $H_{tp}$ | $D_{stp}$ | $F_{st}$ | $F_{stp}$ | $F_{is}$ | $D_{est}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Bohu Lake, China | 75 | 0.1060 | 0.1227 | −0.0002 | 0.1226 | −0.0003 | −0.0014 | −0.0029 | 0.1379 | −0.0004 |
| Liangzi Lake, China | 108 | 0.1069 | 0.1066 | 0.0001 | 0.1067 | 0.0002 | 0.0011 | 0.0022 | −0.0035 | 0.0003 |
| Poyang Lake, China | 337 | 0.1320 | 0.1380 | −0.0002 | 0.1378 | −0.0003 | −0.0013 | −0.0025 | 0.0447 | −0.0004 |
| Potomac River basin | 145 | 0.1123 | 0.1199 | 0.0010 | 0.1211 | 0.0021 | 0.0087 | 0.0172 | 0.0554 | 0.0024 |
| Upper Hudson River basin | 60 | 0.0601 | 0.0603 | 0.0017 | 0.0621 | 0.0035 | 0.0287 | 0.0559 | −0.0264 | 0.0037 |
| Lower Hudson River basin | 94 | 0.1283 | 0.1227 | −0.0003 | 0.1224 | −0.0005 | −0.0021 | −0.0042 | −0.0435 | −0.0006 |
| Chinatown, Manhattan | 67 | 0.1191 | 0.1216 | −0.0026 | 0.1190 | −0.0052 | −0.0212 | −0.0433 | 0.0407 | −0.0059 |
| Philadelphia | 61 | 0.0736 | 0.0765 | −0.0005 | 0.0759 | −0.0010 | −0.0068 | −0.0137 | 0.0435 | −0.0011 |
| Arkansas | 61 | 0.0631 | 0.0651 | −0.0007 | 0.0644 | −0.0014 | −0.0105 | −0.0212 | 0.0404 | −0.0015 |

**TABLE 2 |** Pairwise genetic distances (Fst) between *Channa argus* putative populations.

| | Bohu Lake, China | Liangzi Lake, China | Poyang Lake, China | Potomac River basin | Upper Hudson River basin | Lower Hudson River basin | Chinatown, Manhattan | Philadelphia |
|---|---|---|---|---|---|---|---|---|
| Liangzi Lake, China | 0.083 | | | | | | | |
| Poyang Lake, China | 0.117 | 0.061 | | | | | | |
| Potomac River basin | 0.146 | 0.201 | 0.230 | | | | | |
| Upper Hudson River basin | 0.129 | 0.186 | 0.224 | 0.082 | | | | |
| Lower Hudson River basin | 0.136 | 0.109 | 0.134 | 0.157 | 0.165 | | | |
| Chinatown, Manhattan | 0.186 | 0.138 | 0.125 | 0.197 | 0.223 | 0.099 | | |
| Philadelphia | 0.146 | 0.111 | 0.132 | 0.170 | 0.175 | 0.069 | 0.093 | |
| Arkansas | 0.074 | 0.106 | 0.152 | 0.146 | 0.131 | 0.145 | 0.199 | 0.147 |

In its native range in China, *C. argus* is an important aquaculture species due to its rapid growth rate, strong resistance to disease, and ease of culture in ponds (Yan et al., 2014, 2018). While beneficial in China as an important source of food, these characteristics have likely contributed to the invasion success of *C. argus* in the United States and elsewhere. *Channa argus*

**TABLE 3 |** Upper and lower confidence interval limits for pairwise genetic distances (Fst) between *Channa argus* putative populations.

| | Bohu Lake, China | Liangzi Lake, China | Poyang Lake, China | Potomac River basin | Upper Hudson River basin | Lower Hudson River basin | Chinatown, Manhattan | Philadelphia | Arkansas |
|---|---|---|---|---|---|---|---|---|---|
| Bohu Lake, China | – | 0.090 | 0.124 | 0.154 | 0.139 | 0.144 | 0.191 | 0.154 | 0.081 |
| Liangzi Lake, China | 0.076 | – | 0.067 | 0.206 | 0.194 | 0.119 | 0.145 | 0.120 | 0.113 |
| Poyang Lake, China | 0.108 | 0.055 | – | 0.236 | 0.232 | 0.143 | 0.132 | 0.141 | 0.160 |
| Potomac River basin | 0.139 | 0.190 | 0.218 | – | 0.088 | 0.161 | 0.200 | 0.176 | 0.152 |
| Upper Hudson River basin | 0.122 | 0.176 | 0.213 | 0.077 | – | 0.172 | 0.227 | 0.182 | 0.137 |
| Lower Hudson River basin | 0.130 | 0.099 | 0.125 | 0.147 | 0.156 | – | 0.105 | 0.074 | 0.152 |
| Chinatown, Manhattan | 0.173 | 0.127 | 0.115 | 0.183 | 0.211 | 0.088 | – | 0.097 | 0.206 |
| Philadelphia | 0.140 | 0.102 | 0.122 | 0.161 | 0.166 | 0.063 | 0.082 | – | 0.155 |
| Arkansas | 0.068 | 0.100 | 0.145 | 0.139 | 0.123 | 0.137 | 0.189 | 0.140 | – |

*Upper limits are above the diagonal and lower limits below the diagonal.*

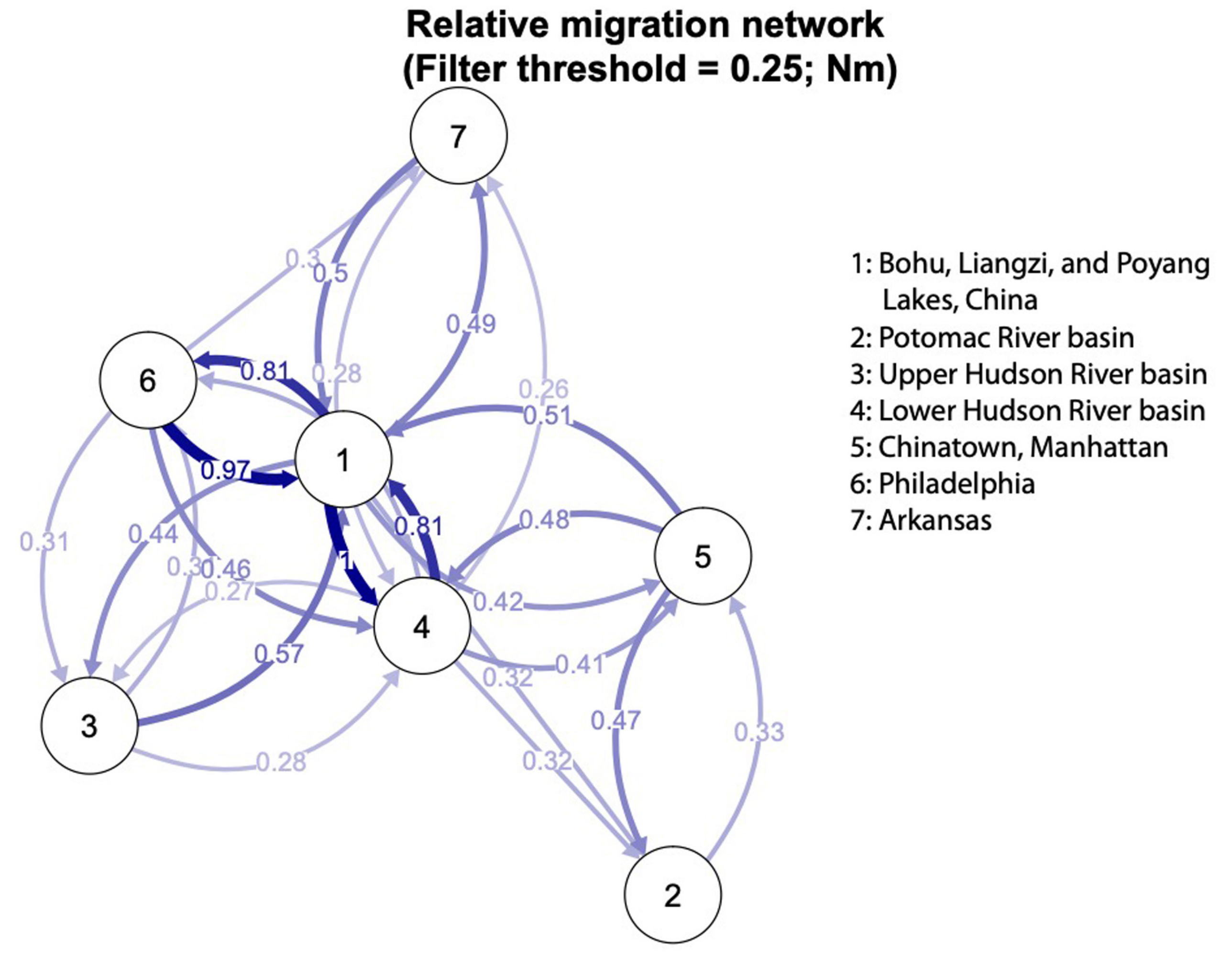

**FIGURE 5 |** Relative migration network of *C. argus* putative populations.

has a large native range that includes China, Russia and Korea (Courtenay and Williams, 2004). One caveat is that our study only included individuals from three source localities that are all from a similar region in China, and therefore our confidence in assigning true source population identity is low unless a high degree of genetic similarity is observed between Chinese and American fishes. Nonetheless, the results of this study are important because they provide evidence that the Bohu and/or

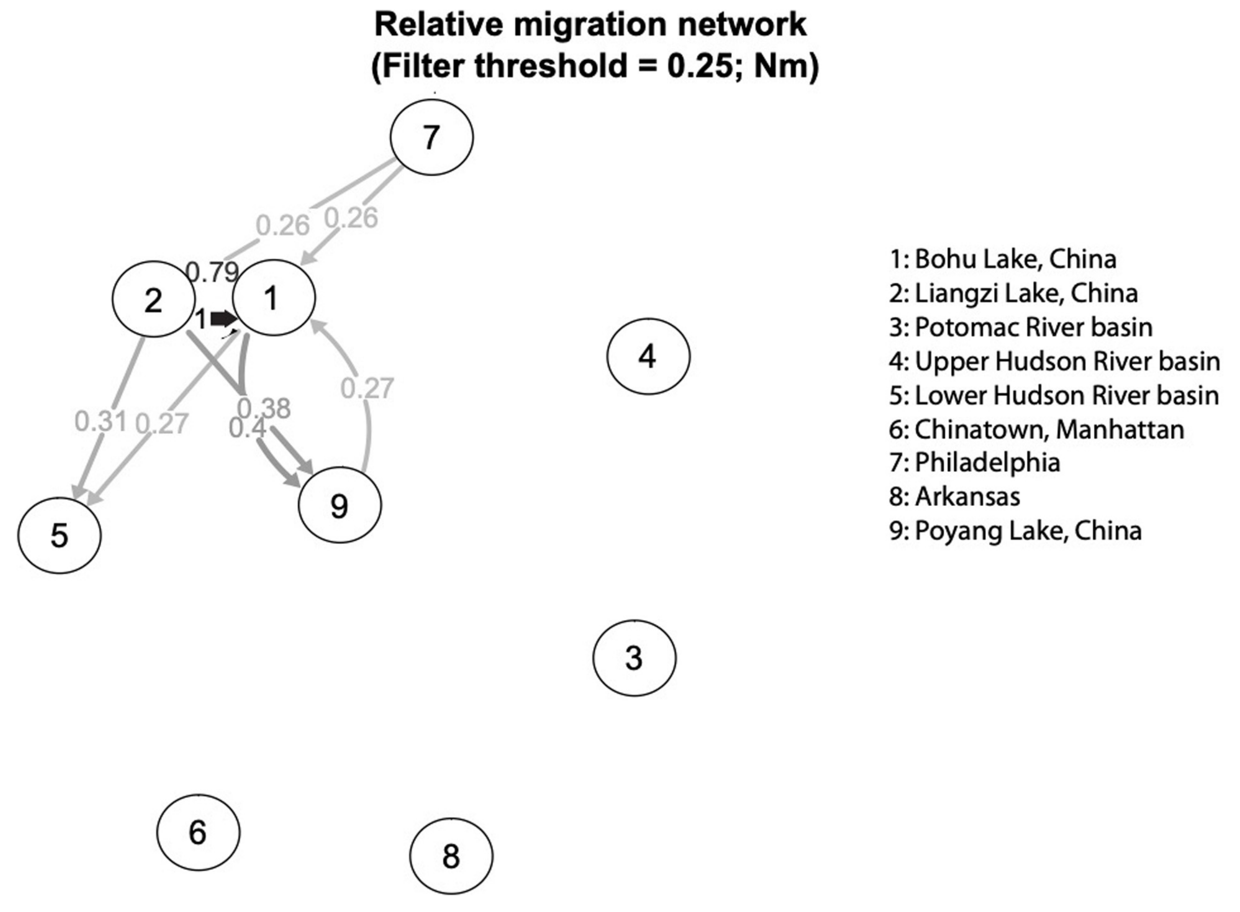

**FIGURE 6 |** Relative migration network of *C. argus* putative populations, assessing each Chinese sampling locality separately.

Liangzi lakes are the likely sources of at least some of the *C. argus* introductions into the United States. In future studies, additional sampling from other sites in the native range beyond central China and the Yangtze River system could help to determine the source(s) of introduction for the other fish in the eastern United States and Arkansas.

Invasive species management is a complex issue that involves ecological, economic, and cultural factors, which often conflict with each other, and thus make decision making difficult (Maguire, 2004). However, the ability to opportunistically obtain samples ideally covering the whole native range and then apply novel genomic methods to compare SNPs from both native and non-native populations, provides a new way for managers to view fine scale population-level data for invasions. *Channa argus* was imported to the United States because it is a popular valuable food source in China, and it was likely introduced into United States waterways by intentional release. Due to its recognition as a species with considerable potential to cause environmental and economic damage, importation and cross-border transport of live individuals was prohibited in the United States in 2002 when it was listed under the Lacey Act. However, despite this regulation, *C. argus* is still sold in areas of the United States where its possession is illegal, illustrating its value as a food source, as well as the possibility of continued live transport in the United States (Fuller et al., 2020). Additionally, *C. argus* is popular for recreational fishing in Meadow Lake, New York, and throughout the Potomac River, and thus contributes to the recreational fishing industry. While *C. argus* may have economic value because of its popularity as a source of food and recreational fishing interest, it has great potential to spread and become established throughout the United States, which will negatively impact native aquatic communities (Fuller et al., 2020). These competing interests illustrate the importance of the results presented here.

To our knowledge, this is one of the first studies using restriction-site-associated digestion sequencing to identify the source of an invasive introduction. This represents a technological advance beyond traditional genetic barcoding and microsatellite analyses, again using modern genomic methods, for analyzing fine-scale links between populations of species in their native and invaded ranges. These results demonstrate that RAD sequencing is an effective method for identifying the source of invasive introductions. This study also demonstrates the power of RAD methods in comparison to traditional microsatellite or mtDNA investigations to resolve fine scale structure (e.g., Wegleitner et al., 2016). Source population information provides insight into invasion pathways and modes of introduction, and therefore is important for management agencies. It will allow for the development of more targeted strategies to prevent further transport of these fishes to the United States. Additionally, it will enable researchers to begin to determine potential sources for biological control for this, and other, harmful aquatic invasive species.

## DATA AVAILABILITY STATEMENT

The data presented in this study are deposited in the NCBI BioSample Database under accession numbers SAMN16703399 through SAMN16703428.

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because: we did not collect or use live animals (only museum tissues) for our genomic work. Thus, no IACUC approval was required.

## AUTHOR CONTRIBUTIONS

AM conceived and designed the experiments. JG, K-JW, and R-JY provided tissues from Chinese sampling locations. CR completed the laboratory work and drafted the manuscript. CR and MG completed the data analyses. AM finalized and submitted the manuscript on behalf of all co-authors. All authors edited subsequent drafts and approved prior to submission.

## FUNDING

This study was funded through internal awards to AM from the College of Science and Engineering at Central Michigan University. Additionally, CR was funded (stipend and tuition) through the Earth and Ecosystem Sciences Ph.D. program at Central Michigan University. This publication is partially funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063, Contribution No. 2021-1123 and PMEL Contribution No. 5197.

## ACKNOWLEDGMENTS

We thank Michael Flaherty, Josh Newhard, Joe Love, Melissa Cohen, Allen Temple, Paul Overbeck, Gabriela Hogue, John Odenkirk, and Justin Homan for contributing *C. argus* tissue samples used in this study. We also thank Tian-Xi Fu and Hai-Ping Chen for assistance with sample collection of the Chinese tissue samples. Additionally, we also thank the Central Michigan University College of Science and Engineering and the Department of Biology for fellowship and assistantship support to CR.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.575599/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
published: 11 February 2021
doi: 10.3389/fevo.2021.627497

# Screening for High-Risk Marine Invaders in the Hudson Bay Region, Canadian Arctic

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The Canadian Arctic is receiving increased ship traffic, largely related to non-renewable resource exploitation and facilitated by climate change. This traffic, much of which arrives in ballast, increases opportunities for the spread of aquatic invasive species (AIS). One of the regions at greatest risk is the Hudson Bay Complex. A horizon scanning exercise was conducted using the semi-quantitative Canadian Marine Invasive Screening Tool (CMIST) to identify AIS of potential concern to the region. This screening-level risk assessment tool, uses documented information to answer questions related to the likelihood and impact of invasion. Species were analyzed by ecological categories (zoobenthos, zooplankton, phytobenthos) and taxonomic groups, with 14 species (out of 31) identified as being of highest relative risk. Crabs, mollusks, macrozooplankton and macroalgae were the taxonomic groups with the highest overall risk scores, through a combination of higher likelihood of invasion and impact scores relative to other taxa. Species that may pose the highest AIS risk are currently mainly distributed on the east and west coasts of the North Atlantic Ocean. Their distributions coincide with source ports and shipping pathways that are well connected to the Hudson Bay Complex. This first horizon scan to identify potential high-risk AIS for the Canadian Arctic incorporated two novel approaches into the CMIST analysis: i) use of the tool to assess two new ecological categories (phytobenthos and zooplankton), and ii) use of averaged CMIST results to interpret general risk patterns of ecological categories. This study is also the first to use CMIST scores to highlight common source regions and connected ports for the highest risk species. In a scenario of climate change and increasing ship traffic, this information can be used to support management actions such as the creation of watch lists to inform adaptive management for preventing AIS establishment, and mitigating associated environmental and economic impacts.

**Keywords: aquatic invasive species, horizon scanning, risk assessment, Canadian Marine Invasive Species Tool, watch list**

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**Specialty section:**
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *09 November 2020*
***Accepted:*** *25 January 2021*
***Published:*** *11 February 2021*

**Citation:**
*Goldsmit J, McKindsey CW, Stewart DB and Howland KL (2021) Screening for High-Risk Marine Invaders in the Hudson Bay Region, Canadian Arctic. Front. Ecol. Evol. 9:627497. doi: 10.3389/fevo.2021.627497*

## INTRODUCTION

To stop biodiversity loss, Aichi Biodiversity Target 9 from The Strategic Plan for Biodiversity 2011–2020 states that invasive species and their pathways need to be identified and managed to take effective actions to prevent introductions and establishments (CBD Secretariat, 2010). Many recent extinctions and losses of biodiversity have been driven by invasive species (Bellard et al., 2016;

Blackburn et al., 2019). Economic impacts due to invasive species have been estimated at up to 12% of the gross domestic product of affected countries (Marbuah et al., 2014). Deleterious effects can occur at ecological levels ranging from populations and communities to habitats, ecosystem functioning, and ecosystem services (e.g., Gallardo et al., 2016a; Anton et al., 2019). A key first step to attain Aichi Biodiversity Target 9, is to identify potential invasive species and assess their likelihood of introduction and impact.

Aquatic invasions are an emerging issue in Arctic ecosystems (Ricciardi et al., 2017), where global change, growing shipping activity, and natural resources exploitation may increase invasion risk (Niimi, 2004; Smith and Stephenson, 2013; Miller and Ruiz, 2014; Melia et al., 2016; Essl et al., 2020). The Canadian Arctic is a vast region where remoteness and harsh climate limit opportunities for year-round monitoring and early detection of aquatic invasive species (AIS). In this area, the identification of high-risk species, pathways, and geographic locations is particularly important for informing targeted preventative and surveillance measures to limit introduction and spread of AIS.

The Canadian Arctic is warming about three times faster than the global rate (Flato et al., 2019), creating conditions favorable for the survival and establishment of new species in the region. The Hudson Bay Complex is an area of the Canadian Arctic where reductions in sea ice cover (duration and concentration) are among the greatest observed in Arctic regions (Stammerjohn et al., 2012; Mudryk et al., 2018). Indeed, sea ice cover there has been declining at a rate of 10.8% per decade since the mid-1990s (Derksen et al., 2018), and ice-free time is projected to double (from 2 to 4 months) by mid-century (Tivy et al., 2011; Mudryk et al., 2018).

Rates of species introduction and AIS establishment are low in the Canadian Arctic relative to temperate regions (Casas-Monroy et al., 2014; Chan et al., 2019). However, new introductions and non-native species are being reported (MacDonald et al., 2010; Mathieson et al., 2010; Goldsmit et al., 2014; Golder (Golder Associates Ltd.), 2018; Dhifallah, 2019; Dispas, 2019) or detected in the environment using genetic tools (Brown et al., 2016; Chain et al., 2016; Grey et al., 2018; Lacoursière-Roussel et al., 2018; Leduc et al., 2019). Ports of call for vessels visiting the Arctic often host species with considerable potential for establishing there. Distribution modeling studies predict that suitable habitat exists in the Canadian Arctic for some potentially high-risk invasive species under current climatic conditions and that Arctic habitats will become increasingly suitable under future change scenarios (Ware et al., 2016; Goldsmit et al., 2018, 2020).

Domestic and international shipping are likely the primary anthropogenic vectors for introducing marine aquatic invasive species to the Canadian Arctic (Chan et al., 2012; Goldsmit et al., 2019). The former plays a fundamental role in supplying local communities and export of mineral resources, and the latter in the export of renewable (e.g., grain) and non-renewable (e.g., ore) resources (Chan et al., 2012; Gavrilchuk and Lesage, 2014; Goldsmit et al., 2019). The risk of introduction is great as ships from both sources transport non-indigenous species in their ballast water and attached to their hulls (Chan et al., 2015; Laget, 2017; Tremblay, 2017; Dhifallah, 2019; Dispas, 2019). Domestic ships, in particular, pose a moderate to high ecological risk in the region (Goldsmit et al., 2019). They often arrive loaded, which reduces the incoming volume of ballast water, but those that do arrive in ballast are exempt from management and undertake shorter transits, which may facilitate the successful transport of viable AIS. Although international vessels typically arrive in ballast, they are required to exchange and/or treat their ballast water (IMO (International Maritime Organization), 2004; Canada Gazette, 2019). However, the efficacy and reliability of various treatment methods for reducing the number of live organisms in vessels can be quite low (DFO (Department of Fisheries and Oceans), 2019) and remains uncertain, particularly under colder conditions, such as those encountered in Arctic waters. Thus, the ecological risk posed by international shipping in Arctic waters may be high. In addition, the trend toward a longer open water season is expected to increase the exposure of local communities to shipping traffic (Andrews et al., 2018). Moreover, significant increases in marine shipping are expected in response to population growth, declining sea ice, and resource extraction (Lasserre, 2018). For example, Baffinland Iron Mines Corporation is currently exporting close to 6 Mt of iron ore annually from its Mary River mine at the northern end of Baffin Island via Milne Inlet, Eclipse Sound and Baffin Bay to markets in Europe and Asia (Baffinland (Baffinland Iron Mines Corporation), 2020a), with a proposed increase to 12 Mt currently under review (Baffinland (Baffinland Iron Mines Corporation), 2020b). A proposal to ship an additional 18 Mt of iron ore annually from the mine via Steensby Inlet, Foxe Basin, and Hudson Strait to markets in Europe and elsewhere has been approved and may be operational by 2028 (Baffinland (Baffinland Iron Mines Corporation), 2020b).

Prevention is key to invasive species management (Lockwood et al., 2007). Once an invasive species has established a reproducing population, it is typically very difficult or impossible to eradicate (Locke and Hanson, 2009). Identifying species that are most likely to harm a particular risk assessment (RA) area is a key step toward preventing introductions and supporting a rapid response if they are introduced (Shine et al., 2010). Procedures such as horizon scanning and risk screening are useful to gather the information needed to identify emerging issues (Amanatidou et al., 2012) and species with the highest likelihood of arrival and establishment, and to anticipate potential impacts (Roy et al., 2014a; Copp et al., 2016; Drolet et al., 2016; Davidson et al., 2017; Verbrugge et al., 2019). Such assessments can improve the identification, quantification and prioritization of invasive species of concern by building watch lists that identify species with the potential to impact biodiversity in a given RA area (Essl et al., 2011; Genovesi and Shine, 2011; Blackburn et al., 2014). This information is useful for prioritizing surveillance, the development of response plans, and species-specific screening tools (e.g., qPCR markers for genetic detection) (Reaser et al., 2020).

This paper outlines a horizon scanning exercise to identify potential higher risk species for the Hudson Bay Complex. This region has conditions predicted to be suitable for the establishment of some marine invasive species of concern (Ware et al., 2016; Goldsmit et al., 2018, 2020). The specific objective of this study was to develop a ranked list of species that could be appropriate to include in watch lists for the Hudson Bay Complex. Using these rankings, it was then assessed: (1) which ecological categories (zoobenthos, phytobenthos, and zooplankton) and taxonomic groups may pose the greatest likelihood of invasion and impact; (2) which ecoregions are most likely to be sources of high-risk species for the RA area; and (3) the importance of each component in the invasion risk calculation (likelihood of invasion and ecological impact) for assessed AIS in the RA area.

## MATERIALS AND METHODS

### Risk Assessment Area

The Hudson Bay Complex is one of eight marine ecoregions of the Canadian Arctic (Spalding et al., 2007). It includes Hudson Strait, Hudson Bay, Foxe Basin, James Bay and Ungava Bay (**Figure 1**). It is characterized by receiving a large volume of freshwater runoff, an important penetration of Arctic marine waters into the system, and a dynamic coastal zone geomorphology (Stewart and Lockhart, 2005, and references therein). Hudson Bay is relatively shallow (150 m mean depth) (Prinsenberg, 1986) and is isolated from open ocean circulation by shallow sills; with local atmospheric conditions forcing inter-annual sea ice cover variations (Hochheim and Barber, 2014, and references therein). A wide range of habitats are available and used throughout the year by a variety of Arctic/Subarctic organisms, together with others that are only seasonal inhabitants such as migratory fishes, marine mammals and birds (Stewart and Lockhart, 2005).

The ecoregion hosts the greatest proportion of ports in the Canadian Arctic (Chan et al., 2012; Goldsmit et al., 2019; **Figure 1**) and the ecological risk to the area is considered high relative to other Canadian Arctic ecoregions (Stewart and Howland, 2009; Goldsmit et al., 2019) as it offers habitat suitable for potential AIS establishment now and under future global change scenarios (Goldsmit et al., 2018, 2020). The risk associated with individual discharges by international transoceanic vessels in the Canadian Arctic is high (Casas-Monroy et al., 2014), thus overall risk can be expected to increase as shipping volumes in the RA area continue to increase in the future (Judson, 2010; Étienne et al., 2013). For example, by ca. 2028 (Baffinland (Baffinland Iron Mines Corporation), 2020b), the Mary River iron ore mine will require 102 cape class ore carriers annually to arrive in ballast and load ore at Steensby Inlet in northeastern Foxe Basin if it is to meet its approved export targets (Baffinland (Baffinland Iron Mines Corporation), 2012). This is roughly 3 times the volume of ballast water currently discharged throughout the eastern Canadian Arctic. In addition, grain shipments from the Port of Churchill also resumed in 2019 and are expected to increase (Franz-Warkentin, 2019).

### Species Selection

For this risk assessment, 100 potentially invasive species were pre-screened based on their biological/ecological traits and considering Arctic environmental conditions related to their potential survival. Only species able to withstand cold temperatures and capable of tolerating brackish and marine water were selected (**Figure 2A**). Information on the species' potential for transport by shipping to the region was also considered. These two selection criteria were included to ensure that the

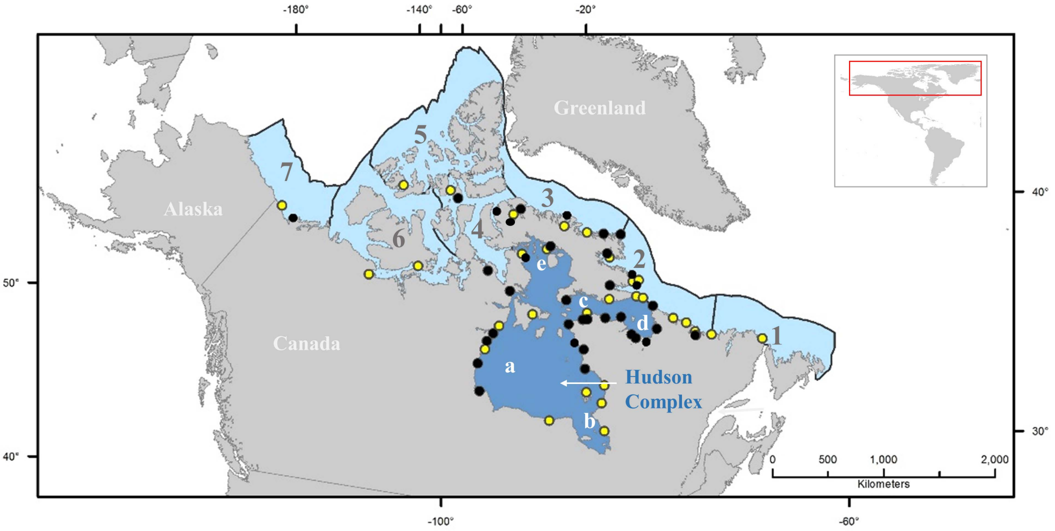

**FIGURE 1 |** Map showing the location of the risk assessment area (Hudson Bay Complex, composed of (a) Hudson Bay; (b) James Bay; (c) Hudson Strait; (d) Ungava Bay; and (e) Foxe Basin). Numbers shown represent the other Canadian Arctic ecoregions as delineated by Spalding et al. (2007): (1) Northern Grand Banks-Southern Labrador; (2) Northern Labrador; (3) Baffin Bay-Davis Strait; (4) Lancaster Sound; (5) High Arctic Archipelago; (6) Beaufort-Amundsen-Viscount Melville-Queen Maud; and (7) Beaufort Sea-continental coast and shelf. Dots represent Canadian Arctic ports known to receive ballast water discharges (black), and ports without registered discharges of ballast water but that could be affected by biofouling (yellow) (Chan et al., 2012; Goldsmit et al., 2019; DFO (Department of Fisheries and Oceans), 2020).

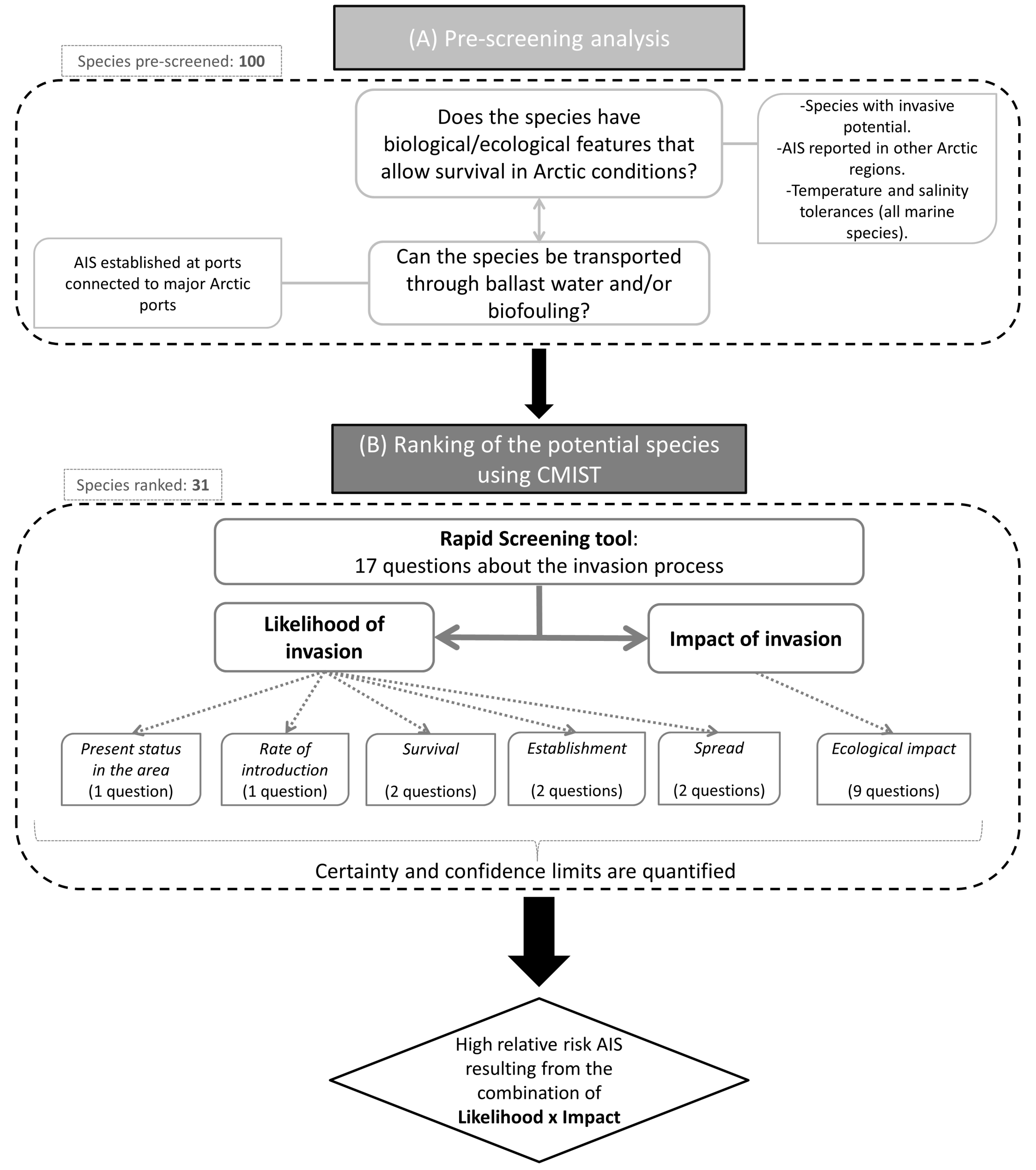

**FIGURE 2 |** Overview of the species selection (**Panel A:** Pre-screening analysis) and assessment process using the CMISt tool (**Panel B:** Ranking of species).

assessment was realistic in that it considered species with chances of surviving Arctic conditions and a means of anthropogenic transport to the Arctic. Data used for this pre-screening step were gathered from the published and gray literature (Hines et al., 2000; Ruiz et al., 2006; Molnar et al., 2008; Chan et al., 2012, 2016; Geller and Ruiz, 2013; Chain et al., 2016; Ware et al., 2016; Young, 2016; Turbelin et al., 2017) and global invasive species lists (National Exotic Marine and Estuarine Species Information System NEMESIS[1]; Invasive Species Compendium[2]; the European Network on Invasive Alien Species NOBANIS[3]; and the Global Invasive Species Database GISD[4]).

A total of 39 species were thus selected for ranking with the Canadian Marine Invasive Species Tool (CMIST) (Drolet et al., 2016) to assess their likelihood of invasion and potential impacts in the Hudson Bay Complex. Only 31 ended up being completely ranked (**Table 1**) since sufficient detailed information required to answer screening questions was missing for the remaining (or closely related) species (5 phytoplankton and 3 zooplankton

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[1] www.invasions.si.edu/nemesis/

[2] www.cabi.org/isc

[3] www.nobanis.org/

[4] www.issg.org/database

**TABLE 1** | Species ranked using the CMIST tool.

| Species | Common name | Taxa | Ecological group | Taxonomic group |
|---|---|---|---|---|
| *Amphibalanus amphitrite* | Striped barnacle | Crustacea | Zoobenthos | Barnacle |
| *Amphibalanus eburneus* | Ivory barnacle | Crustacea | Zoobenthos | Barnacle |
| *Amphibalanus improvisus* | Bay barnacle | Crustacea | Zoobenthos | Barnacle |
| *Austrominius modestus* | Australian barnacle | Crustacea | Zoobenthos | Barnacle |
| *Botrylloides violaceus* | Violet Tunicate | Tunicata | Zoobenthos | Tunicate |
| *Botryllus schlosseri* | Golden star tunicate | Tunicata | Zoobenthos | Tunicate |
| *Caprella mutica* | Japanese skeleton shrimp | Crustacea | Zoobenthos | Amphipod |
| *Carcinus maenas* | Green crab | Crustacea | Zoobenthos | Crab |
| *Chionoecetes opilio* | Snow crab | Crustacea | Zoobenthos | Crab |
| *Ciona intestinalis* | Vase tunicate | Tunicata | Zoobenthos | Tunicate |
| *Cordylophora caspia* | Freshwater hydroid | Cnidaria | Zoobenthos | Other |
| *Eriocheir sinensis* | Chinese mitten crab | Crustacea | Zoobenthos | Crab |
| *Gammarus tigrinus* | Tiger scud | Crustacea | Zoobenthos | Amphipod |
| *Littorina littorea* | Common periwinkle | Mollusca | Zoobenthos | Mollusk |
| *Marenzelleria viridis* | Red-gilled mudworm | Polychaeta | Zoobenthos | Other |
| *Membranipora membranacea* | Coffin box bryozoan | Bryozoa | Zoobenthos | Other |
| *Molgula manhattensis* | Sea grape | Tunicata | Zoobenthos | Tunicate |
| *Mya arenaria* | Soft shell clam | Mollusca | Zoobenthos | Mollusk |
| *Paralithodes camtschaticus* | Red king crab | Crustacea | Zoobenthos | Crab |
| *Pontogammarus robustoides* | Scud | Crustacea | Zoobenthos | Amphipod |
| *Styela clava* | Club tunicate | Tunicata | Zoobenthos | Tunicate |
| *Codium fragile* spp. *fragile* | Dead man's fingers | Chlorophyta | Phytobenthos | Macroalga |
| *Dumontia contorta* | Dumont's tubular weed | Rhodophyta | Phytobenthos | Macroalga |
| *Sargassum muticum* | Japanese wireweed | Phaeophycea | Phytobenthos | Macroalga |
| *Undaria pinnatifida* | Wakame | Phaeophycea | Phytobenthos | Macroalga |
| *Acartia (Acanthacartia) tonsa* | No common name found | Copepoda | Zooplankton | Copepod |
| *Aurelia limbata* | Brown banded moon jelly | Cnidaria | Zooplankton | Macrozooplankton |
| *Centropages typicus* | No common name found | Copepoda | Zooplankton | Copepod |
| *Eurytemora affinis* | No common name found | Copepoda | Zooplankton | Copepod |
| *Eurytemora carolleeae* | No common name found | Copepoda | Zooplankton | Copepod |
| *Mnemiopsis leidyi* | Warty comb jelly | Ctenophora | Zooplankton | Macrozooplankton |

species). The final set of ranked species included both benthic (zoobenthos and phytobenthos) and planktonic (zooplankton) organisms that could be transported by ship traffic, either in ballast water or as biofouling. Of the 31 species selected for ranking, three are established in the RA area: *Aurelia limbata*, *Dumontia contorta*, and *Eurytemmora affinis* (**Table 1**).

## Risk Assessment Using CMIST

CMIST is a screening-level RA tool that uses documented information and expert opinion to semi-quantitatively assess the risk of aquatic non-indigenous species (Drolet et al., 2016) (for both species known to be invasive elsewhere in the world or not). It consists of 17 questions related to the likelihood and impact of invasion (hereafter, Invasion and Impact, respectively). Each question is scored, and a level of certainty for each questions incorporated into final score values. It has been applied to the east and west coasts of North America to assess the risk of single (Moore et al., 2018) or multiple (DFO (Department of Fisheries and Oceans), 2017; Therriault et al., 2018) species, and has been shown to provide accurate predictions of invasive species establishments and impacts (Ogilvie, 2017). Questions relate to the present status of the species in the area of interest, rate of introduction, survival, establishment, spread, and negative ecological impacts (**Figure 2B**). Each question is scored from 1 (low) to 3 (high). Mean values of scores are calculated for Invasion (questions 1 to 8) and Impact (questions 9 to 17). These means are then multiplied to yield a final risk score per species that can range from 1 (lowest) to 9 (highest). In this study, CMIST scores were assigned by assessors based on a combination of expert knowledge and the best-available data for each species assessed (even information on closely related species can be used). CMIST also scores the certainty related to each question score, from 1 (low) to 3 (high), to account for confidence on the scoring according to the quality of information available at the time of assessment. To adjust certainty and aid interpretation, a Monte Carlo randomization procedure is used to generate upper and lower 95% confidence limits for risk scores (for details on calculation of mean adjusted values, refer to Supplementary Material 2 in Drolet et al., 2016). Mean adjusted values of Invasion and Impact, and mean CMIST scores were analyzed to identify highest risk species and ecological/taxonomic groups. Species with the highest relative risk (HRR species) were defined as those scoring ≥2.0 in both risk components (adjusted Invasion and Impact) (i.e., all species that fell in the upper right quadrant of the heat matrix, **Supplementary Figure 1**).

Information used to answer the CMIST questions for each species was drawn from published articles, government reports, gray literature, and global invasive species websites, as described above. Scores were consensus-based, with all authors assessing and participating in risk scoring for all CMIST questions. Note that the ecological impacts included in the analysis are those considered to negatively impact ecosystems; potential positive impacts, such as establishment of new fisheries resources, were not considered.

Some CMIST questions were modified for assessment in an Arctic environment. For example, for Question 16, 'What level of impact could the species have on aquaculture and commercially fished species in the assessment area?', subsistence fisheries were considered as they are particularly important in Arctic regions, whereas aquaculture is not. Interpretation of some questions was also modified from the original CMIST guidance to provide clearer direction for scoring, for example: (i) Question 2 (related to arrival): scores were adapted according to the number of potential vectors and known distribution of the species in connected ecoregions, (ii) Question 13 (related to diseases and parasites): additional guidance on the presence of mechanisms for arriving with the host was added, and (iii) Question 14 (related to hybridization): modifications related to the presence of known native species in the same genus were added (details given in **Supplementary Table 1**). Refer to Drolet et al. (2016) to see general guidelines for CMIST.

## Horizon Scanning Analysis With HRR Species and Source Ecoregions

Distribution of HRR species richness among ecoregions was calculated and plotted on a global map. Both known native and invaded ranges were included to evaluate the number of HRR species in each source ecoregion. Connectivity between the RA area and source regions was examined at the vessel-level according to last port of call and at the tank-level with respect to ballast origin (which may differ from the last port of call) from international and domestic ports. This information was obtained from the shipping database used in Goldsmit et al. (2019) and included last port of call and ballast water source of vessels that visited Hudson Bay Complex ports over a 10-year period (2005–2014). The proportion of connected ports that occurred within ecoregions containing HRR species was calculated, as were the proportion of discharged ballast and arrivals that originated from those ecoregions.

# RESULTS

For the 31 species assessed, CMIST adjusted overall scores ranged from 3.38 to 6.28 (**Figure 3**). A total of 14 HRR species was identified for the Hudson Bay Complex: (1) *Chionoecetes opilio*; (2) *Paralithodes camtschaticus*; (3) *Acartia (Acanthacartia) tonsa*; (4) *Mya arenaria*; (5) *Littorina littorea*; (6) *Codium fragile* spp. *fragile*; (7) *Sargassum muticum*; (8) *Aurelia limbata*; (9) *Mnemiopsis leidyi*; (10) *Carcinus maenas*; (11) *Marenzelleria viridis*; (12) *Membranipora membranacea*;

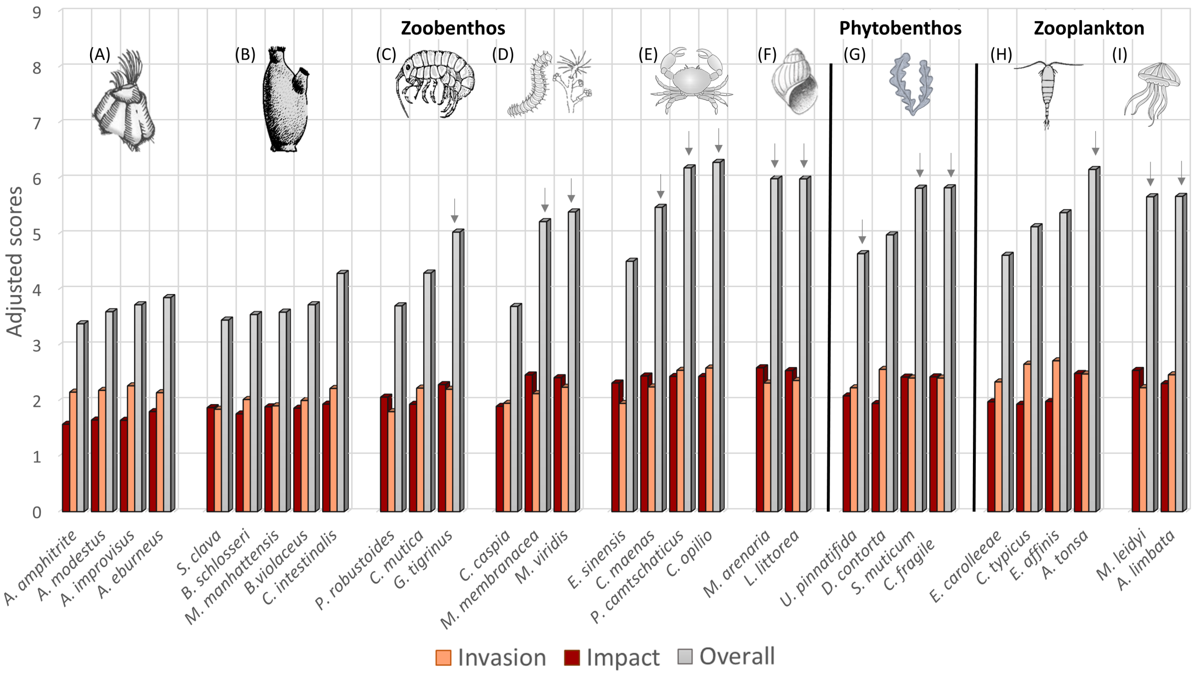

**FIGURE 3 |** Adjusted Invasion, Impact, and CMIST overall risk scores for ecological categories and taxonomic groups assessed for the Hudson Bay Complex marine ecoregion, including Zoobenthos: **(A)** barnacles, **(B)** tunicates, **(C)** amphipods, **(D)** other zoobenthos, **(E)** crabs, **(F)** mollusks; Phytobenthos: **(G)** macroalgae; and Zooplankton: **(H)** copepods, **(I)** macrozooplankton. Arrows identify HHR (scores ≥2.0 in Invasion and Impact).

(13) *Gammarus tigrinus*, and (14) *Undaria pinnatifida* (**Figure 3**, **Supplementary Figure 1**, and **Table 1**). This list includes almost half of the species that were pre-screened from zoobenthos and zooplankton ecological categories and three of the four species in the phytobenthos category. Note that different combinations of Invasion and Impact scores may yield similar CMIST risk scores (**Figure 3**). For example, *D. contorta* and *G. tigrinus* have similar CMIST risk scores (4.98 and 5.03, respectively), but greater differences in their Invasion (*D. contorta* = 1.95 and *G. tigrinus* = 2.28) and Impact scores (*D. contorta* = 2.56 and *G. tigrinus* = 2.20).

The contributions of Invasion and Impact for individual species may be seen when plotted against each other in a heat matrix, highlighting those for which both components have scored high (upper right quadrant, **Supplementary Figure 1**) and in graphic form showing overall adjusted CMIST scores (**Supplementary Figure 2**). The same was done at the ecological and taxonomic levels by grouping species score values for the different categories (**Figure 4**). Variation in scores for zoobenthos is greater than that for the other two ecological categories as mean taxonomic group values vary greatly (differences of up to 2.35 on mean taxonomic group scores for zoobenthos, while a variation of only 0.35 was observed between zooplankton taxonomic group means) (Note that there was only one taxonomic group for phytobenthos) (**Figures 3**, **4**). This variation in individual scores seems to be somewhat related to ecological category size. In general, zooplankton and phytobenthos have similar mean values for Invasion and Impact, whereas zoobenthos have a wider range

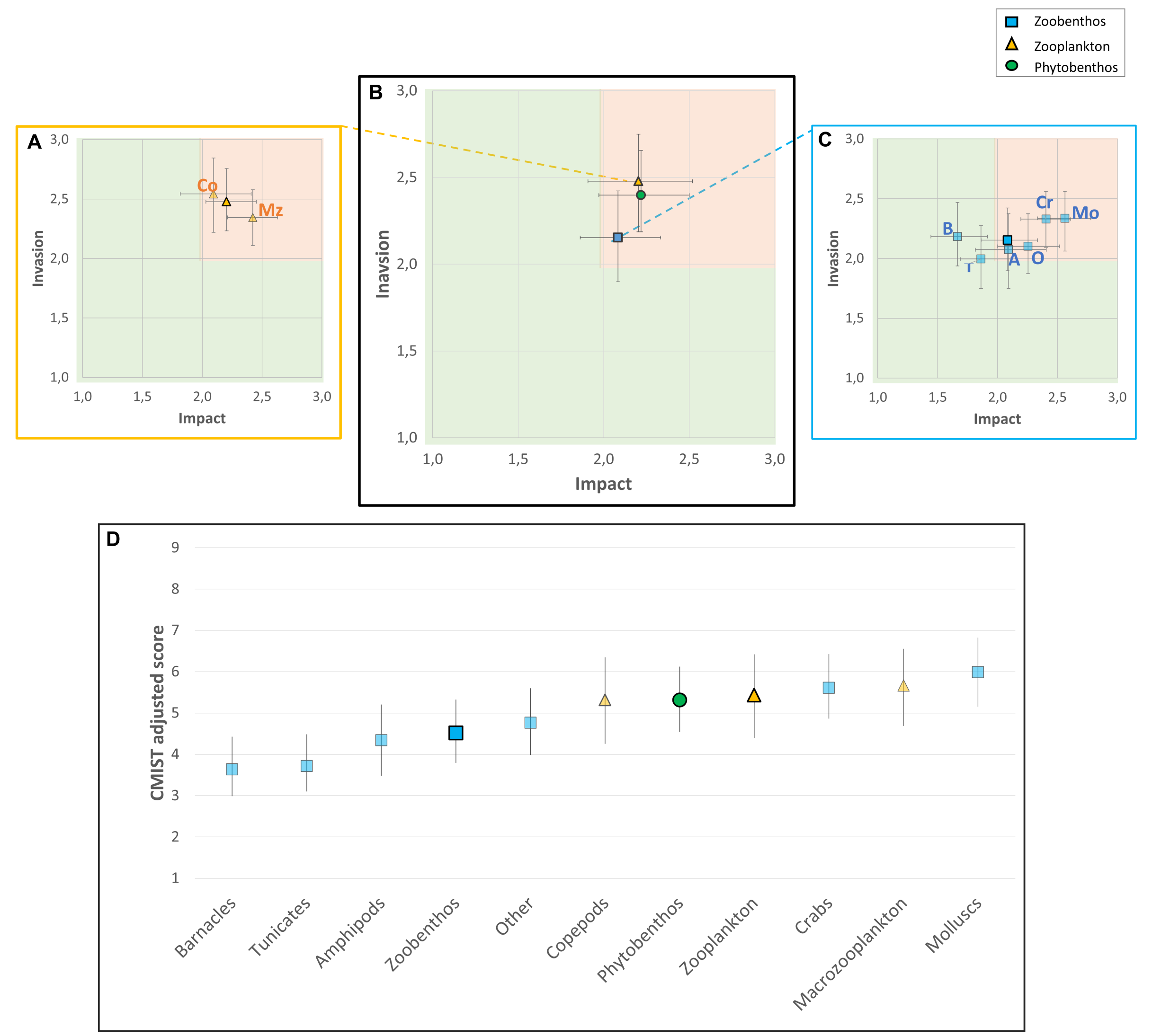

**FIGURE 4 |** Heat matrices depicting adjusted average values of likelihood and impact of invasion scores by ecological groups **(A)** and taxonomic groups in the Hudson Bay Complex **(B,C)**, and ranked average CMIST risk scores for ecological and taxonomic groups **(D)**. Error bars represent the mean of upper and lower 95% confidence limits of each category/group. Symbols of ecological categories are in bold while taxonomic groups therein are in lighter colors (Co: copepods; Mz: macrozooplankton; B: barnacles; T: tunicates; A: amphipods; O: other zoobenthos; Cr: crabs; Mo: mollusks).

of mean values, which is a function of differences in taxonomic group characteristics (**Figures 3**, **4**). For zoobenthos, crabs and mollusks had the highest mean combination of Invasion and Impact, while tunicates and barnacles had the lowest (**Figure 4** and **Supplementary Figure 2**). Variation in Invasion and Impact among taxonomic groups may have differing effects on final CMIST scores (as was also seen at the species-level). For instance, barnacles had higher Invasion but lower Impact likelihoods relative to tunicates (**Figure 4C**), resulting in the groups ending up with very similar mean CMIST scores (**Figure 4D**).

In total, the native and invaded distributions of the 14 HRR species span 60 of the global marine ecoregions (**Figure 5**). Up to 11 of the identified HRR species may be found in each of these ecoregions (**Figure 5**). Of the 60 ecoregions, 22 are connected to the RA area through single or multiple ballast water discharges or vessel arrivals (**Figure 5**). The richest sources of HRR species for the Hudson Bay Complex were on the east and west coasts of the North Atlantic (**Figure 5**). The principal ecoregions showing the highest HRR species richness were the Virginian, Gulf of Maine/Bay of Fundy, Scotian Shelf, and Gulf of St. Lawrence/Eastern Scotian Shelf in the Northwest Atlantic, and the Celtic and North Seas in the Northeast Atlantic (**Figure 5**). These ecoregions include 50.4% of the ports that are connected to the RA area by domestic and international vessels that discharged ballast water at ports in the Hudson Bay Complex between 2005 and 2014 (**Figure 5**). Single and multiple discharges from these source ecoregions represent 79.3% of the total ballast water discharged and 51.4% of arrivals in the RA region during this time period. The Northern California ecoregion also supports 8 of the HRR species but it does not have ports directly connected by shipping to the Hudson Bay Complex.

Overall, considering the ensemble of questions for the 31 species assessed, about 20% of the CMIST question results were scored as low, 42% moderate, and 38% high (corresponding to risk scores of 1, 2, and 3 respectively) (**Figure 6** and **Supplementary Table 1**). The degree of certainty related to these scores generally ranged from moderate to high (**Figure 6**). Questions 8 (related to anthropogenic dispersal) and 17 (related to known invasiveness of the species) scored the highest for all species (and generally with high certainty), since these species are known AIS that may be transported by anthropogenic vectors. In contrast, Question 1 (related to the presence of the species in the RA area) scored the lowest (with moderate certainty), since data on species presence in the RA region is limited and because invasions have likely been limited to date, thus most species are not known AIS for the region (**Figure 6**).

## DISCUSSION

This study highlights AIS that could be of major concern for the Hudson Bay Complex and their potential main source regions through the first application of the rapid screening approach, CMIST, in a polar RA area. Although all species included in the assessment were pre-selected based on their ability to withstand colder temperatures and their potential for transport in pathways with connections to the Hudson Bay Complex, screening with CMIST identified a subset of species with higher relative risk (14 of the 31 assessed species). The approach of averaging and assembling analyses to examine results from an ecological category perspective revealed that zooplankton and phytobenthos had similar high Invasion, Impact, and overall

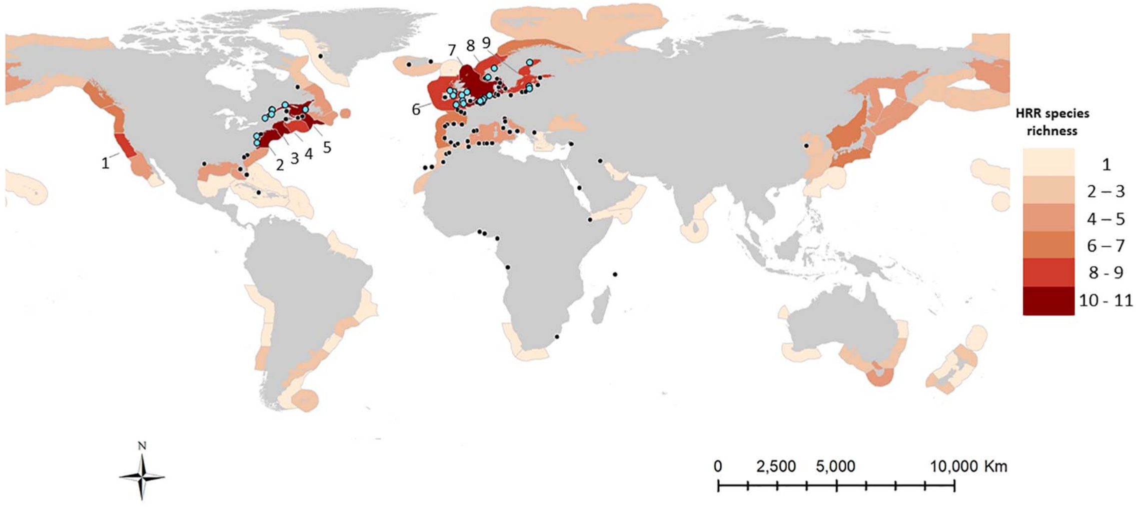

**FIGURE 5 |** Map illustrating source ecoregions of highest risk species for the Hudson Bay Complex. HRR species richness (number of HRR species present in their native and invaded ranges. Species included: *C. opilio, P. camtschaticus*, *A. tonsa*, *M. arenaria, L. littorea*, *C. fragile*, *S. muticum*, *A. limbata*, *M. leidyi*, *C. maenas*, *M. viridis*, *M. membranacea*, *G. tigrinus*, and *U. pinnatifida*). Ecoregions are as delineated by Spalding et al. (2007) (1: Northern California, 2: Virginian, 3: Gulf of Maine/Bay of Fundy, 4: Scotian Shelf, 5: Gulf of St. Lawrence/Eastern Scotian Shelf, 6: Celtic Seas, 7: North Sea, 8: Southern Norway, 9: Baltic Sea). Black circles represent last port of call and ballast water source ports that were connected to ports in the Hudson Bay Complex (single or multiple discharge events); blue circles represent ports situated in locations with highest AIS richness that registered multiple discharge ballast water events. Port and ballast water discharge information is from Goldsmit et al. (2019).

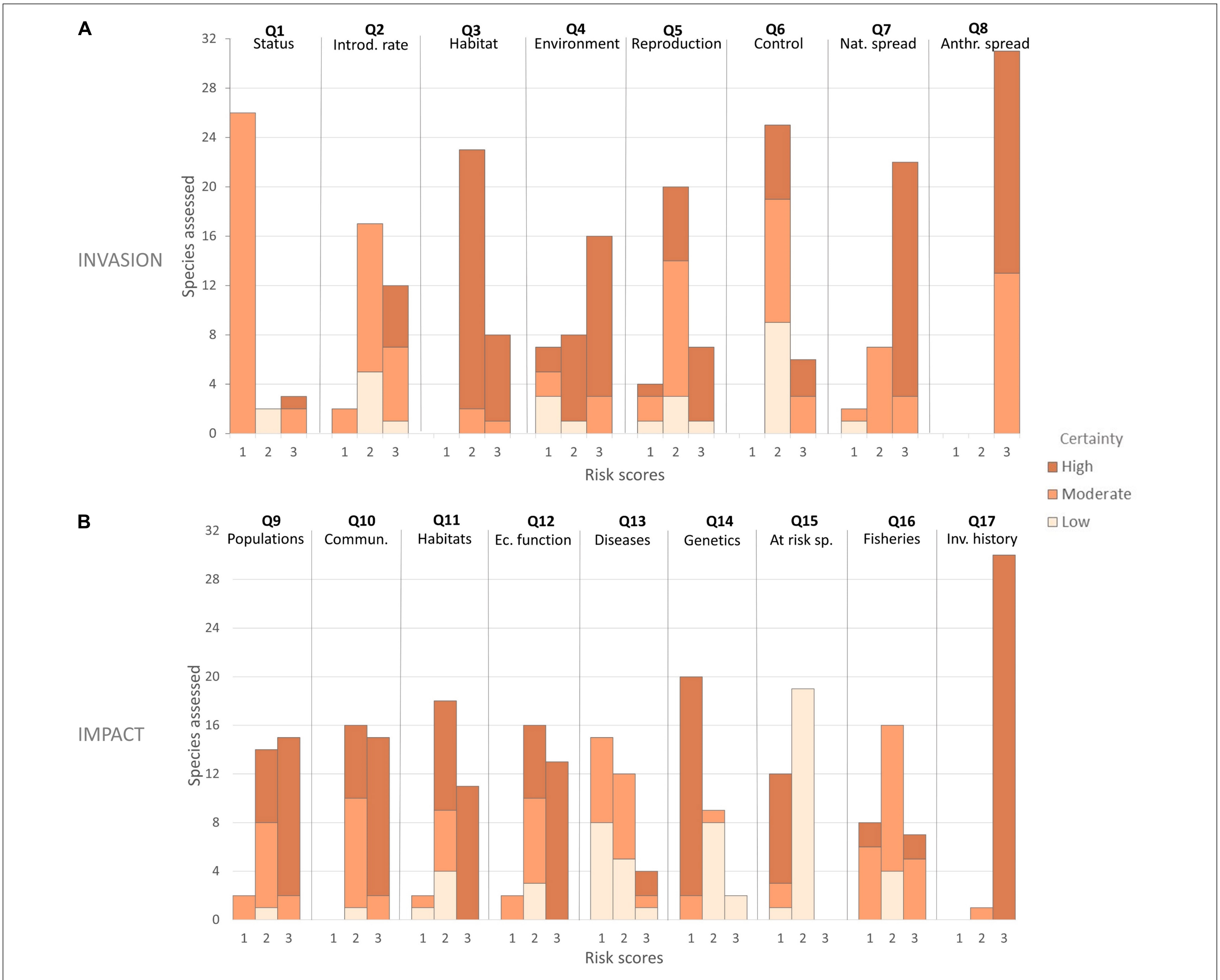

**FIGURE 6 |** Frequency of risk scores used in the set of 31 species assessed using CMIST in the RA area, together with their degree of certainty. Risk scores from 1 (low) to 3 (high) describe the relative risk of AIS in the RA area (e.g., for Question 1, three species received a risk rating of 3 for high (x-axis), the certainty of these rankings was high for one species (dark bar shade) and moderate for two (medium bar shade). Panel **(A)** shows the scores of Questions 1–8 related to Invasion: (1) present status, (2) rate of introduction, (3) survival-habitat, (4) survival-environment, (5) establishment-reproduction, (6) establishment-control, (7) spread-natural, and (8) spread-anthropogenic; Panel **(B)** shows Questions 9–17 related to Impact: (9) on populations, (10) on communities, (11) on habitats, (12) ecosystem function, (13) parasite and diseases, (14) genetics, (15) at risk species, (16) aquaculture/fisheries, (17) past invasion history). See **Supplementary Table 1** for the full text of each question; see also Drolet et al. (2016). Certainty values score from low (mostly uncertain) to high (very certain).

risk scores. In contrast, the average risk values of zoobenthos were lower when considered collectively as a group, but there was high inter-taxonomic grouping variability. In general, taxonomic groups such as crabs, mollusks, macrozooplankton, and macroalgae had relatively higher risk for invasion in the Hudson Bay Complex. Distributions of higher relative risk species were concentrated mainly along the east and west coasts of the North Atlantic Ocean, which have a high proportion of ports connected to the Hudson Bay Complex by shipping and could therefore serve as important source regions for AIS.

This study incorporates two novel approaches in the way the CMIST tool is applied. The first relates to the ecological and taxonomic groups assessed. CMIST has been applied previously to invertebrates (mainly benthic) (Drolet et al., 2016; Moore et al., 2018; Therriault et al., 2018), but this is the first time it has been applied to other groups, including phytobenthos and zooplankton. This is a reasonable approach since the CMIST questions are not taxon-specific but, rather, relate directly to the invasion process and known impact of the assessed species (DFO (Department of Fisheries and Oceans), 2015; Drolet et al., 2016). The second approach is related to the use of mean scores across the species assessed to analyze patterns by clusters of ecological and taxonomic groups. Risk assessment of taxonomic groups has been done at regional (Roy et al., 2014a; Verbrugge et al., 2019) and global scales, emphasizing AIS impact by taxonomic and functional groups (Gallardo et al., 2016a; Anton et al., 2019), but has not been plotted or analyzed using the combination of likelihood and impact of invasion. CMIST scores were also used to highlight common source regions and connected ports for HRR species. This study thus shows new ways of applying and analyzing CMIST results to evaluate ecological- and taxa-specific patterns.

## HRR Species in the Hudson Bay Region

Fourteen invasive marine species were identified as posing the highest relative risk to the Hudson Bay Complex. In this context, species and groups of particular note included crabs (green crab *C. maenas*, snow crab *C. opilio*, and red king crab *P. camtschaticus*), mollusks (common periwinkle *L. littorea*, and soft-shell clam *M. arenaria*), macrozooplankton (warty comb jelly *M. leidyi* and brown banded moon jelly *A. limbata*), and macroalgae (dead man's fingers *C. fragile* spp. *fragile*, Japanese wireweed *S. muticum*, and wakame *U. pinnatifida*). Of these, only one species, *A. limbata*, is already established in the RA area. These findings are corroborated by environmental niche models and ecophysiological threshold models, which have shown that the majority of HRR species are predicted to find suitable habitat in some regions of the RA area under current and/or projected climate change scenarios (Ba et al., 2010; Crafton, 2014; Ware et al., 2016; Goldsmit et al., 2018, 2020; Lins et al., 2018). Additionally, a species-specific ecological risk assessment of the Canadian Arctic using *L. littorea* and *M. arenaria* showed that ports situated in the Hudson Bay Complex (Churchill and Deception Bay), are presently under moderate to high relative risk of invasion given the current vessel traffic in the region, particularly with respect to domestic vessels (Goldsmit et al., 2019).

HRR species are presently distributed in regions that are well connected by shipping traffic to the RA area. These pathways provide ongoing opportunities for their transport into the RA area, making them so called "door knockers" (future invasive species identified in horizon scanning exercises that have not yet been introduced but that could be expected to arrive in the near future) (Roy et al., 2014b; Boršić et al., 2018). These door knockers are presently distributed and highly concentrated in ecoregions situated along the east and west coasts of the North Atlantic Ocean. Both coasts have some of the highest global AIS richness (Geraldi et al., 2020), and include organisms in both their native and invaded ranges. Potential transport of these species between source ecoregions and the Hudson Bay Complex is further strengthened by the presence of numerous connected ports and the fact that there have been multiple ballast water discharges into the RA area from nearly half of those. This connectivity is likely to further increase given that the number of voyages to the Arctic has increased over the last few years (Dawson et al., 2018; Lasserre, 2019) and is predicted to continue rising under future climate change scenarios (Smith and Stephenson, 2013; Melia et al., 2016; Andrews et al., 2018).

Door knocker species have already been found in ships visiting Canadian Arctic ports. *A. tonsa*, for example, was found in ballast water samples from vessels arriving in Deception Bay (Dispas, 2019). The same study found *A. limbata* at the port of Churchill in 2015 (Dispas, 2019) while studies that used metabarcoding sequencing reported signals of *M. arenaria* and *A. limbata* in Churchill (Chain et al., 2016; Grey et al., 2018). Some of these species are already established in other regions of the Arctic, including *C. opilio* in Barents and Kara seas, *P. camtschaticus* in Barents Sea, *M. arenaria* and *C. fragile* spp. *fragile* on the Iceland Shelf, and *M. manhattensis*, *M. viridis* and *S. muticum* in the Norwegian Sea (Orlov and Ivanov, 1978; Berger and Naumov, 2002; Sokolov and Milyutin, 2006; Shakirova et al., 2007; Falk-Petersen et al., 2011; Gederaas et al., 2012; Sundet, 2014; Thorarinsdottir et al., 2014; Zimina, 2014; Dvoretsky and Dvoretsky, 2015; Cohen, 2016; Chan et al., 2019; Espelien, 2020). Door knocker species should be taken seriously considering connectivity due to shipping and the fact that some are already established in other Arctic regions. Additionally, two of these door knocker species (*C. maenas* and *U. pinnatifida*), are also listed as potential species that could threaten biodiversity and ecosystems in another polar environment (the Antarctic Peninsula) (Hughes et al., 2020).

## Ecological Categories and Taxonomic Groups

Assessment of the broader phytobenthos and zooplankton categories yielded similar, high overall risk scores, while zoobenthos was lower but with great inter-group variability, depending on taxonomic group. The highest relative risk scores calculated for the Hudson Bay Complex were within the taxonomic groups for crabs, mollusks, macrozooplankton, and macroalgae. These findings are consistent with studies that have identified crabs and mollusks as the two dominant groups of marine invasive species (Molnar et al., 2008; Ruiz et al., 2015), and crustaceans as one of the most successful invasive species groups (Hänfling et al., 2011). The invasive success of these groups has been attributed to their generalist (eurytolerant and omnivorous) and r-selected life-history characteristics (Hänfling et al., 2011 and references therein). Shipping has been highlighted as one of the most important pathways of introduction, both via ballast water and biofouling, for all these taxonomic groups (Oliveira, 2007; Molnar et al., 2008; Hänfling et al., 2011; Ruiz et al., 2015).

Impacts of invasive crab, mollusk, macrozooplankton, and macroalgae species may be substantial and significantly affect various levels of ecosystems. Invasive crustaceans may trigger cascading effects that affect ecosystem services (e.g., biodiversity, water quality) by changing energy fluxes and nutrient cycles (Hänfling et al., 2011 and references therein). Crabs and mollusks are among the groups that have been the cause of large overall declines in the number of native taxa (Anton et al., 2019). Macrozooplankton species may also impact various levels of the food web. For example, predation on fish eggs, fish larvae, and zooplankton by *M. leidyi* as well as competition with the latter 2 groups has caused the collapse of planktivorous fish stocks in the Baltic Sea (Daskalov et al., 2007; Oguz et al., 2008; Ojaveer et al., 2018). Predatory marine invasive species are of particular concern as they may have stronger effects on native communities and lead to larger ecological impacts than AIS belonging to other trophic levels (Gallardo et al., 2016a; Anton et al., 2019). And lastly, invasive macroalgae can change richness and diversity of native species, decrease the cover of other macroalgae, and even change the habitat since they may modify the existing architectural structure (Schaffelke et al., 2006 and references therein; Wallentinus and Nyberg, 2007). In addition to ecological impacts, introductions of species from these groups have resulted in substantial economic impacts (Pimentel et al., 2005; Colautti et al., 2006; Lovell et al., 2006; Marbuah et al., 2014).

## Risk Assessment Components, Horizon Scans, and Watch Lists

Across the complete suite of species assessed, likelihood of invasion ranged from moderate to high for most species, due, in part, to the fact that all are known AIS that may be transported via ballast water and/or biofouling. However, this risk component was likely affected by the pre-screening process that selected cold-tolerant species. This risk component may also have been influenced by the fact that few species were established in the RA area, although scores for the three that established varied widely and did not differ noticeably from non-established species, suggesting this was not the case. Likewise, scoring of impact of invasion was likely affected by the fact that all assessed species are known invaders from other regions of the world, with considerable information in the literature about their known negative ecological impacts. Nevertheless, information about ecological effects of invasive species in the marine ecosystem is limited compared to other ecosystems (Crystal-Ornelas and Lockwood, 2020). Given this, and that most of these species are not yet present in the RA area, certainty scores varied widely, depending on the question and species assessed. While impacts caused elsewhere can be a good predictor of the potential impact in a new region (Hayes and Barry, 2008), environmental similarity must be considered, together with habitat characteristics and species composition of each ecoregion (Kumschick and Richardson, 2013). The need to improve the accuracy and consistency of impact scoring in risk assessments has been identified previously (Kenis et al., 2012; Kumschick and Richardson, 2013) and is an important consideration, particularly when comparing across studies. Accordingly, some modifications from the original CMIST guidance were made to better assess regional impact. Nevertheless, CMIST can be particularly informative in assessing relative risk to prioritize marine invaders that are not yet reported in a particular RA area (DFO (Department of Fisheries and Oceans), 2015). CMIST also has the advantages of transparency, consistency, and flexibility to allow for continuous improvement when compared to other screening tool methods (Srëbalienë et al., 2019).

Certainty, which is influenced by the quality and quantity of information, was incorporated into the adjusted values and confidence limits for the score for each species. An advantage of CMIST is that it allows certainty to be quantified and translated into confidence limits, a feature most risk assessment tools lack (Koop et al., 2012; Drolet et al., 2016). This is achieved by predicting the probability of possible combinations of score and certainty to a different answer that an assessor might have provided and generating the range of potential scores associated with the 95% confidence limits (Drolet et al., 2016, 2017). This characteristic helps improve interpretation and usability in management (DFO (Department of Fisheries and Oceans), 2015). While CMIST may be overparameterized, it is much less-so than other tools (DFO (Department of Fisheries and Oceans), 2015; Drolet et al., 2017), and its favorable points (e.g., performance, low inter-assessor variability, distinction between invasion elements, certainty quantification, etc.) make it a good option to assess the risk associated with door knocker species that could be introduced to the Hudson Bay Complex.

Over the past decade, European countries have been undertaking horizon scans to produce watch lists to highlight the principal species of concern for their regions (e.g., Shine et al., 2010; Roy et al., 2014b, 2015; Gallardo et al., 2016b; Matthews et al., 2017; Carboneras et al., 2018; Paganelli et al., 2018; Peyton et al., 2019; Killi et al., 2020). These efforts are related to the objectives of a European Union regulation (1143/2014) and the Commission Delegated Regulation (EU) No 2018/968 (2018), which are to control/eradicate priority species and prevent the introduction and establishment of new invasive species by managing pathways of introduction. This states that species to be added to the "Union list" must have, as a precondition, been evaluated through risk assessment (European Union, 2018). These types of regulations are not in force under Canadian legislation, making all efforts to identify potential invasive species using science-based risk assessment tools, such as in the present study, more valuable. However, under the International Convention for the Control and Management of Ship's Ballast Water and Sediments, adopted by the International Maritime Organization (IMO) in 2004 and which entered into force in September 2017, newer vessels originating from outside of Canada's Exclusive Economic Zone are required to manage their ballast water through treatment to reduce risks for species introductions (IMO (International Maritime Organization), 2021). These measures should help prevent the arrival of new species through this particular vector.

## CONCLUSION

Three of the 14 door knockers species identified in this assessment (*C. maenas, M. leidyi*, and *U. pinnatifida*) are included in the Global Invasive Species Database' list of "100 of the World's Worst Invasive Alien Species"[5] (Lowe et al., 2000). Actions to prevent their arrival and establishment should be undertaken. CMIST analysis provided a standardized structure for interpreting ecological information from the Hudson Bay region in relation to specie's requirements and potential effects. This tool can also be used to develop watch lists for management actions based on the relative ranking of species in other regions [e.g., black and gray watch lists; see Essl et al. (2011) and Blackburn et al. (2014)]. To be useful, this type of assessment to identify potential threats must be followed by appropriate actions (Sutherland and Woodroof, 2009).

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[5] http://www.iucngisd.org/gisd/100_worst.php

The high-risk species identified here are of particular concern and managers should mitigate risks by taking preventative actions, monitoring for arrivals, and planning for early responses if initial measures fail. Management of invasive species can have a range of economic benefits, including protecting biodiversity and maintaining ecosystem health (Hanley and Roberts, 2019). The effects of invasive species on native diversity in aquatic ecosystems and remote regions with low accessibility, such as the Canadian Arctic, are poorly understood (Florencio et al., 2019). Anticipating and preventing potential AIS establishment and associated environmental and economic costs will be increasingly important as climatic conditions change and shipping traffic increases.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JG, CM, and KH contributed to the conceptualization. JG performed the formal analysis, visualization, and wrote the original draft. KH and CM obtained funding for the work and provided resources and supervision for the project. CM, DS, and KH reviewed and edited it. All authors contributed to the methodology (risk assessment scoring) and the investigation, read and approved the submitted version.

## FUNDING

We are grateful for funding from the Canadian High Arctic Research Station (1516-036), Polar Knowledge Canada (PKC-NST-1617-0016A), Fisheries and Oceans Canada (AIS Monitoring Program, Arctic Science Fund, Results Fund, Strategic Program for Ecosystem-Based Research and Advice), the Nunavut Wildlife Management Board (NWMB) (Nunavut Wildlife Research Trust #3-15-12), Nunavik Marine Region Wildlife Board (NMRWB), World Wildlife Fund (WWF), and Quebec-Ocean.

## ACKNOWLEDGMENTS

We would like to thank David Drolet for his availability to discuss the CMIST tool and provide insightful comments. We also would like to thank Gesche Winkler for her expertise and advice on scoring of zooplankton species. We appreciate the time and comments of reviewers. This work benefited from comments of two reviewers and from feedback received during presentations of draft results to the International Council for Exploration of the Seas (ICES) Expert Working Groups on Ballast Water and Other Shipping Vectors and Introductions and Transfers of Marine Organisms. The author sequence follows the 'first-last author-emphasis' norm. A report in the Canadian Data Report of Fisheries and Aquatic Sciences series (https://science-libraries.canada.ca/eng/fisheries-oceans/publications/) entitled "Screening for high-risk marine invaders in the Hudson Bay Region, Canadian Arctic: Compilation of background information, rationale, and references used to answer questions with the Canadian Marine Invasive Species Tool (CMIST)" contains all the scoring rationale and background information used for this paper.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.627497/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 13 April 2021
doi: 10.3389/fevo.2021.641686

# A Dynamic Modeling Framework to Evaluate the Efficacy of Control Actions for a Woody Invasive Plant, *Hakea sericea*

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Invasive alien species (IAS) are a significant component of global changes, causing severe economic and biodiversity damage. In this regard, *Hakea sericea* is one of the most widespread IAS throughout the Mediterranean region, including Portugal. The difficulty surrounding its management is exacerbated by post-fire situations, signifying a challenging task for managers. To assist in this effort, we used a system dynamic approach to model the population dynamics of *Hakea sericea* regarding the combinations of wildfire risk and control scenarios, which differ in periodicity, type of interventions, and cohort age. The ultimate goal of this study was to assess the effectiveness and costs of control efforts at reducing the abundance of this IAS. A Natura 2000 site Alvão/Marão (code PTCON0003) in northern Portugal, severely invaded by *Hakea sericea*, served as the study site. The modeling results demonstrate that *Hakea sericea* is likely to continue spreading if left uncontrolled. Although it may not be possible to ensure eradication of *Hakea sericea* from the study, repeated control actions aimed at the entire IAS population could be very effective in reducing its area. From a practical standpoint, removing all plants 24 months after each fire event followed by subsequent monitoring appears to be the most cost-effective strategy for managing *Hakea sericea*. Considering the modeling results, the dynamic modeling framework developed is a versatile, instructive tool that can support decision-making aimed at effective management of *Hakea sericea*.

**Keywords: system dynamics, silky hakea, biological invasions, invasive species management, post-fire vegetation dynamics**

***Edited by:***
*Ross Taylor Shackleton,*
*University of Lausanne, Switzerland*

***Reviewed by:***
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***Specialty section:***
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

***Received:*** *14 December 2020*
***Accepted:*** *23 March 2021*
***Published:*** *13 April 2021*

***Citation:***
*Morais MC, Gonçalves B and Cabral JA (2021) A Dynamic Modeling Framework to Evaluate the Efficacy of Control Actions for a Woody Invasive Plant, Hakea sericea. Front. Ecol. Evol. 9:641686. doi: 10.3389/fevo.2021.641686*

## INTRODUCTION

Changing weather patterns and the speed of these changes exert a direct influence on the ecosystems, including the ability of exotic species to become established and invasive when introduced into a new environment. Invasive alien species (IAS) are widespread phenomena recognized as one of the main global threats to biodiversity (Early et al., 2016), with escalating impacts at ecological, economic, and human health levels (Hulme, 2006; Simberloff et al., 2013; Marbuah et al., 2014). To tackle this increasing problem, the European Commission published a dedicated Regulation (no. 1143/2014) on IAS that focuses on the need to take management measures for IAS that are widespread (European Union, 2014). Traditionally, IAS management in natural ecosystems has focused on removing the target invader under the assumption that its impacts would dissipate and the ecosystem would recover after its removal (Pearson and Ortega, 2009), but this is not always realistic or feasible (Zavaleta et al., 2001; Marchante et al., 2011). The extent and rate of ecosystem recovery depend on the propagule pressure, type, and frequency of disturbance, among other factors (Foxcroft et al., 2011). Due to the complexity of external drivers influencing IAS spread and impact (Hulme, 2006), IAS control and management is challenging and costly, both economically and environmentally (Hyder et al., 2008; Hulme, 2009), which raises concerns for managers, conservationists, and other stakeholders working with IAS. The interaction between the most relevant ecological components during the invasion process generates significant and increasingly complex influences on the ecosystems (Le Roux et al., 2020), which further complicates IAS management.

Given that it is impractical to deal with all invasive species and invaded populations at once, prioritization of actions is an important strategy to support cost-effective resource allocation (Krug et al., 2010; Gallardo and Aldridge, 2013) and is essential for successful IAS management (McGeoch et al., 2016; Lohr et al., 2017). One of the tools applied in decision-making is ecological modeling, which can be implemented at a relatively low cost in terms of money, effort, and capacity to recreate hypothetical management scenarios (Day et al., 2018). These tools have become indispensable in better understanding, predicting, and controlling biological invasions (e.g., Broenniman and Guisan, 2008; Buchadas et al., 2017). The need for correctly addressing uncertainty, which is inherent to any invasion process (Lewis et al., 2016), has fostered the application of dynamic modeling approaches (e.g., Buchadas et al., 2017). Dynamic models can capture the complexity of interactions among key ecological components by combining environmental conditions, effects of time, and stochastic factors that are difficult to understand otherwise (Jørgensen, 1999). Therefore, this type of models has the potential to support decision-making in IAS management (Santos et al., 2015; Büyüktahtakın and Haight, 2018), for example, for risk evaluation (Guisan et al., 2013), spread dynamics (Ferrari et al., 2014; Martins et al., 2016), management effectiveness (Hyder et al., 2008; Chalak et al., 2011; Portela et al., 2020) of IAS, and restoration of invaded ecosystems (Hall et al., 2020). System dynamics (SD) is a process-based and problem-oriented modeling able to study, analyze, and visualize the behavior of complex systems, in which time is a critical component (Mashaly and Fernald, 2020). This methodology considers the relationships between variables and subsystems, providing insights into potential consequences of system perturbations and future uncertainties (Mirchi et al., 2012). In SD, the system structure is composed of state variables and flows which influence each other, including feedback mechanisms (Mashaly and Fernald, 2020) that attempt to capture the structural functioning in systems affected by long-term environmental changes, such as the impacts resulting from the IAS (Buchadas et al., 2017). In this sense, SD modeling is an excellent tool for solving a range of specific environmental problems (Turner et al., 2016), including those related to IAS management (BenDor and Metcalf, 2006).

It is widely recognized that IAS control and management are costly endeavors, and in the majority of situations, it is an important barrier to successful IAS control (Kettenring and Adams, 2011; Dana et al., 2019). Therefore, a better understanding of using the scarcity of resources is essential in the decision-making process. The difficulty in measuring costs, its context-dependence (IUCN, 2018), associated with the complex nature of invasion dynamics (Epanchin-Niell, 2017) make it a challenging (Kerr et al., 2016; Reyns et al., 2018), but necessary task for improving long-term management of IAS. Here, we develop a SD model for the analysis of the effectiveness and costs of control efforts of *Hakea sericea* (silky hakea), one of the worst woody IAS in Portugal. In South Africa, where this IAS has been problematic for over 100 years, biological control with several agents (Gordon and Fourie, 2011) has proven to be the most successful method. Still, it is not yet an option in Europe. In the country, the use of the "fell and burn" technique, which comprises felling of adult plants, leaving them for 12–18 months and then burning the vegetation, also proved to be a very effective control method, leaving minimal follow-up (Esler et al., 2010). However, in Portugal, the use of this methodology is scarce due to the limited knowledge on the interactions between fire, ecosystem, and the IAS. Control of this IAS relies almost exclusively on mechanical removal (e.g., chainsaws, brush cutters, skid steer brush cutters, and bulldozers), which is hugely expensive. To help managers design effective and efficient allocation of resources, we model the impact of wildfires associated with several control options on the abundance of *Hakea sericea* and control costs. Although previous studies have documented that fire is a key driver *Hakea sericea* invasion, its influence on the success of control efforts is not explored, and this is the primary focus of the present work. A sensitivity analysis (SA) was also carried out to explore the effect of uncertainty on the abundance of *Hakea sericea*. We apply the SD model to the management of *Hakea sericea* in a Natura 2000 site (Alvão/Marão, Northern Portugal), where invasion by this IAS is particularly relevant due to being a management priority. We expect that the outputs of the proposed modeling framework will provide crucial information on the potential magnitude of *Hakea sericea* invasion in a study area and contribute to the implementation of spatial-temporal management scenarios and strategies aimed at effective long-term management of *Hakea sericea*.

## MATERIALS AND METHODS

### Study Species

*Hakea sericea* (Proteaceae) is native to south-eastern Australia and has become invasive in South Africa, New Zealand, and several European countries, such as Portugal, France, and Spain (EPPO, 2017). This serotinous species can form dense, extensive, almost monospecific stands that can alter vegetation composition and structure (Richardson et al., 1989). In South Africa, in Cape fynbos vegetation, dense stands of *Hakea sericea* lead to significant reductions in cover (van Wilgen and Richardson, 1985) and richness (Richardson et al., 1989) of native species. Its impacts also include alterations of fuel properties and abundance, which can modify the fire regime (van Wilgen and Richardson, 1985). The expansion of this IAS is intimately linked to fire, which stimulates the release and scatters of winged seeds that germinate in the post-fire environment (Wilson et al., 2020). In Portugal, *Hakea sericea* generally flowers in its third year of life, during winter, between December and February. Fruit development, which becomes visible in late February, continues for several months and mature fruits emerge in June (personal observations).

## Study Site Description

The Alvão/Marão Natura 2000 network, located in the north of mainland Portugal (41°39′N, 7°83′W), was selected as the study area. The vegetation in this area is predominated by oaks (*Quercus robur* and *Quercus pyrenaica*), pines (*Pinus pinaster*), and a variety of shrub and herb species, mainly belonging to the genera *Erica* and *Ulex*. At the beginning of the 20th century, *Hakea sericea* seedlings were purposefully planted in the area to form mature hedges. The occurrence of wildfires and insufficient management practices facilitate its spread. Major increases in the *Hakea sericea* invasion occurred after 2013 as a consequence of an intense wildfire. Nowadays, this IAS occupies different altitudinal zones, especially those previously dominated by *Pinus pinaster*. It occurs in dense stands (>75% cover) and as isolated individuals dispersed in the area.

The climate in the study area is of Mediterranean type with an Atlantic influence (Csb in the Köppen classification). Data from the closest weather station (41°18′N, 7°44′W) indicates that the mean annual precipitation during 1981-2010 was 1,023 mm, being more abundant in autumn and winter. The average temperatures range from 6.3 (January) to 21.7°C (August), and the mean maximum (28.6°C) and minimum (2.8°C) temperature occur in August and January, respectively.

## Model Conceptualization

A SD framework focusing on the post-fire dynamics of *Hakea sericea* was developed within the software STELLA (iSEE systems Inc., Version 9.0.3). The model comprises five interactive sub-models, respectively, pertaining to the vegetation ecological succession, population dynamics of *Hakea sericea*, fire events and burnt area dynamics, management control efforts, and cost estimates, as shown on the conceptual diagram (**Figure 1**). The model runs on a monthly time step for 50 years to assist the long-term management of this IAS. The fire and control efforts sub-models can be included (turned-on) or excluded (turned-off) in each simulation run.

The dynamics of vegetation and *Hakea sericea* sub-models aim to recreate the changes in vegetation structure (i.e., herbs, shrubs, and trees) and composition of the invaded population [seedlings, young plants with no fruits (age < 3 years old), and adult plants (age > 3 years old)] over time in response to fire and control efforts. In both sub-models, the post-fire succession was based on the temporal rates that reproduce the number of months needed by each class to reach the respective dominance (Bastos et al., 2016). Data used for parameterization of the post-fire succession of vegetation was compiled from Moreira et al. (2001) and Mouillot et al. (2005), whereas the parameterization of the post-fire succession of *Hakea sericea* population was based on EPPO (2017) and Le Maitre et al. (2008).

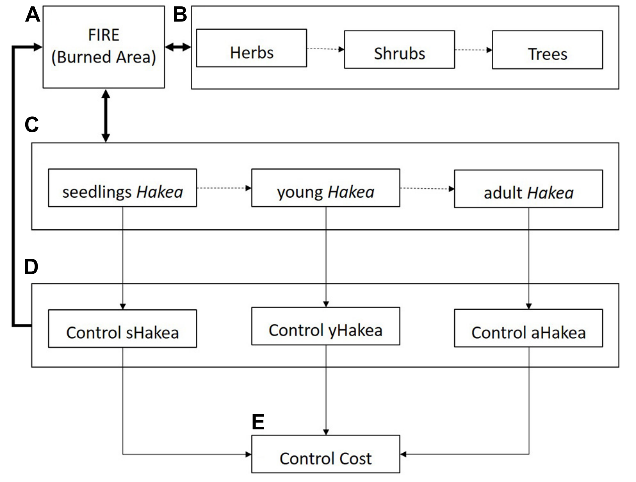

**FIGURE 1 |** General conceptual diagram with the structure and organization of the sub-models: **(A)** fire occurrence and extent, **(B)** vegetation ecological succession, **(C)** population dynamics of *Hakea sericea*, **(D)** management of control efforts, and **(E)** cost estimates. The fire and control sub-models influence interactively the competitive process between the *Hakea sericea* and the other vegetation cover dynamics, as indicated by bold arrows.

The sub-model of fire occurrence and extent characterizes the likelihood of fire occurrence based on temperature and precipitation as the two most crucial weather determinants, obtained from the closest weather station for the 1981–2010 period. In the model, we assumed that mean monthly temperatures exceeding 15°C and monthly precipitation below 20 mm create conditions favorable to fire, according to the fire statistics made available by the ICNF (2017). This sub-model also had in account the fire frequency based on the average number of fire events of the study area, and fire extent, determined using a random number between 0.1 (low fire extent) and 1.0 (extreme fire extent).

In the design of the management of control efforts sub-model, we considered the technique commonly used to control *Hakea sericea* in the study area, which consists of mechanical felling of young and adult plants. The sub-model also considers the timing of occurrence (before or after a fire), frequency (i.e., removal interval), intensity (i.e., the proportion of plants removed per control event, which can assume values between 0 and 1.0, where 1.0 means that all plants were removed), and additional follow-up monitoring.

The cost estimates sub-model addresses the expense invested in each control effort per hectare. It was determined by the product of the area subjected to control (after proper conversion to ha) and the cost/ha of the control method used. For simplicity, we considered four control methods (initial removal of adult plants using heavy equipment, removal of young plants and dead plant matter after a fire event using brushcutters, removal of young plants using brushcutters, and hand-pulling of young plants). The costs of each method, in Euros/ha, were based on actual quotes provided by local contractors.

In total, the proposed modeling framework includes fourteen dynamic state variables (**Table 1**), divided into five main groups, with one variable related to the occurrence of fire, three variables related to the vegetation structure (herbs, shrubs, and trees), three variables based on *Hakea sericea* age stratification, represented by three life stage cohorts (seedlings, young plants, and adult plants), two variables associated to the control of young and adult plants, and, finally, three variables related to the cost estimates. Specification of the state variables included in the model is presented in **Table 1**. The initial values of these variables were based on literature knowledge and pre-existing field data of the study area. The full explanation of processes (**Supplementary Appendix 1**), equations (**Supplementary Table 1**), and variables (**Supplementary Table 2**) included in the model construction are available as **Supplementary Electronic Material**.

## Management Scenarios

In order to reduce the computational complexity of the simulation exercise and to accommodate more realistic management practices, we assumed the following conditions: (i) control of adult plants of *Hakea sericea* occurs only once, at the beginning of the simulation period or 12, 24, or 36 months after each fire event; (ii) control of young plants of *Hakea sericea* occurs only after a fire event; (iii) control of young and adult plants occur at an intensity of 1.0; (iv) follow-up monitoring occurs 10 months after each post-fire control. We also included a management scenario where no control option was applied (scenario 1). In total, twelve management scenarios were simulated, consisting of combinations of age cohorts (young plants vs. adult plants), frequencies of post-fire removal (0, 12, 24, and 36 months after a fire event), and the execution or not of follow-up monitoring (**Table 2**).

For each scenario, 25 independent stochastic simulations were carried out for the simulation period, and the average values of the abundance of *Hakea sericea* (%) and costs were calculated.

**TABLE 1 |** Specification of the state variables included into the model construction, their description, initial values, and measure units.

| State variable | Description | Unit |
|---|---|---|
| HERBS | Area occupied by herbs. Initial value = 2,000 | $m^2$ |
| SHRUBS | Area occupied by shrubs. Initial value = 4,000 | $m^2$ |
| TREES | Area occupied by trees. Initial value = 2,000 | $m^2$ |
| sHAKEA | Area occupied by seedlings of *Hakea sericea*. Initial value = 0 | $m^2$ |
| yHAKEA | Area occupied by young plants of *Hakea sericea*. Initial value = 0 | $m^2$ |
| aHAKEA | Area occupied by adult plants of *Hakea sericea*. Initial value = 2,000 | $m^2$ |
| AreaCyHAKEA | Area of young plants of *Hakea sericea* subjected to control efforts | $m^2$ |
| AreaCaHAKEA | Area of adult plants of *Hakea sericea* subjected to control efforts | $m^2$ |
| AreafHAKEA | Area of *Hakea sericea* subjected to control efforts after fire events | $m^2$ |
| AreaFollowHAKEA | Area of *Hakea sericea* subjected to follow measures after fire events | $m^2$ |
| BAREA | Total area affected by fire plus *Hakea sericea* removal | $m^2$ |
| EndsHAKEA | Duration of soil seedbank | month |
| TafControl | Time of control adult plants of *Hakea sericea* after a fire event | month |
| TyfControl | Time of control adult plants of *Hakea sericea* after a fire event | month |

## Data Analysis

Statistical analysis was performed using the software package IBM SPSS version 26 for Windows (Orchard Road-Armonk, NY, United States). Management scenarios were compared in terms of efficacy and costs using a one-way analysis of variance (ANOVA), followed by Duncan's multiple range test, at a 95% confidence level.

To evaluate how changes in the main parameters affected the estimated efficacy of each management scenario, a local SA by one-parameter-at-a-time technique (OAT) (Czitrom, 1999) was performed. For this, the different plant cover conversion rates and number estimates of fire events were adjusted with changes of ±10 and ±50% from the original values (Ligmann-Zielinska, 2013) and the results with and without variation (reference results) were expressed in percentage of each state variable variation. The results are positive or negative, considering the response trend of the selected state variables, representing the percentages of change in the *Hakea sericea* abundance between simulations with and without variation in the parameter under study. The percentage absolute value represents the distance to the state variables' reference results. Implementation of the OAT

**TABLE 2 |** Management scenarios evaluated by model simulations.

| | | No control | Control options | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Cohort age | | | | | | | Follow-up |
| | | | Adult plants | | | | Young plants | | | |
| | | | Time (month) of execution after fire | | | | | | | |
| | | | 0 | 12 | 24 | 36 | 12 | 24 | 36 | |
| Scenarios | 1 | X | | | | | | | | |
| | 2 | | X | | | | | | | |
| | 3 | | | | | | X | | | |
| | 4 | | | | | | | X | | |
| | 5 | | | | | | | | X | |
| | 6 | | | | | | X | | | X |
| | 7 | | | | | | | X | | X |
| | 8 | | | X | | | X | | | |
| | 9 | | | | X | | | X | | |
| | 10 | | | | | X | | | X | |
| | 11 | | | X | | | X | | | X |
| | 12 | | | | X | | | X | | X |

technique in the current work required 14 model simulations for each management scenario.

## RESULTS

### Post-fire *Hakea sericea* Dynamics

The results of scenario 1 showed that unplanned fires altered the structure and composition of the vegetation, creating favorable conditions for the spread of *Hakea sericea*. At the beginning of the simulation period, *Hakea sericea* comprised 20% of the total vegetation of a sampling area and, after 25 simulations throughout 50 years, this proportion increased by 30% (**Table 3**). In the same period, herbaceous vegetation increased from 20 to 34%, at the expense of the other growth forms, whose relative abundance decreased. The occurrence of wildfires caused significant tree abundance loss, which almost disappeared within 50 post-fire years.

### Management Scenarios

The primary goal of any management plan for invasive species is to eliminate or reduce its population. The results yielded by the twelve management scenarios considered in this study (that differ in time between control efforts, cohort age, and inclusion of follow-up monitoring) were very heterogeneous. The majority of them did not produce desired outcomes (**Figure 2**).

The absence of control measures (scenario 1), as well as the low frequency of rounds of control (scenarios 2 and 5), had counterproductive effects since it allowed the IAS to increase in abundance (**Figure 2**). Removal of all plants 36 months after a fire event (scenario 10) caused a minimal decline in the relative abundance of *Hakea sericea*. In contrast, increasing the frequency of control efforts to 12 of 24 months after a fire event resulted in pronounced decreases in *Hakea sericea* abundance (**Figure 2**). Of the eight possible management strategies, half of them focused only on the control of young plants to prevent them from reaching reproductive maturity (scenarios 3, 4, 6, and 7). In comparison, the remaining four strategies also included control of adult plants (scenarios 8, 9, 11, and 12). When control efforts were only employed on young plants, the *Hakea sericea* abundance decreased by around 90%, stand about 3–4%, at the final of the simulation period. In turn, removing young and adult plants of *Hakea sericea* 12 or 24 months after a fire event and follow-up monitoring at 10 months after the first intervention (scenarios 11 and 12) significantly increased control efficacy, keeping its abundance below 0.5%.

**TABLE 3 |** Proportion of plant cover areas (abundance) at the beginning and at the end of the simulation period (50 years) under the occurrence of wildfires.

| Main variable | Abundance (%) | |
|---|---|---|
| | Initial | End |
| Herbs | 20 | 34.1 ± 16.2 |
| Shrubs | 40 | 35.3 ± 18.1 |
| Trees | 20 | 0.10 ± 0.12 |
| *Hakea sericea* | 20 | 25.6 ± 3.0 |

*At the end of the simulation period, values are means ± standard deviation.*

The estimated costs associated with each management scenario were also determined, and the results are shown in **Figure 3**. The economic costs of controlling *Hakea sericea* were highly variable, ranging from 650 €/ha to approximately 11,000 €/ha. Less expensive strategies included those referred in scenarios 2 (650 €/ha), 5 (3,100 €/ha), 4 and 7 (around 6,000 €/ha), but had limited controlling effects on *Hakea sericea*. In contrast, scenarios 11 and 12, which successfully brought the species down to abundances lower than 1%, presented control costs around 10,000 euros/ha. Similar economic costs ($P < 0.001$) were observed in scenarios 6, 8, and 9 but with less efficiency.

### Sensitivity Analysis

The results from the OAT SA (**Supplementary Appendix**) showed that, without control management, the parameters related to the temporal conversion rates of seedlings and young plants of *Hakea sericea* cause the main changes in the *Hakea sericea* abundance. In turn, the number estimates of fire events were the parameter with the primary influence on the outputs of almost all selected management scenarios.

## DISCUSSION

The dynamic model developed in this study allowed us to determine the best management strategy for minimizing the *Hakea sericea* abundance in the presence of stochastic unplanned fires and different management strategies. According to the current fire regime in the study area and in the absence of control measures aimed at *Hakea sericea*, the abundance of this IAS may increase in the coming decades. The large increase in relative abundance yielded by the model (about 30% more than the initial value) suggests that *Hakea sericea* will take advantage of fire disturbances. This finding can be partially explained by the extraordinary capacity of this species to release its seeds after a fire event. *Hakea sericea* possesses a large aerial seedbank composed of heat-resistant fruits accumulated throughout its lifetime (Brown and Whelan, 1999), resulting in high propagule pressure, typical of successful invaders (Simberloff, 2009). Fire occurrence generally results in the opening of fruits and the release of abundant seeds within a few days (personal observations), facilitating its establishment and invasion in the absence of canopy cover and/or ground layer vegetation. Moreover, the seeds can also be dispersed by the wind across a wide area, supporting a quick spread of the species (Richardson et al., 1987; EPPO, 2017). Similar IAS expansion after a fire has been documented for other invasive species, such as *Acacia* sp. (Souza-Alonso et al., 2017), *Pinus radiata* (Richardson and Brown, 1986), *Arundo donax* (Coffman et al., 2010), *Chromolaena odorata* (Dew et al., 2017), or *Cenchrus ciliaris* L. syn *Pennisetum ciliare* (L.) Link (Jarnevich et al., 2019). From an economic point of view, curbing such expansion will require more resources, thus increasing management costs. The increasing post-fire abundance of *Hakea sericea* will also have detrimental effects on the habitat composition and structure and

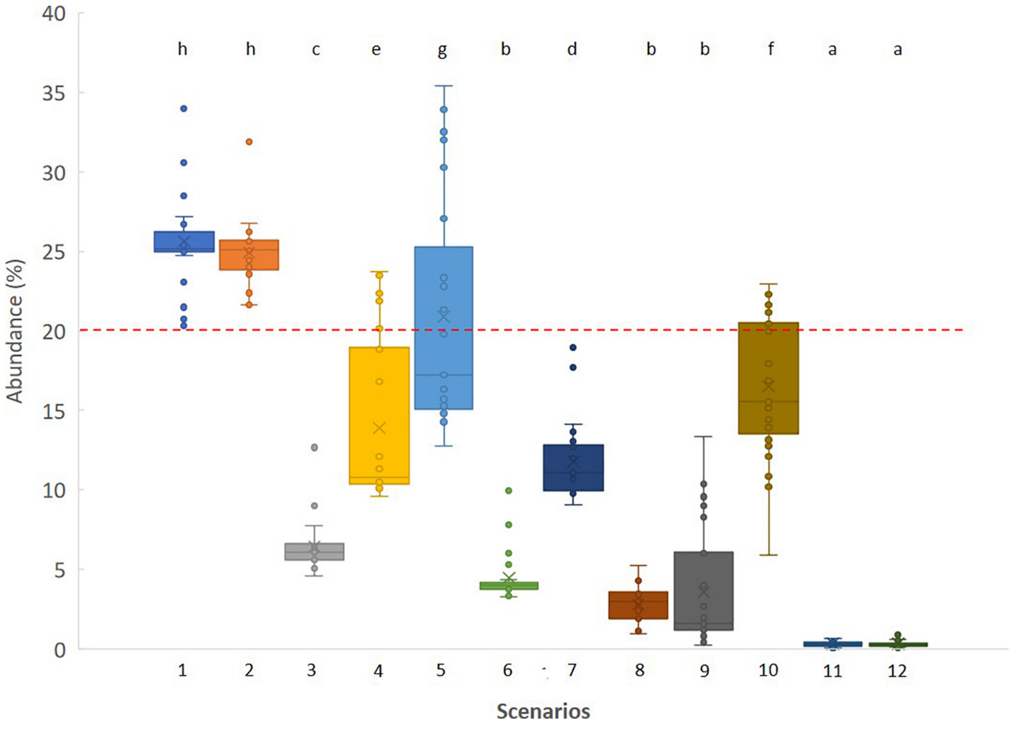

**FIGURE 2 |** Box and whisker plot of the relative abundance of *Hakea sericea* (%) after 50 independent simulations for the tested management scenarios. Different lowercase letters indicate significant differences ($P < 0.05$) between management scenarios. The dashed line at 20% indicates the initial abundance of *Hakea sericea*.

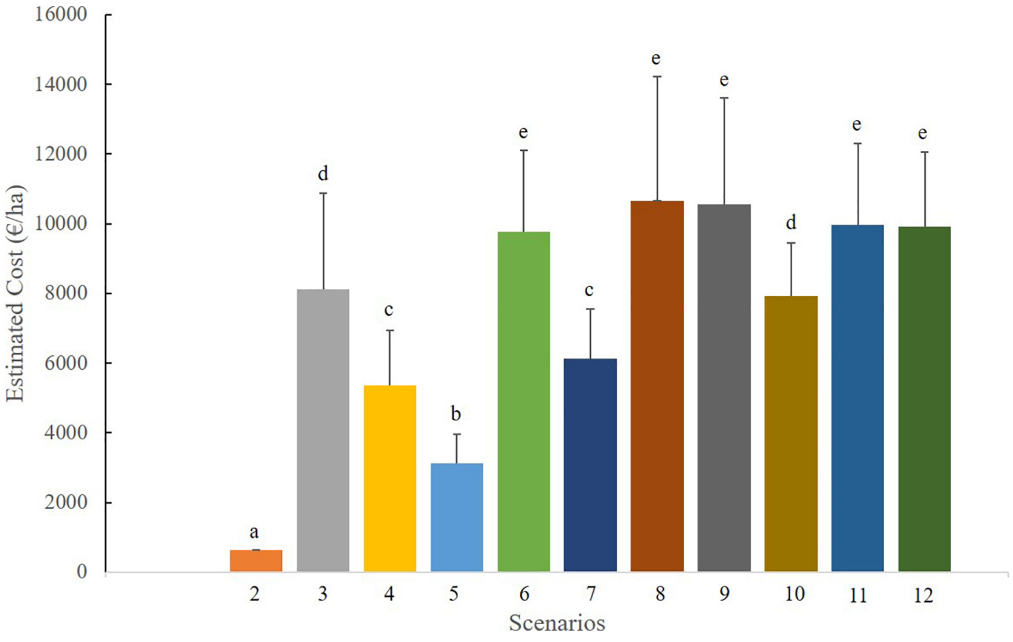

**FIGURE 3 |** Estimated costs (Euros/ha) of the tested management scenarios. Data are means ± standard deviation. Different lowercase letters indicate significant differences ($P < 0.05$) between management scenarios.

native plants' succession. In particular, our results highlighted a reduction of shrub vegetation and a poor representation of tree species after the simulation period, reflecting long recovery times for this lifeform. In addition, it creates favorable opportunities for *Hakea sericea* to establish and spread. The existence of undesired synergies between disturbances, such as fire and IAS, supports the importance of incorporating such stochastic effects when making management decisions.

In our study, none of the management strategies tested resulted in the total eradication of *Hakea sericea.* This fact is not surprising since complete eradication has been most successful only at early invasion stages or in small islands (Gherardi and Angiolini, 2007). For IAS that are widespread and abundant, as *Hakea sericea* is in Portugal, the management goal is generally to reduce their populations to a level that would substantially reduce their ecological impact (Prior et al., 2018; Nunes et al., 2020). The management strategies tested here yielded different outcomes depending upon the frequency of control efforts, and the age of the plants controlled. Our findings indicate that it is more effective to concentrate efforts on controlling the entire population rather than focusing only on a specific age cohort. Similarly, controlling only IAS at the early stages of development (young plants), although helpful in preventing the development of a seedbank and thus the establishment and spread of this IAS, was not effective in reducing the overall abundance of *Hakea sericea* at the end of the simulation period. As a consequence of poor treatment efficacy, future management resources will be needed. This goal is more likely to be achieved when the entire invasive population (young and adult plants) is controlled at short time intervals after a fire event.

Tang et al. (2010) concluded that longer periods between control efforts result in lower management efficacy, and our results corroborated this assertion. Our 50-years simulation showed that *Hakea sericea* abundance was significantly reduced with more frequent control efforts, i.e., at 12 to –24 month intervals. *Hakea sericea* generally produces viable seeds at 3-year-old. For this reason, it is reasonable to argue that differences in management efficiency between 1 or 2 and 3-year intervals should coincide with the maturity of plants, indicating that understanding the biology of the target IAS is vital for making the right management decisions. The same conclusion was drawn by Dew et al. (2017) when evaluated the seasonal efficacy of clearing *Chromolaena odorata*. These authors concluded that clearing efficacy was higher when executed during flowering season than during seed dispersal.

*Hakea sericea* quickly germinates after fires, emphasizing the importance of monitoring the growth of the new generation of plants. Our results indicate that when follow-up monitoring was included in the model, the control efficacy increased. This finding is in accordance with other studies (Lindenmayer et al., 2015; Dew et al., 2017), which have also shown that follow-up control is essential for maintaining the IAS at low levels. In our work, complete eradication of *Hakea sericea* is unlikely to occur, suggesting that additional follow-up treatments will be necessary. Generally, this operation would involve more resource allocation (Marais and Wannenburgh, 2008), which, in some situations, could be neglected, leading to the proliferation of the IAS with consequent unsuccessful results of management plans (Cheney et al., 2019). According to our results, when follow-up monitoring was done as a complement activity of post-fire control of *Hakea sericea*, the estimated costs tend to be slightly higher. However, it is also expected that the economic impact of successive follow-up treatments will dissipate over time (Marais and Wannenburgh, 2008).

Our simulation results clearly show that the economic resources' requirements for the control of *Hakea sericea* are directly dependent on the control efficacy of the management strategy. Therefore, it is crucial that resources are allocated effectively. Strategies focused on a single control event, although less expensive, were ineffective and could contribute to perpetuating *Hakea sericea* persistence in the study area. On the contrary, strategies focused on controlling burnt areas within 12 or 24 months after fire with follow-up operations declined significantly the abundance of the IAS, but required more resources. The SA demonstrated that an increment of fires in the study area was strongly associated with decreases in *Hakea sericea* abundance, highlighting the importance of adjusting the management strategies with the particularities of the study area. However, due to the fire-prone characteristics of this IAS, continuous follow-up monitoring will be necessary.

When analyzing the overall performance and costs of all scenarios, control efforts implemented 24 months after a fire event followed by subsequent monitoring seemed to be the most cost-effective way of managing *Hakea sericea*, since it yielded the same benefits as the annual control, at a similar cost.

## CONCLUSION

The SD framework developed as a part of this investigation can be adopted to support decision-making in IAS management since the simulation results reproduce realistically the dynamics of plant structural composition and are respond with credibility throughout contrasting scenarios. It provides crucial information about the temporal dynamics of the invaded population and the efficacy of several management strategies under the risk of unplanned fires. Complete eradication of *Hakea sericea* is unlikely within the next 50 years. Nonetheless, combining control efforts with the occurrence of fires can greatly improve the control efficacy of this problematic IAS. Control efforts performed at 2-years intervals followed by continuous monitoring can substantially reduce the abundance of this IAS, to very low levels, below 0.5%, compared to the current situation of 25% of abundance. Due to the simplicity of the framework, it can be easily adapted to other areas by adjusting its parameters to the peculiarities of each study site. Therefore, we highlight the interplay between model-based research and ecological monitoring to anticipate, with scientific credibility, the ecological responses associated with the control of IAS and test the effectiveness of ongoing management programs.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

MM and JC conceived and designed the simulation model. MM analysed the data and wrote the manuscript with contributions from all other authors. All authors have read and approved the submitted version of the manuscript.

## FUNDING

This work was supported by national funds by Portuguese Foundation for Science and Technology (FCT), under the project UIDB/04033/2020. MM is supported by a post-doctoral grant (SFRH/BPD/103604/2016) from FCT.

## ACKNOWLEDGMENTS

We would like to thank Paula Morais from Instituto de Conservação da Natureza e Florestas (ICNF) for providing field data for the work. We also grateful to Rita Bastos for her assistance with the sensitivity analysis and to three reviewers for their helpful comments.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.641686/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Ecology and Evolution

ORIGINAL RESEARCH
published: 13 April 2021
doi: 10.3389/fevo.2021.631214

# Non-indigenous and Invasive Freshwater Species on the Atlantic Islands of the Azores Archipelago

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Freshwater systems on remote oceanic islands are particularly vulnerable to biological invasions. The case of freshwater ecosystems in the Azores Archipelago is especially relevant considering the islands' youth and remoteness, and low natural connectivity. This study presents a review of the introduction and presence of non-indigenous freshwater species in the Azores, retrieved from various historical records, paleoenvironmental reconstructions, published records, and field data from two decades of the Water Framework Directive (WFD) monitoring programs. At least 132 non-indigenous freshwater species have successfully established in the Azores, belonging to several taxonomic groups: cyanobacteria (10), synurophytes (1), desmids (1), diatoms (20), plants (41), invertebrates (45), amphibia (2), and fishes (12). Intentional and accidental introductions have been occurring since the establishment of the first human settlers on the archipelago, impacting freshwater ecosystems. The first reported introductions in the Azores were intentional fish stocking in some lakes. Non-deliberate introductions have recently increased through transport-contaminants (51%) associated with the aquarium trade or agricultural products. In the Azores, the highest number of non-indigenous species occur on the largest and most populated island, São Miguel Island (116), followed by Flores (68). Plants constitute the most representative group of introduced species on all islands, but invertebrates, diatoms, and fishes are also well established on most islands. Among invertebrates, non-indigenous arthropods are the most well-established group on all islands except on the smallest Corvo Island. Many non-indigenous species will likely benefit from climate change and magnified by globalization that increases the probability of the movement of tropical and subtropical species to the Azores. Present trends in international trade, importations, and enhanced connectivity of the archipelago by increasing flights and shipping will probably promote the arrival of new species. Augmented connectivity among islands is likely to improve non-indigenous species dispersal within the archipelago as accidental transportation seems to be an essential pathway for non-indigenous freshwater species already present in the Azores.

**Keywords: non-indigenous species, invasive species, oceanic islands, freshwater ecosystems, Azores archipelago**

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***Specialty section:***
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *19 November 2020*
***Accepted:*** *19 March 2021*
***Published:*** *13 April 2021*

***Citation:***
*Costa AC, Balibrea A, Raposeiro PM, Santos S, Souto M and Gonçalves V (2021) Non-indigenous and Invasive Freshwater Species on the Atlantic Islands of the Azores Archipelago. Front. Ecol. Evol. 9:631214. doi: 10.3389/fevo.2021.631214*

# INTRODUCTION

Human activities have for centuries promoted the transport of multiple species across huge biogeographical barriers (Gippoliti and Amori, 2006; Clavero and Villero, 2014), and this has accelerated exponentially since the beginning of the twentieth century (Vander Zanden and Olden, 2008; Clavero and Villero, 2014). The increasing introduction rate and spread of non-indigenous species are among the most critical threats to biodiversity and ecosystem services (Vitousek et al., 1996; Sala et al., 2000). Even though biological introductions may cause no detectable or long-term impact (Williamson and Fitter, 1996), some non-indigenous species, especially the invasive ones, usually display high spreading rates in the introduced environment causing significant impacts, from the alteration of habitats, replacement of native species through predation and competition, the transmission of diseases, and effects on human health and economy (Pimentel et al., 2000; Cowie, 2001; Blackburn et al., 2014; Gallardo et al., 2016). Identifying these invasive species is crucial for prioritizing management efforts (Ricciardi and Atkinson, 2004). Their control is often more practical, cheaper, and more effective soon after detection, and for some, eradication might be possible (Simberloff, 2009; Simberloff et al., 2011).

Freshwater ecosystems provide many benefits to humankind, and the induced changes (e.g., by invasive species) in the goods and services they provide can have a substantial impact on the human well-fare (Gherardi, 2007). Nevertheless, freshwater ecosystems are among the systems most heavily affected by non-indigenous species introduction (Amat-Trigo et al., 2019). The degradation of these ecosystems has caused non-indigenous species to establish and become invasive more easily than in other environments (Sala et al., 2000). Many of these species are effective colonizers that exhibit rapid adaptation in degraded aquatic or riparian habitats characterized by communities with a reduced competition that facilitate such adaptation (Conlan, 1994; MacNeil et al., 2004). The disturbance is commonly assumed to release resources and provide opportunities for invaders (Lozon and MacIsaac, 1997; Davis et al., 2000). Moreover, some invaders that inhabit human-disturbed environments in their native range might have a greater ability to adapt to human-disturbed environments than resident species (Niemelä and Mattson, 1996), giving them the advantages for successful invasion (Shea and Chesson, 2002). Also, systems already impaired by non-indigenous species are susceptible to additional disturbance, as non-indigenous species often facilitate each other's establishment and/or their continued existence, increasing the likelihood and the magnitude of the global environmental impact inflicted by biological invasions (Gherardi, 2007).

Freshwater ecosystems are highly vulnerable to anthropogenic and natural introductions of species and their subsequent spread (Gherardi et al., 2008b; Strayer, 2010; Havel et al., 2015; Tricarico et al., 2016). The effects of intensive human usage and hydromorphological changes to aquatic systems, such as the impoundment of rivers (e.g., dams and weirs, water removal), water quality deterioration (e.g., pollution, eutrophication, acidification), habitat degradation and fragmentation (e.g., channelization and land-use change), resources overexploitation (Ricciardi, 2001), as well as climate change (Rahel and Olden, 2008) have been enhancing the dispersal of aquatic organisms (Gherardi et al., 2008a; Oscoz et al., 2010). Both anthropogenic habitat disturbance and the introduction of non-indigenous species are today the main drivers of biodiversity change in these ecosystems (Didham et al., 2005).

Aquatic non-indigenous organisms encompass a great variety of taxonomic groups, including microorganisms, plants, sponges, cnidaria, flatworms, molluscs, crustaceans, fishes, birds, amphibians, reptiles, and mammals (see García-Berthou et al., 2007; Nunes et al., 2015). However, most of the freshwater non-indigenous species that have been deliberately introduced are fishes and plants (Pimentel et al., 2005). Most freshwater species introduced in Europe are native to northern America and arrived in France, United Kingdom, or Germany, and spread from there to southern Europe, e.g., Portugal and Spain (García-Berthou et al., 2005; Boix et al., 2007). For example, the pumpkinseed [*Lepomis gibbosus* (Linnaeus, 1758)] and mosquito fishes (*Gambusia* spp.), which are American fish species (García-Berthou et al., 2005), are very well-established in Europe. One of the major pathways of freshwater species introduction is aquarium species trade, which accounts for 21% of world freshwater fish introductions (Andrews, 1990; Gozlan, 2008; Maceda-Veiga, 2013; Ishikawa and Tachihara, 2014; Nunes et al., 2015) and secondarily, aquaculture (Gherardi et al., 2008b; Nunes et al., 2015). In Europe, introductions related to ornamental trade were mostly freshwater plants (Keller et al., 2011). More than 400 non-indigenous aquatic and semi-aquatic species of plants are currently traded in Europe, and many are considered potentially invasive in European freshwater habitats (Hussner, 2012). Most of those introductions arrived in Portugal via Spain (García-Berthou et al., 2005). Nonetheless, some accidental freshwater introductions in Portugal seem to be related to escapes from cultivation sites and disseminated along watercourses. For example, red swamp crayfish [*Procambarus clarkii* (Girard, 1852)] might have arrived in Portugal from escapes in aquaculture facilities in Spain to the Guadiana river (Gherardi et al., 2002). Most imports to the Azores came from mainland Portugal, through commercial shipping and flights to the archipelago, mainly arriving on São Miguel island (Calado et al., 2014).

Oceanic islands are highly vulnerable to invasive species due to the low levels of diversity, lack of competitors and predators, and the resulting availability of ecological niches (Simberloff, 1995; Sax, 2001; Covich, 2010), offered by the existence of non-saturated assemblages (see Cornell and Lawton, 1992). Moreover, species on islands have small populations with restricted genetic diversity, and this, coupled with limited habitat availability, increases their vulnerability to environmental stresses, including the introduction of non-indigenous species (Russell et al., 2017). Therefore, insular freshwaters are among the most vulnerable ecosystems to invasive species (Raposeiro et al., 2009; Costa et al., 2013; Raposeiro et al., 2017).

The geographic setting of oceanic islands and the Azores archipelago presents a considerable distance across open ocean from a continental source which hampers natural dispersal and species colonization (Bilton et al., 2001; MacArthur and Wilson, 2001). In the Azores, isolation, small island area, young geology, and numerous volcanic eruptions have acted as strong biogeographical filters, resulting in low diversity of native biotic assemblages and a high percentage of freshwater faunal endemism (11% – Raposeiro et al., 2012), when compared to continental systems (Hughes, 2006). Since the establishment of the first human settlements in the islands (official Portuguese colonization in 1432 CE), pressure on the ecosystems has increased exponentially, mainly associated with landscape disturbance due to changes in land use which have resulted in habitat degradation and fragmentation and the introduction of non-indigenous species (Triantis et al., 2010; Connor et al., 2012; Ferreira et al., 2017; Raposeiro et al., 2017; Rull et al., 2017; Vázquez-Loureiro et al., 2019).

The consequences of introduced species have been an object of discussion in several studies (Mooney and Hobbs, 2000; Ricciardi, 2003; Bohlen et al., 2004), including in island ecosystems (Reaser et al., 2007), but the introduction of non-indigenous species and the impact of these in the highly vulnerable insular freshwater systems of the Azores has not yet been thoroughly addressed (Raposeiro et al., 2011a). The inventory of non-indigenous species in the archipelago and knowledge of their introduction pathways, establishment, and spread potential is vital to predicting threats to freshwater native biodiversity and to developing management strategies for local freshwater environments (Raposeiro et al., 2009; Lamelas-López et al., 2017).

This paper updates the knowledge on all non-indigenous freshwater species in the Azores through a broad taxonomic approach from unicellular phytoplankton to vertebrates, presenting what is known of their introduction history, pathways, origins, and ecological and socioeconomic impacts in the archipelago. Furthermore, species' invasion risk and management actions are discussed.

## Study Area

The Azores archipelago comprises nine islands of volcanic origin located in the middle of the northern Atlantic Ocean (**Figure 1**), between the latitudes, 36° 45′ N and 39° 43′ N and the longitudes 24° 45′ W and 31° 17′ W, about 1500 km off mainland Portugal (Santos et al., 2004). This archipelago is particularly rich in freshwater ecosystems due to volcanic geomorphology and climatic conditions that prevail in altitude with a total land surface area of 2,325 km$^2$ drainage corresponding to 763 hydrographic basins (Cruz and Soares, 2018) and many small (maximum length of 29 km) streams (Raposeiro et al., 2013). Following its discovery in 1439, extensive deforestation began in coastal areas of hydrographic basins to establish human settlements that extended in the early 20th century. The intensification of agricultural activity, the excessive application of agrochemicals, building roads, effluent discharge of livestock farms, and the release or non-deliberate introduction of non-indigenous species are some of the main factors currently affecting the water quality and ecosystems services provided by these islands' freshwater habitats (Pereira et al., 2014; Raposeiro et al., 2014).

# MATERIALS AND METHODS

The GBIF Backbone Taxonomy was used to harmonize the taxonomy of the studied groups (GBIF Secretariat, 2019). For the present paper, freshwater species were considered those organisms that complete their entire life cycle in the water [e.g., diatoms (Bacillariophyceae), molluscs (Mollusca), crustacea (Crustacea), fishes (Actinopterygii), cyanobacteria (Cyanobacteria), synurophytes (Synurophyceae) and desmids (Desmidiaceae)], animals that live in aquatic habitats at some point in their life cycle [e.g., some arthropods (Arthropoda), amphibia (Amphibia) and floating, submerged and helophyte plants (Tracheophyta) (Thorp et al., 2014; Bellinger and Sigee, 2015; Dodds and Whiles, 2019)].

Indigenous and non-indigenous species were categorized following criteria in Essl et al. (2018); indigenous species from the Azores were considered those not related to human-modified habitats or activities, occurring in native habitats, and also present in other Macaronesian archipelagos. Species that have human-mediated movement across biogeographic barriers from their presumed native/indigenous origin are considered non-indigenous. In the Azores, this biogeographic filter is evident due to its distance to the mainland (around 1,500 km) and the Atlantic Ocean's physical barrier. Possible pathway analysis and their absence from pristine habitats had to be put into the equation to establish the species as non-indigenous. The review of the introduction and presence of non-indigenous freshwater species in the Azores considered all available records to date (see **Supplementary Material 1**), retrieved from various sources as historical and contemporary records, paleoenvironmental reconstructions, and field data from WFD monitoring programs in place for the last two decades.

According to the Convention on Biological Diversity (Convention on Biological Diversity, 2014), each species' introduction pathway was determined, distinguishing intentional and/or non-deliberate introductions. The species introduction mechanism as importation, transport vector or dispersal corridor association and natural spread from a previously invaded region were considered and addressed to one of five groups (as the CBD 6th pathway is not locally applicable): Release – an intentional introduction for human use in the natural environment (e.g., biological control, fishery, hunting); Escape – the movement of non-indigenous species from confinement (e.g., aquaria, botanic gardens, zoos) to the wild; Transport-contaminants – the non-deliberate movement of organisms transferred through intentional trade (e.g., pets, food diseases, seeds); Transport-stowaway – the movement of organisms attached to transporting vessels and associated equipment and media (e.g., ballast water, boats, fishing equipment's); and Unaided – secondary natural dispersal of organisms that have been introduced elsewhere through pathways 1–5.

Some of the non-indigenous species established in Azorean freshwater habitats were categorized as invasive species following

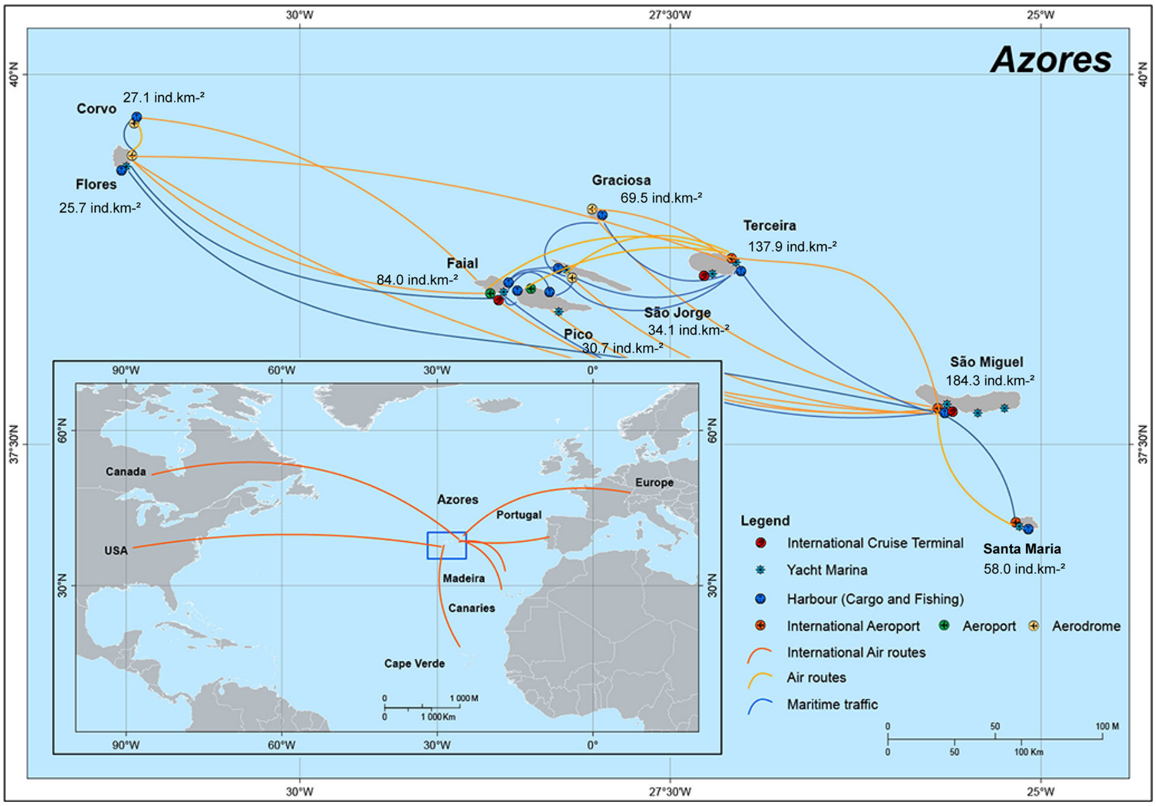

**FIGURE 1 |** Location of Azores Archipelago on North Atlantic Ocean. Principal routes of entry for non-indigenous species onto the islands are presented.

the definitions of the International Union for Conservation of Nature (IUCN), US National Aquatic Invasive Species Act (NAISA), and the Convention on Biological Diversity (CBD). Thus, invasive species are herein considered as non-indigenous species whose introduction and/or spread outside their natural past or present distribution has led to their establishment and spread in an ecosystem or a natural or semi-natural habitat, being an agent of a change and threat to native biodiversity, economy, environment, human health, recreation, or public welfare.

We used information on the invasive potential of non-indigenous species from Delivering Alien Invasive Species Inventories for Europe (DAISIE), European Alien Species Information Network (EASIN), Global Invasive Species Database (GISD) databases to established them as invasive or non-invasive species. Moreover, field and published data about their spread capacity and proliferation, feeding habits, predation and competition behavior, and preferred habitat were also used as complementary information to define the invasive status of those species and determine their possible negative impact on archipelago's ecosystems.

## Literature Review and Historical Records

Historical data can provide important insight to understand biological invasions (Willis and Birks, 2006). The assignment of introduced status to the Azores islands species has also been inferred using historical records, including those from the first 17th century chronicles and reports from naturalist and scientific expeditions of the 19th century. Data on species were extracted from these sources and completed with information retrieved from different peer-reviewed published papers, gray literature, reports, and studies carried out in Azorean freshwater systems. Species introductions associated with developing human economic activities in the archipelago and clear evidence for direct human mediation were considered deliberate introductions, releases, or escapes. The more obvious cases are related to agricultural and ornamental plants introductions (Williamson, 1996; Heywood, 2012). Ornamental plants and fishes deliberately introduced in Azorean lakes for leisure, stocking, and fishing purposes, were the most prevalent, especially during the late 18th century (see Raposeiro et al., 2017 and references associated). Species that might have arrived in the archipelago due to indirect consequences of human actions, such as accidental transport related to habitat modification, eliminating indigenous competitors or predators, were also considered. The date of introduction was considered the date of the first record reported in the literature or the publication date when the introduction date was not mentioned.

## Paleolimnology Records

Long-term data are essential to assign indigenous and non-indigenous species status and detect the exact date of a species introduction (Moser, 2004; Willis and Birks, 2006; Smol, 2014).

To overcome the scarcity and incomplete historical records in the Azorean islands, environmental reconstructions based on long continuous sequences of natural archives (sediments older than 1450 AD) were used to establish species presence in pristine conditions before human settlement. Data from recent paleolimnological studies in the Azores (São Miguel, Pico, and Flores islands) that have been focused on climatic and environmental reconstruction using biological proxies, e.g., pollen, plant remains, frustules of diatoms, water fleas, and chironomids (van Leeuwen et al., 2005; Connor et al., 2012; Raposeiro et al., 2017; Rull et al., 2017; Vázquez-Loureiro et al., 2019) were considered for this new approach. For example, van Leeuwen et al. (2005) unequivocally confirm the status of *Selaginella kraussiana* (Kunze) A. Braun as native on the Azores islands. As a consequence, species only collected in sediments post-1450 AD were considered non-indigenous. Despite the usefulness of paleolimnological records as an essential tool to understand native biota, the preservation of organisms in the sediments depends on the type of organism and the environmental conditions at the time of sedimentation (Heiri et al., 2009; Smol, 2014). So, the absence of species in the paleolimnological registry does not, *per se*, qualifies them as non-native. To overcome this, paleolimnological data was only used to access the status of diatoms, which are well preserved in lake sediments. Only the species that were consistently present in the sediment after human arrival was considered non-native, while all species that occurred sporadically were excluded.

## Field Records

Field data from WFD monitoring programs carried out between 2000 and 2020 covering several water masses on all islands were also used to compile plants, macroinvertebrates, microalgae, and cyanobacteria data. Due to the different distribution of water masses among islands, the number of sampling events is not the same for every island: 4 on Faial, 12 on Terceira, 55 on Corvo, 60 on Santa Maria, 212 on Pico, 421 on Flores, and 1101 on São Miguel. Records of recent fish releases on different islands were obtained by net-fishing field data for various projects (authors' unpublished data).

# RESULTS AND DISCUSSION

## Taxonomic Groups and Area of Origin of Non-indigenous Species

At least 132 non-indigenous species are established in Azorean freshwater ecosystems (see **Supplementary Material 1**), belonging to different taxonomic groups (**Table 1**). Plants (41), invertebrates (45), diatoms (20), and fishes (12) presented the highest number of records, followed by cyanobacteria (10), amphibia (2), synurophytes (1), and desmids (1). Plants and arthropods are the most representative contributing with 31.1 and 19.7%, respectively, of the total number of non-indigenous species, followed by diatoms (15.2%) and fishes (9.1%) (**Table 1**). Freshwater non-indigenous fauna represents a total of 59 species, of which 23.7% are vertebrates. Invasive species account for 51.5% (68 species) of Azorean non-indigenous freshwater species (**Table 1**). All amphibians and fishes, except for the native eel *Anguilla anguilla* (Linnaeus, 1758) are considered invasive species in the archipelago. Plants and mollusks also presented a higher percentage of invasive species (82.9 and 66.7%, respectively) than the other groups (**Table 1**). More than 60% of vascular plant flora in the terrestrial realm, all the mammals (except the Azorean bat) and reptiles are reported to be non-indigenous (Silva et al., 2008). As for marine species, the number of non-indigenous species reported for the Azores by Tsiamis et al. (2019) is 53 species, most of them macroalgae and invertebrates.

**TABLE 1 |** Number and percentage (in brackets) of freshwater non-indigenous (NIS) and invasive species in different taxonomic groups.

| Group | Non-indigenous species (% of total NIS) | Invasive species (% for the group) |
|---|---|---|
| Cyanobacteria | 10 (7.6%) | 5 (50.0%) |
| Synurophyceae | 1 (0.8%) | 0 (0.0% |
| Desmidiaceae | 1 (0.8%) | 0 (0.0%) |
| Bacillariophyceae | 20 (15.2%) | 1 (5.0%) |
| Tracheophyta | 41 (31.1%) | 34 (82.9%) |
| Platyhelminthes | 4 (3.0%) | 2 (50.0%) |
| Nematomorpha | 1 (0.8%) | 0 (0.0%) |
| Cnidaria | 2 (1.5%) | 1 (50.0%) |
| Annelida | 6 (4.5%) | 2 (33.3%) |
| Mollusca | 6 (4.5%) | 4 (66.7%) |
| Arthropoda | 26 (19.7%) | 5 (19.2%) |
| Amphibia | 2 (1.5%) | 2 (100%) |
| Actinopterygii | 12 (9.1%) | 12 (100%) |
| Total | 132 | 68 (51.5%) |

The Azorean non-indigenous species are predominantly Palearctic (mostly invertebrates, amphibians, and fishes) and unknown (mostly cyanobacteria, diatoms, and desmids) in origin. Neotropic and Nearctic regions are also represented in non-indigenous species in the Azores in plants, Platyhelminthes, Mollusca, and fishes (**Figure 2**). According to historical records, some non-indigenous species might have been transported inadvertently by the Portuguese during the initial human colonization of the islands (archeophytes, i.e., introduced before 1500; Mandak and Pysek, 1998). However, the latest introductions in the late 19th century were deliberate releases with economic purposes for fish stocking or as ornamental plants for gardens. The first record of a species introduction is the goldfish [*Carassius auratus* (Linnaeus, 1758)] in 1792 (Ribeiro et al., 2009) (**Figure 3**), which is also the first record for freshwater species' introduction in Portugal (Kottelat and Freyhof, 2007). It is often difficult to be sure whether humans have introduced insular species or whether they are, in fact, native. Paleolimnology records helped solve this question, especially in well-preserved groups as diatoms, plants, and some invertebrates. In the Azores, the significant impacts revealed by the sedimentary record are concurrent with the Portuguese colonization, providing evidence for strong anthropogenic landscape transformations leading to eutrophication (Connor et al., 2012; Raposeiro et al., 2017; Rull et al., 2017). Eighteen diatom taxa only appear in the

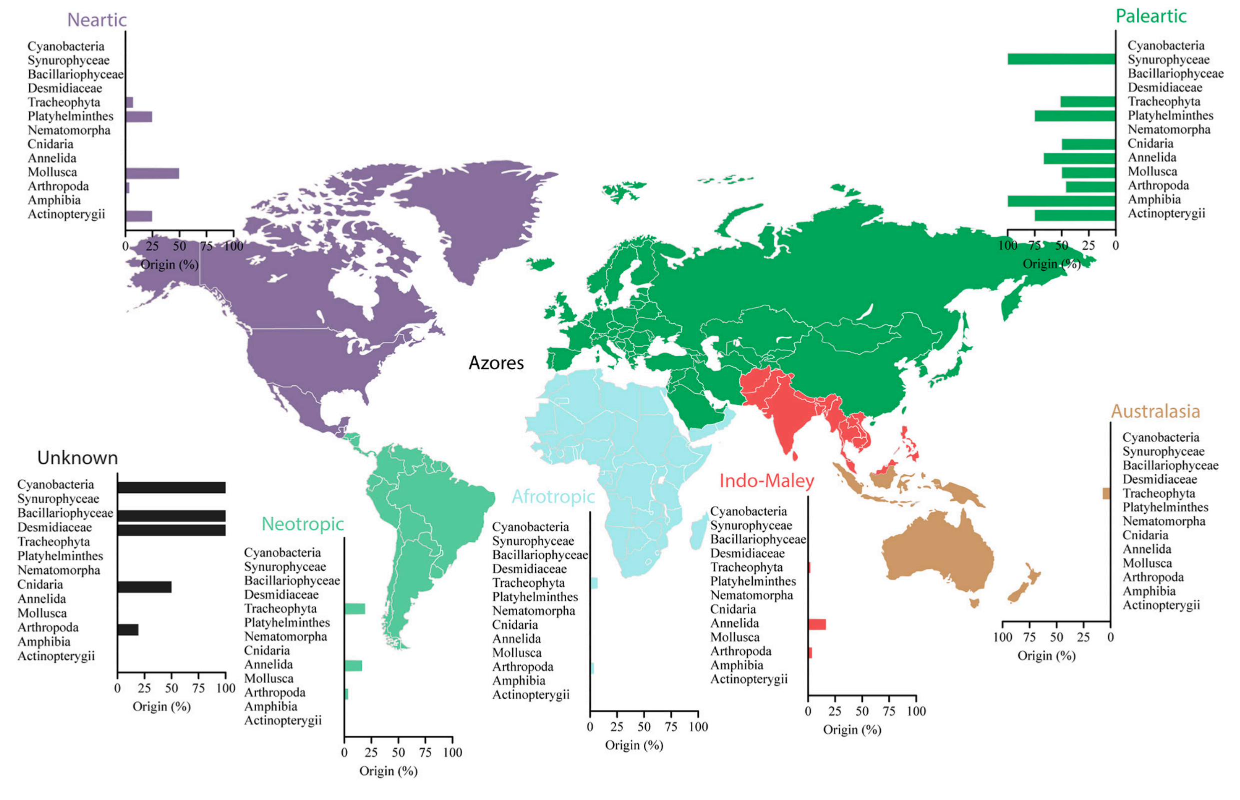

**FIGURE 2 |** Percentage of freshwater non-indigenous species from different native distribution areas recorded in the Azores.

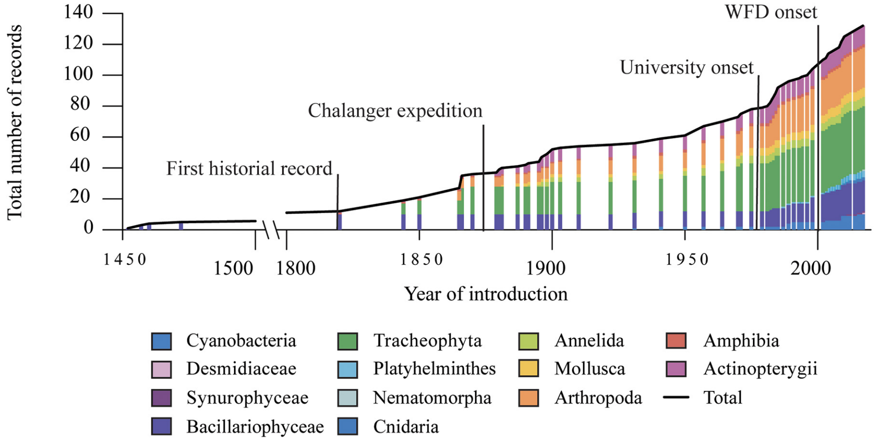

**FIGURE 3 |** Records of non-indigenous species introduced in Azorean freshwaters from 1450 to 2020 over 50 years intervals.

records after the Portuguese settlement providing evidence that these species are non-indigenous [e.g., *Gomphonema minutum* (C.Agardh) C.Agardh, *Fragilaria crotonensis* Kitton, *Asterionella formosa* Hassall].

Fishes and plants represented the groups for which first introductions have been reported (**Figure 3**) since the 19th century. The onset of the 19th-century naturalist expeditions to the archipelago, e.g., Challenger, encompass a growing number of studies on freshwater biota, increasing the number of non-indigenous species recorded. The number rose again in the second half of the 20th century when more studies on the lakes were carried out (**Figure 3**) due to the local university's establishment and when the international airport in São Miguel started its regular operation. The number of freshwater species reported vastly increased in the last two decades, with new records of non-indigenous species resulting from the extensive sampling efforts in freshwater ecosystems due to WFD monitoring programs' implementation. During this period, the records for cyanobacteria also started to become relevant.

## Non-indigenous Species Distribution in the Archipelago

In the Azores archipelago, the highest number of non-indigenous species occurs on São Miguel Island (116), followed by Flores (68), Pico (65), and Terceira (56) (**Figure 4**). Although plants are the most represented group of introduced species on all islands, from 31.0% in São Miguel to 69.0% in São Jorge, invertebrates, diatoms, and fishes are also well established in São Miguel, Santa Maria, Pico, Flores, and Corvo islands. Non-indigenous species do not present a clear distribution pattern linked to human factors such as population density and/or the number of ports. Taxonomic distribution differences among islands are also not apparent (**Figure 4**). These results seem to be related to the sampling efforts associated with WFD monitoring programs during the last two decades in several islands (see field records in the section "Materials and Methods"). However, Terceira, Graciosa, São Jorge, and Faial showed higher percentages of non-indigenous plants (60.7, 63.0, 69.0, and 58.5%, respectively) than the rest of the groups (**Figure 4**). São Miguel and Flores are also the islands with higher habitat availability for freshwater species. Therefore, a higher number of successful introductions can be expectable as mentioned by several authors (Raposeiro et al., 2011a, 2013; Gonçalves et al., 2015). Habitat availability could also explain the distribution of specific groups, such as cyanobacteria and diatoms. Most non-indigenous cyanobacteria and several diatoms are planktonic and therefore restricted to islands with lakes. A similar situation is observed in the fish group, where most of the species were introduced in the lakes of São Miguel island during several decades, from where they were more recently spread to the rest of the archipelago.

Among invertebrates, non-indigenous arthropods are the most well-established group on all islands (from 18.5% in Pico to 26% in Graciosa) except for Corvo where arthropods only represent 4.2% of introductions (**Figure 4**). The poor records on this island may be related to a lower number of studies, limiting the data available for this group.

Most invasive species are restricted to just one archipelago island (**Figure 5**), mainly on São Miguel, Flores, and Pico islands (Raposeiro et al., 2011b; Gonçalves et al., 2015). Half of invasive fish and amphibia and all invasive Annelida and Platyhelminthes are only present on São Miguel island (**Figure 5**). Being the largest and most populated island, São Miguel has greater connectivity with mainland Portugal, Europe, and America (**Figure 1**), becoming the main entrance of invasive species in the archipelago. This island is the main entry point of traded goods in the archipelago, functioning as a distribution hub for other islands. São Miguel is also the island with the most significant contribution to the archipelagos economy reflected in the economic indicators as importation/exportation of agriculture and fisheries' products or tourism (FMS, 2013). The increased human pressure in São Miguel island leads to a higher habitat degradation posing more opportunities for opportunistic non-indigenous species to establish (Silva and Smith, 2004; Cardoso et al., 2013). This island has also hosted a higher number of studies (Johansson, 1976; Borges et al., 2010), and it has thus been more intensively sampled, which might also be reflected in the present results. Invasive plants, fishes, and arthropods present a larger dispersion in Azorean freshwater habitats, with several species established in eight islands (**Figure 5**). Amphibians occur on nine islands; however, this extended distribution is represented only by the green frog, *Pelophylax perezi* (López-Seoane, 1885). Other invasive species, Mollusca, Cnidaria, and Cyanobacteria, are scattered on three or four islands (**Figure 5**).

## Principal Introduction Pathways

Most non-indigenous species were probably accidentally introduced to the Azores archipelago, mainly inadvertently

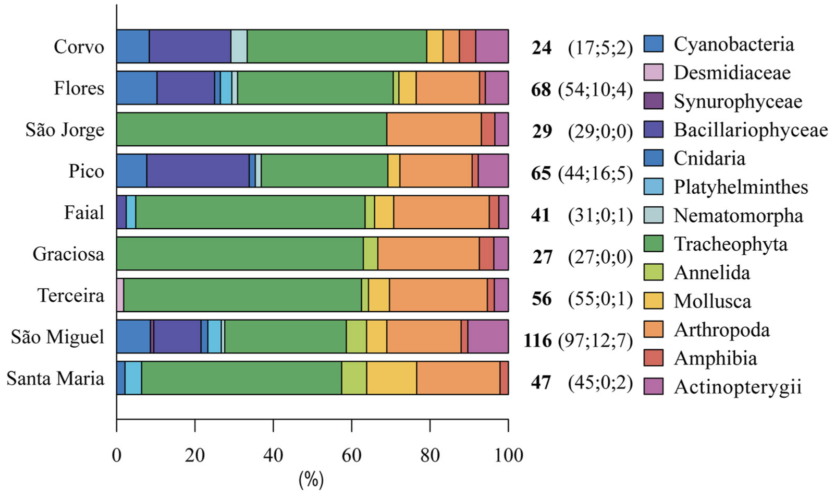

**FIGURE 4 |** Percentage and **total number** (number of literature records; the number of paleolimnology records; field records) of non-indigenous species included in different taxonomic groups registered in freshwaters habitats for each Azorean island.

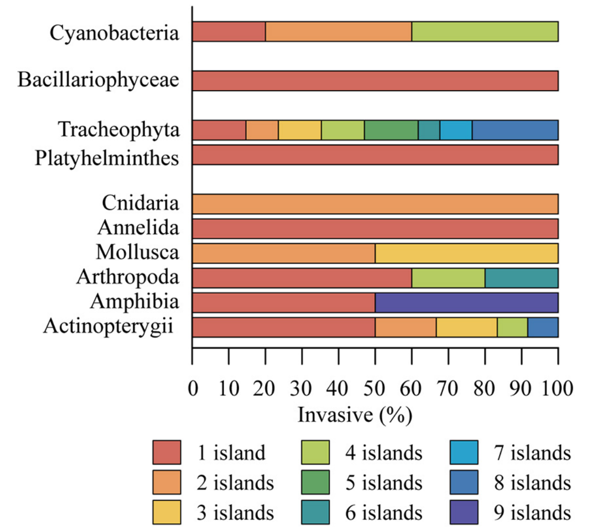

**FIGURE 5 |** Percentage of invasive species of the different taxonomic groups present in one to nine islands. Synurophytes, Desmids, and Nematomorpha were not included due to the absence of invasive species in these groups.

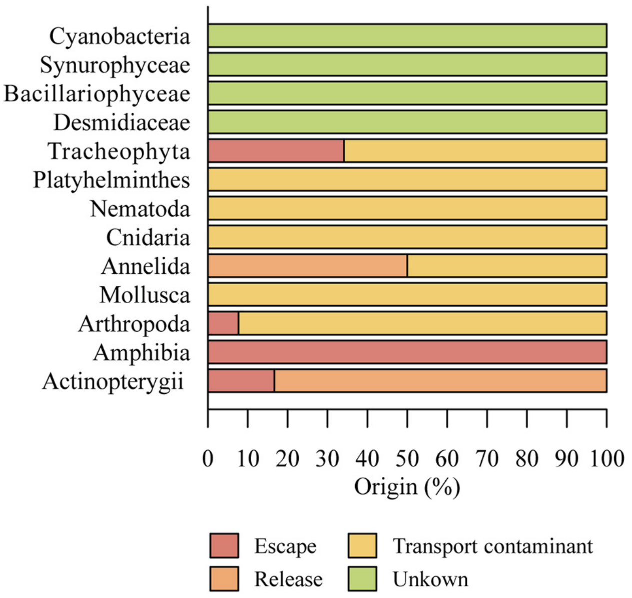

**FIGURE 6 |** Main introduction pathways of non-indigenous species in the Azores.

by the aquarium trade, attached to plants, as eggs, or in resistant life stages ("Transport-contaminant" pathway), such as Mollusca [e.g., *Ferrissia fragilis* (Tryon, 1863), *Physella acuta* (Draparnaud, 1805) and *Galba truncatula* (O. F. Müller 1774)], Platyhelminthes (e.g., *Dugesia* sp.) and Cnidaria (e.g., *Hydra vulgaris* Pallas, 1766 and *Craspedacusta sowerbii* Lankester, 1880). Arthropods may have been accidentally transported with agricultural products, including food, or packing material, including Coleoptera (mainly species of Hydrophilidae) and Diptera. Agricultural trade is also involved in the introduction of associated pests, such as the turfgrass pest *Tipula oleracea* Linnaeus, 1758 ("Transport-contaminant" pathway) (**Figure 6**).

Ornamental trade was inadvertently involved in the release and spread of many aquatic plant species that might have been imported for use in private or botanical gardens, an important leisure activity of the 19th century in islands as São Miguel, Terceira, and Faial. These aquatic species such as *Zantedeschia aethiopica* (L.) Spreng, *Nymphaea alba* L. or *Eichhornia crassipes* Mart. (Solms) escaped, invading large extensions of freshwater habitats ("Escape" pathway) (**Figure 6**). Another example of species that might have been introduced via domestic aquarium trade, probably by releases in private tanks and later escapes, eventually ending up in native aquatic ecosystems, is the crayfish, *P. clarkii*.

Some species might have been transported accidentally on fishing equipment, airplane wheels, and shoes, among others ("Transport-stowaway" pathway), but this introduction pathway is not easy to determine. The introduction pathway for most non-indigenous species in Azorean freshwaters was categorized as transport-contaminant movement (51.0%) (**Figure 6**). In addition to these accidental introductions, other species have been intentionally introduced. Since the late 18th century, intentional release is the main introduction pathway for fishes such as *Cyprinus carpio* Linnaeus, 1758, *Perca fluviatilis* Linnaeus, 1758, and *Esox lucius* Linnaeus, 1758 among others, attributed to angling activities in Azorean lakes. A well-known example of deliberate introduction is the release of *Gambusia holbroki* Girard, 1859 for biological control of mosquito populations on the mainland and Cabo Verde, another Macaronesian archipelago (Cabral and Marques, 1999; Salgueiro et al., 2019). However, in the Azores, the introduction of *G. holbrooki* was probably related to escapes from private aquaria. After the last known *Rutilus rutilus* (Linnaeus, 1758) introduction in 1983 in Lake Azul (Raposeiro et al., 2017), deliberate releases into the wild stopped. Annelids introduction pathway seems to be escapes related to leeches for medical purposes in the late 19th century (Chaves, 1949). Nevertheless, releases (10.0%) and escapes (15%) are less significant introduction pathways for non-indigenous freshwater species in the Azores (**Figure 6**) when compared with Transport/contamination pathway.

As for Cyanobacteria, Synurophytes, Diatoms, and Desmids, the introduction pathways remain uncertain. Natural dispersion of freshwater microalgae and cyanobacteria is mainly related to transportation by migratory waterbirds (Proctor, 1959) or other organisms (e.g., insects, mammals) (Kristiansen, 1996; Coste and Ector, 2000), water or wind (Sharma et al., 2007). Especially on remote oceanic islands, like the Azores, migratory waterbirds, which can transport microorganisms to very distant places, are probably the most important natural vectors of microalgae and cyanobacteria (Guerne, 1887; Proctor, 1959). Although the presence of non-native microalgae and cyanobacteria could be explained by the interplay of these natural dispersion mechanisms with ecological changes in target areas that enable their establishment (Cellamare et al., 2010), human facilitated transport (e.g., introduction of non-indigenous aquatic plants and fishes) is the most probable pathway of their invasion into new areas across the globe (Cellamare et al., 2010; Kaštovský et al., 2010) and in the Azores.

The international airport in Ponta Delgada (São Miguel) was inaugurated in 1969, and in the following three decades, escapes and transport/contaminant pathways were more critical than introductions. After 2000, escapes became a less clear pathway, which might be related to law enforcement related to living imports. Other pathways such as escapes and transport/contaminant, the first related to ornamental and aquariology trade, and the second with agriculture/livestock importations, are still very relevant and primary pathway in recent years (**Supplementary Material 1**).

## Ecological and Economic Impacts

It is widely accepted that invasive species affect biodiversity and ecosystems and have socio-economic impacts (Pimentel et al., 2000). Traditionally, ecologists and invasion biologists have solely focused on the impacts of invasive species on biodiversity and ecosystem functions (Sala et al., 2000; Courchamp et al., 2017). However, the adoption of ecosystem services where biodiversity is considered within the context of human well-being has emphasized the need to consider people's health, wildlife, and domestic animals (Pejchar and Mooney, 2009). Most of the time, it is challenging to quantify long-term ecological impacts because freshwater ecosystems adjust and evolve in response to invasions. However herein we present some examples on ecological and economical effects of species introductions with special emphasis in the Azores.

The introduction of predators (fishes) on the Azores lakes had marked effects on the trophic dynamics and ecological state of formerly fishless lakes. Particularly evident was the negative effect of *C. auratus* and *C. carpio* both of which have altered the trophic dynamics and the relative importance of benthic and pelagic production, contributing to the increase of turbidity, leading to a change in oxygen conditions of the hypolimnion of the deep lakes, and increasing the eutrophication processes in the lakes (Skov et al., 2010; Raposeiro et al., 2017). Additionally, direct predation has caused the disappearance of several native macroinvertebrate and zooplankton species (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017).

In the Azores, the introduction of Lymnaeidae snails [e.g., *G. truncatula* and *Radix peregra* (Müller, 1774) vectors of *Fasciola hepatica* Linnaeus, 1758] have contributed to significant revenue losses in livestock farms in São Miguel (Frias Martins, 1991), which highlights the importance to consider health and ecosystem services aspects in locally accessing introductions' impacts.

Economic impacts are also associated with landscape deterioration due to the decline and impoverishment of ecosystem services (Fei et al., 2014). The introduction of non-indigenous cyanobacteria and plants such as *Egeria densa* Planch. has decreased water quality and increased turbidity of Azorean lakes, negatively impacting leisure recreational activities undertaken both by tourists and the local population (Santos et al., 2012; Cruz et al., 2015; Cordeiro et al., 2020). Moreover, climate changes may promote the spread of non-indigenous species that act as hosts of parasites and transmit human illness.

Despite the high number of non-indigenous species that may negatively affect ecology and economy, the introduction of some species may also have had socio-economic benefits like enhanced recreational fishing in Azorean lakes by fish stocking (Hunt et al., 2017).

### Cyanobacteria, Diatoms, Desmids, and Synurophytes

Little is known about the distribution of freshwater cyanobacteria, desmids, synurophytes, and diatom species in the Azores (Jorgen Kristiansen, 1996; Foissner and Hawksworth, 2009). Nevertheless, cyanobacterial blooms were recorded for the first time in Azorean lakes, namely Sete Cidades and Furnas (e.g., Santos et al., 2005; Gonçalves, 2008; Cruz et al., 2015) during the late 1980s. Several well-known bloom-forming species associated with eutrophication, such as *D. scheremetieviae, M. aeruginosa, M. flosaquae* were not only recorded for the Azores between 1989 and 1991, but became dominant in several lakes. When these microorganisms become invasive, they contribute to the eutrophication of aquatic ecosystems (Hillebrand and Sommer, 2000), altering the structure of native communities significantly and leading to loss of biodiversity (Chapin et al., 2000; Korneva, 2014).

In general, invasions by microorganisms are poorly understood and, until recently, their impact on the environment has been underestimated (Foissner and Hawksworth, 2009; Kaštovský et al., 2010).Many species of cyanobacteria can produce toxins harmful to the ecosystem, and when present in drinking or recreational waters might lead to human health problems (Christoffersen and Kaas, 2000; Funari and Testai, 2008; Oscoz et al., 2010) that can vary from psychological effects, discomfort, nuisance, and phobias, to skin irritations, allergies, poisoning, disease and even death (Bayliss et al., 2017; Peyton et al., 2019). Examples of the latter can be posed by the invasive species *Microcystis aeruginosa* (Kützing) Kützing, *Microcystis flosaquae* (Wittrock) Kirchner, *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault, *Aphanizomenon gracile* Lemmermann and *Dolichospermum scheremetieviae* (Elenkin) Wacklin, L. Hoffmann & Komárek, found in many lakes in the archipelago, often with high abundance (Santos et al., 2005; Cordeiro et al., 2020; Luz et al., 2020).

In addition to the predominance of cyanobacteria in most eutrophic lakes, which manifests the most significant degradation of these ecosystems' biological quality, non-indigenous diatoms can also cause considerable damage to the environment. The invasive *A. formosa* and non-indigenous *F. crotonensis*, are widely distributed species whose populations have been increasing in numerous lakes worldwide (Gonçalves, 2008; Sivarajah et al., 2016). The species *A. formosa* has at times been the most abundant diatom in several Azorean lakes (Gonçalves, 2008). The synurophyte *Synura petersenii* Korshikov and the desmid *Micrasterias papilifera* Brébisson ex Ralfs are also considered non-indigenous and were recently found in one lake in São Miguel and Terceira islands, respectively.

## Plants

Among the 41 plant species (see **Supplementary Material 1**), free-floating macrophytes such as the water hyacinth *E. crassipes* interfere with water utilization resources (Cook, 1990; Vereecken et al., 2006). Water hyacinth has invaded freshwater systems on five continents, and it is expected to expand in consequence of global warming (Kriticos and Brunel, 2016). In Portugal, the possession and sale of water hyacinth were prohibited by Law Decree no 165/74 (1974). Its mats with complex radicular structures prevent light penetration and water oxygenation with severe consequences to the autochthonous fauna and flora. Despite its presence on several islands of the archipelago (currently present in five of the nine islands), it has only been found in water tanks and ponds as ornamental, or on temporally waterlogged areas in Sete Cidades lakes (São Miguel Island). The local containment of this species is essential as it may constitute a threat for many small lakes in the Azores (Kriticos and Brunel, 2016).

The non-indigenous duckweeds *Landoltia punctata* (G. Meyer) D. H. Les & D. and *Lemna minor* L. can be aggressive invaders in aquatic ecosystems, whose colonies cover the surface of the water, causing oxygen depletion (Landolt, 1986). These plants should be controlled before they cover the entire water surface. Although they have a high dispersal capacity, populations in the archipelago are small and sparse.

Two species of Hydrocharitaceae recently introduced to the archipelago also stand out, *Egeria densa* and *Elodea canadensis* Michx. The first is disseminated worldwide and is capable of high-speed growth (Oliveira et al., 2005) due to fragmentation and posterior vegetative reproduction. *E. densa* is a very resistant species and tolerates an extensive range of nutrient, oxygen, carbon dioxide, and pH conditions (Matthews et al., 2014). In the Azores, it is present in three islands, but problems have been mainly reported in Sete Cidades and Furnas lakes (São Miguel Island) where the eutrophic conditions have been enhancing its growth. *E. canadensis* was first reported in 1970 for São Miguel island (Santos et al., 2005). These species introductions have been related to escapes from aquaria or deliberate ornamental plantations in natural ponds and subsequent dispersion by fragments through water flow or associated with human activities. Their impacts include restrictions on recreational activities, rising flooding risk, and interfering with some infrastructure such as turbines (Oliveira et al., 2005; Matthews et al., 2014).

A number of non-indigenous dicotyledonous helophytes develop on temporarily flooded soils, such as *Apium nodiflorum* (L.) Rchb.fil., *Nasturtium officinale* W.T.Aiton, *Persicaria hydropiper* (L.) Spach and Poaceae *Glyceria fluitans* R.Br. and are common species inhabiting small watercourses. Similarly, the emergent and submergent macrophytes (helophytes) can flourish in fens and temporarily or permanently flooded areas (Rivas-Martínez et al., 2001). In the Azores, these macrophyte communities, mainly composed of non-indigenous species, are favored by removing forest cover and the abusive use of water resources for both humans and livestock (Rodrigues et al., 2004). This ecotone has been extended in many aquatic margins where livestock access creates disturbed areas that facilitate invasive species spreading, such as *Cyperus* spp. and *Typha* spp.

Certain herbaceous invasive species, non-strictly aquatic, prefer wetland habitats, such as *Ranunculus* spp., *Mentha* spp. and *Tradescantia fluminensis* Vell., and form dense populations in moist and shady areas. With a short reproductive maturation and high levels of seed dispersal, these species are common on most islands. These reproductive strategies constitute a competitive advantage over native flora that inhabit similar environments.

## Invertebrates

Non-indigenous invertebrate species that may cause ecological and socioeconomic impacts in Azorean freshwaters are represented by Platyhelminthes, Cnidaria, Annelida, Mollusca, and Arthropoda (**Table 1**). The species that have the most serious negative effects in freshwater ecosystems are described in detail.

*Craspedacusta sowerbii* Lankester, 1880 (Cnidaria, Hydrozoa) native from China (Jankowski, 2001), shows a cosmopolitan distribution due to its introduction in many freshwater habitats (Jankowski et al., 2008) on all continents except Antarctica (Rayner, 1988). Most of these introductions have been accidental and associated with fauna trade or ornamental plants (Jakovčev-Todorović et al., 2010). In 2010 some individuals were found in Congro lake, São Miguel Island (Raposeiro et al., 2011c). Recently, *C. sowerbii* has been discovered on other islands. *C. sowerbii* feeds on zooplankton (Smith and Alexander, 2008; Moreno-Leon and Ortega-Rubio, 2009) and may impact aquatic food webs by removal of a significant part of the zooplankton population, leading to changes in the structure of plankton community (Smith and Alexander, 2008) and cascading effects on primary producers (Brooks and Dodson, 1965; Carpenter and Kitchell, 1984; Williamson et al., 1989). Moreover, blooms of *C. sowerbii*, that often occur under eutrophic conditions and high temperatures, may trigger severe impact on the ecosystem (Davis, 1955; Jakovčev-Todorović et al., 2010).

*Ferrissia fragilis* (Mollusca, Gastropoda) is a native from North America and was probably introduced to the Azores by aquarists and/or associated with ornamental plants ("Transport-contaminant" pathway). This species was first observed on São Miguel Island in Sete Cidades Lake in 2004 (Raposeiro et al., 2011b). Since then, it has been found on Santa Maria, Graciosa, and Pico islands. Freshwater habitats where *F. fragilis* are present are usually characterized by high nutrient concentrations where these snails are typically found on submerged leaves of the introduced plant *E. densa* in shallow littoral shores. *F. fragilis* can also be found in submersed periphyton-covered stones or on plant detritus in weak flow areas (Raposeiro et al., 2013). The impact of this species is not clear (Raposeiro et al., 2011b). The impact in the Azores is probably masked by other introduced freshwater gastropods (Backhuys, 1975; Frias Martins, 1991; Raposeiro et al., 2012).

*Galba truncatula* (Mollusca, Gastropoda) introduction to the archipelago is possibly associated with imported sheep from mainland Portugal or aquarium trade (Duggan, 2010). Its introduction may have also been mediated by Nearctic birds or insects (Raposeiro et al., 2011a). The invasive potential of

Lymnaeids species may be related to marked resistance to desiccation which increases their survival probability (Chapuis and Ferdy, 2012). When released in new environments, even a single individuals can develop a population as Lymnaeids can be self-fertilized (Escobar et al., 2011; Lounnas et al., 2018). Snails belonging to the Lymnaeidae family (Hurtrez-Boussès et al., 2001; Mas-Coma et al., 2005), such as *G. truncatula* and *R. peregra,* both introduced in the archipelago, are intermediary hosts for the Trematoda F. *hepatica* that contaminates part of São Miguel, Flores, and Santa Maria islands causing significant socioeconomic losses associated with damage to dairy livestock (Barbosa et al., 2019).

*Procambarus clarkii*, a crayfish native from North America and Mexico, is considered globally one of the most invasive aquatic species (Meineri et al., 2014; Arce and Diéguez-Uribeondo, 2015). In Portugal, it is forbidden under the Law Decree no 565/99 (1999) to keep and rear this species. *P. clarkii* was reported for the first time in São Miguel Island in 1994 (Correia and Costa, 1994; Costa et al., 1997), and it has since spread to Terceira Island. Its introduction in the Azores may be related to the aquarium trade, with an escape or release from a private aquarium or tank. This crayfish can actively disperse by land (Gherardi et al., 2000; Ramalho and Anastácio, 2014) and spread by passive vectors such as vehicles and animals (Águas et al., 2014; Anastácio et al., 2014). Its short life cycle, rapid growth, digging activity, and high populational densities facilitate its establishment (Gherardi and Acquistapace, 2007). In lakes in São Miguel island, *P. clarkii* is associated with the invasive species *E. densa* contributing actively to this plant fragmentation and dispersion. The presence of the red swamp crayfish in the archipelago is restricted to highly impacted systems, making its impact evaluation difficult, but it is probably lower than on the mainland. Interestingly, *P. clarkii* is now absent from Lagoa do Peixe, the small lake where its presence was first detected in São Miguel island, which seems to be a first record for a population extinction of this species.

Other non-indigenous species categorized as invasive in Azores freshwaters are the platyhelminth *Dugesia tigrina* (Girard, 1850); the annelids *B. sowerbyi* and *Eiseniella tetraedra* (Savigny, 1826); the gastropod *P. acuta*; the crustacean *Argulus foliaceus* (Linnaeus, 1758); and diptera considered urban and agricultural pests, as *Culex pipiens* Linnaeus, 1758 and *T. oleracea*.

### Vertebrates

Non-indigenous amphibians in the Azores include, the frog *P. perezi*, introduced in 1820 and scattered on all the islands and by the crested newt *Triturus cristatus carnifex* (Laurenti, 1768) already present in 1922 on São Miguel (Svenberg, 1975), and both considered as invasive in the region. Due to the Azores' oceanic geography, fishless lakes were common before human settlement, and the only native freshwater fish is *A. anguilla*, a common inhabitant of Azorean streams. In Azorean lakes, fishes' introduction had a strong effect on macroinvertebrates communities, mainly due to the absence of native predators, with direct impacts on the diversity and abundance of prey populations (e.g., native invertebrates) (Skov et al., 2010; Raposeiro et al., 2017). Among the non-indigenous fishes introduced in the Azores (**Supplementary Material 1**), we mention the most abundant species with a negative impact on Azorean freshwaters.

*Cyprinus carpio* is the most abundant fish species in Azorean lakes, and is present on Flores, Pico and São Miguel islands (Gonçalves et al., 2006; Bio et al., 2008; Raposeiro et al., 2017). The first record of introduction dates from 1890 in São Miguel Island (Chaves, 1911). Recent introductions of fishes in the Azores have been for recreational fishing purposes (Anastácio et al., 2019), and dispersion among aquatic systems and islands is due to human action either by introductions from breeding facilities (e.g., trout) or by anglers' translocations. *C. carpio* has a detritivorous bottom-feeding strategy consuming benthic invertebrates, removing sediments from the bottom, uprooting the macrophytes leading to the increase of water turbidity (Parkos et al., 2003; Miller and Crowl, 2006) and consequently, contributing to decrease water quality and habitat degradation (Lougheed et al., 1998; Buchaca et al., 2011). Moreover, *C. carpio* has a substantial impact on benthic communities by releasing nutrients from sediments thus and indirectly promoting algae blooms (Ribeiro et al., 2009; Raposeiro et al., 2017). *C. carpio* may also have socio-economic impacts through decreasing high value fish species by outcompeting with them and reducing recreational activities' attractiveness. Increasing nutrient availability through sediment disturbance and excretion by fish may directly affect primary producers (quantity and diversity) and subsequent bottom–up consequences on food webs (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017).

*Micropterus salmoides* is a piscivorous species introduced in 1898 for fishing purposes. Nowadays, it is well distributed in Pico, São Miguel, Flores, and Corvo Island (unpublished data). This species may impact the ichthyofauna and amphibians, causing top-down consequences in trophic webs (Takamura, 2007).

*Perca fluviatilis* is planktivorous fish introduced for angling in São Miguel's lakes in 1898, an activity long fomented by Forestry Services. Thus, anglers can act as dispersion vectors for some non-indigenous species, fishes, and accompanying species. *P. fluviatilis,* as a zooplanktivorous fish, may promote the decrease of native zooplankton densities, lowering grazing pressure on phytoplankton with resulting increased chlorophyll-a concentration, reduced water clarity, and enhanced eutrophication in Azorean lakes (Skov et al., 2010; Buchaca et al., 2011).

## Management and Conservation Actions

Climate change and the increasing magnitude and frequency of introductions of species across geographic barriers resulting from international trade (see Hulme, 2009) are likely to change their establishment, spread, abundance, physiology, or phenology, potentially altering humans' health impacts (Bayliss et al., 2017). Many non-indigenous species will likely benefit from climate change as some of their ecological traits provide high plasticity and adaptation abilities to cope with changing conditions (Hellmann et al., 2008). Global change may lead to new public health concerns as globalization increases the likelihood of disease vectors' movement and facilitates the transmission of tropical and subtropical pathogens to higher latitudes and other Atlantic archipelagos (Seixas et al., 2019). Trade plays a vital role in the spread of invasive species and has arguably contributed to the recent acceleration of biological invasions (Seebens et al., 2015). The magnitude of merchandise imports is a determinant of the number of invasive species (Hulme, 2009), evidenced by correlations between invasive species richness and economic indicators (Dalmazzone, 2013). This has been proved stronger for islands than for continents, reflecting the more significant proportion of imports and higher establishment of invasive species (Hulme, 2009). Considering the observed trends in international trading, importations, and enhanced connectivity of the Azores archipelago as a result of the increasing number of flights and shipping (Vieira et al., 2019), unintentional introductions may accelerate beyond control if some preventive measures are not enforced (Howeth et al., 2016) due to enhanced propagule pressure. Higher connectivity among islands (**Figure 1**) is likely to improve non-indigenous freshwater species' dispersal within the archipelago as accidental transportation seems to be an essential pathway for the non-indigenous freshwater species present in the Azores.

An important focus should be developing a biosecurity program addressing different sorts of species importation, improving the existing legislation and customs controls, and public campaigns to ensure good practices for watersheds users. For example, the "Clean Drain" movements, applied in the United States, New Zealand, and the United Kingdom, empowered recreational and other water users to promote biosecurity best practice to reduce the risk of accidental introduction and spread of aquatic IAS, encouraging people to check, clean and dry all equipment and clothing thoroughly (Beyer et al., 2011; Anderson et al., 2015). A relevant problem to address is the introduction of ornamental species. The ornamental plant industry needs "new" varieties of plants to offer to the public. Still, at the same time, there must be mechanisms to prevent non-indigenous species' entry with high invasive potential. The large number of species coming from aquariums is worrying, and strict control of importation for business purposes must be put in place, and information and prevention campaigns should be carried out among the general public and anglers. The awareness-raising campaign could also include citizen science initiatives directed at key species that should be included in an early warning monitoring program. It is widely accepted that citizen science can play a significant role in public engagement. Their observations are crucial to informing policy on biodiversity conservation from government decisions to those made by local conservation managers (Theobald et al., 2015; Anderson et al., 2017). This is particularly relevant in restricting and preventing biological invasions (Theobald et al., 2015; Anderson et al., 2017; Chandler et al., 2017). A wealth of species occurrence data generated by citizen scientists enables surveillance of emerging and established invaders at larger spatial extents. Strictly regulating – or even prohibiting – the trade of species highly likely to become invasive, together with early alert and rapid response systems, is generally considered the most successful management strategy (Leung et al., 2002).

In parallel, monitoring of aquatic ecosystems would allow early detection of new species. To do this effectively, it is necessary to provide high quality and up-to-date information. Monitoring staff must be well trained in species identification to avoid confusion as occurred in the past, such as the case of clover fern *Marsilea azorica* Launert & J. Paiva (Schaefer et al., 2011). This species was described in 1983 and included as 'critically endangered' on the IUCN red list and as 'strictly protected' species by the Bern Convention and the European Union's habitats directive, but was later identified by Schaefer et al. (2011) as *Marsilea hirsuta* R.Br., a non-indigenous species in the archipelago. A similar problem arose with *Potamogeton lucens* Nolte, subsequently determined by Kaplan and Zdenek (2005) as *Potamogeton schweinfurthii* A.Benn.

In the Azores case, the moderate climate without large annual fluctuations makes it possible for many species to potentially acclimatize (Walther et al., 2009; March-Salas and Pertierra, 2020), which would be more difficult elsewhere. Despite its oceanic isolation, the archipelago is halfway between the Americas and Europe, doubling the possible routes of entry for invasive species that can rapidly spread in the islands. Therefore, regarding the flora, most non-indigenous aquatic plants in the Azores should have monitoring plans due to the risk of rapid dispersal in lakes and water courses, and eradication should be advised for newly established species with limited distribution (Sharov, 2004). This should be considered, for instance, for controlling the water hyacinth *E. crassipes* in the Azores. The percentage of non-indigenous plants (69%) in the Azorean flora is relatively high (Silva and Smith, 2004). Some of these such as the terrestrial *Hedychium gardnerianum* Ker Gawl., *Clethra arborea* Vent., or *Hydrangea macrophylla* Thunb. although not strictly aquatic plants, strongly influence the Azorean freshwater ecosystems' ecotone zones. Their presence at the margins of water courses, transport of rhizome fragments, deliberate introduction (hedges) allied with their aggressive nature, and strong presence in the archipelago will create severe problems in the structure, native status, and succession of these ecosystems. This complete alteration of riparian phytocenosis is of paramount importance since it provides the habitat and food for many organisms and influences aquatic microbial community composition (Ferreira et al., 2017).

Eutrophication is a slow natural process that has been dramatically accelerated by human activities, such as the runoff of excess fertilizer or sewage effluent in the Azores. Anthropogenic eutrophication is typically associated with higher primary productivity, higher oxygen demand, lower species richness, and species abundance changes (Engelhardt, 2011). One of the leading causes of this eutrophication in the Azores is the agricultural and livestock use of the territory, mainly focused on cattle. The alterations caused by livestock in the riparian areas are mostly three: physical destruction of the habitat by trampling, selective grazing of the vegetation, and excess supply of nutrients and seeds of non-indigenous species by excrements. This complex interaction of factors can lead over time to the complete alteration of delicate aquatic ecosystems by favoring invasion of non-indigenous plants in the riparian galleries and their proliferation in the water, as is the case of *E. densa* and non-indigenous cyanobacteria blooms.

Management actions against freshwater weeds were applied in some Azorean lakes (e.g., Sete Cidades lakes) using mechanical harvesting. Although large amounts of weed biomass were removed from the lakes (Santos et al., 2012) no ecological improvement was detected in these lakes. Mechanical approaches to control *E. densa* are known to be ineffective and can even enhance its dispersal and spread (Pennington, 2009). Massive removal of lake macrophytes can also resuspend lake sediments and release sediment-sequestered nutrients, favoring phytoplankton growth (Sayer et al., 2010; Quilliam et al., 2015) and enhancing eutrophication. Therefore, the removal of large stands of weeds in water bodies with massive proliferation is not recommended. However, removing non-indigenous macrophytes should be prioritized in recently invaded water bodies to contain or even eliminate them in the early invasion stages.

Another important factor contributing to eutrophication is the internal recycling of nutrients (Sondergaard et al., 2001). Fishes play an essential role in this process (Horppila et al., 1998; Buchaca et al., 2011), especially in ecosystems where they were naturally absent, as is the case of Azorean lakes (Skov et al., 2010; Raposeiro et al., 2017). Efforts were made in one lake (Lake Furnas, São Miguel Island) to reduce fish abundance to minimize eutrophication, and increase water quality (Bio et al., 2008). Despite the promising results of the first attempt to control fish populations in Azorean lakes, this approach was only applied for a short period (Bio et al., 2008). However, habitat restoration and implementation of land-use changes and more sustainable livestock and agriculture practices within some watersheds can not only fight the eutrophication problem but could also help manage the invasive species that benefit from nutrient-enriched conditions and impaired habitats. Some efforts have been put in place, e.g., on São Miguel, through watershed management plans, to tackle this problem (Cruz et al., 2015), but more robust measures have to be enforced to control of the freshwater invasive species spread.

A very positive point of Portuguese legislation in force on invasive species (Law Decree no 92/2019, 2019) is that investment is made in preventive culture. Monitoring, early detection, and rapid reaction mechanisms are put in place to contain the spread of invasive species. Despite including more invasive species than the previous law (Law Decree no 565/99, 1999), many species appear in this document as invasive only for the autonomous region of Madeira, leaving out the Azores, as it is the case of *Adiantum raddianum* C.Presl, *Adiantum hispidulum* Sw., *Colocasia esculenta* (L.) Schott, *Holcus lanatus* L.*, Z. aethiopica and Crocosmia x crocosmiiflora.* The Regional Legislative Decree n.o 15/2012/A (2012) aims to regulate the import, holding, and introduction into the territory of the Autonomous Region of the Azores of non-indigenous species, in annex XI (Animal specimens whose introduction is permitted in the Autonomous Region of the Azores). However this decree concerning pets allows the entry into the islands of two groups of animals whose dispersion in the aquatic systems of the archipelago is problematic: "(e) Turtles (reptiles of the Chelidae family) and (f) Freshwater aquarium fish when produced in captivity." Another point to note is the absence in Annex IX (List of species of fauna and flora invasive or at known ecological risk) of a fish list, which does appear in national law (Regional Legislative Decree n.o 15/2012/A, 2012). Moreover, in recent years, efforts have been made to reinforce controls at border levels by customs in local airports and ports.

River basin management plans implemented in the framework of WFD should also be an instrument for invasive species control. Even though non-indigenous species are not explicitly referred in the WFD, the directive aims to restore pristine communities in European water bodies, which implies that invasive species must be removed from or controlled within these ecosystems. Unfortunately, most European countries do not include invasive species in WFD assessments, and many do not take them into account in the status classification (Boon et al., 2020). Although in the Azores invasive species are not used for the ecological status classification, they negatively impact water bodies, and measures to control invasive plants in transitional waters were proposed in the Azores river basin management plan (AHA-DRA, 2015). Due to their impact on native communities and ecological quality, invasive species can preclude the achievement of WFD environmental objectives of good water status in water bodies. Therefore, more actions to control invasive species must be considered in future river basin management plans.

## FINAL REMARKS

In island freshwater ecosystems, it is challenging to predict vulnerability to non-indigenous species. Still, it is crucial to compile a detailed list of species, distribution, and associated environmental and historical information. Using this information combined with alternative approaches, like paleolimnological reconstruction, a comparative analysis of past introductions could be a significant step to understand the consequence of invasive species on insular freshwater systems. Detailed and general knowledge of the principal pathways and efforts to enhance environmental conditions would minimize invaders' success within fragile insular ecosystems. Also, control measures such as checking the consignment both by air and sea for non-indigenous species would prevent new species' entrance. In contrast, a more conscious and educated behavior from all users (e.g., tourists, anglers, and aquariologists) and management measures to improve water quality will prevent the spread of present invasions. Furthermore, systematic monitoring of these habitats and biota should be carried out to provide additional information that is essential for improving freshwater management, sustainable development, and ensuring the functioning and services of freshwater ecosystems.

Managing non-indigenous species on remote oceanic islands requires a well-coordinated strategy among all stakeholders. In the future, we must take into account that expanding international trade, tourism, transport, and climate change will probably facilitate the entry, spread, and establishment of non-native species through new pathways. Future actions such as political awareness and compromise and public awareness and education concerning species introductions are needed to tackle this problem.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

AC and PR contributed to the conception and design of this study. All the authors contributed to the manuscript with essential inputs from AB (fauna species lists and data compilation), PR (data treatment), and SS (microalgae and cyanobacteria data compilation), largely contributed to the manuscript writing, and approved the submitted version. VG contributed microalgae, cyanobacteria and management, and ecosystem data analysis. MS contributed plants and management sections.

## FUNDING

Part of this study was financed by Portuguese National Funds, through FCT - Fundação para a Ciência e a Tecnologia, the European Union, QREN, FEDER, COMPETE, by funding the CIBIO/InBIO (project UID/BIA/50027/2020 and POCI-01-0145-FEDER-006821), DISCOVERAZORES Project (PTDC/CTA-AMB/28511/2017P), P. M. Raposeiro and M. S. Souto (DL57/2016/ICETA/EEC2018/25 and ICETA 2019/56). This study was also financed by PRIBES project (Direcção Regional do Ambiente – LIFE17 IPE/PT/000010).

## ACKNOWLEDGMENTS

The surveys were performed to comply with the current laws of Portugal. We want to thank all the collaborators from FRESCO – Freshwater Ecology research group from CIBIO-A (University of the Azores), which somehow helped gather data for this paper. Thanks are also due to Erik Zettler for his comments and language revision. We also thank the three reviewers and the editor whose comments/suggestions helped to improve and clarify this manuscript.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.631214/full#supplementary-material

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 15 April 2021
doi: 10.3389/fevo.2021.639161

# Monitoring Extreme Impacts of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in El Estrecho Natural Park (Biosphere Reserve). Showing Radical Changes in the Underwater Seascape

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OPEN ACCESS

***Edited by:***
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***Reviewed by:***
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***Specialty section:***
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

***Received:*** *08 December 2020*
***Accepted:*** *12 March 2021*
***Published:*** *15 April 2021*

***Citation:***
*García-Gómez JC, Florido M, Olaya-Ponzone L, Rey Díaz de Rada J, Donázar-Aramendía I, Chacón M, Quintero JJ, Magariño S and Megina C (2021) Monitoring Extreme Impacts of Rugulopteryx okamurae (Dictyotales, Ochrophyta) in El Estrecho Natural Park (Biosphere Reserve). Showing Radical Changes in the Underwater Seascape. Front. Ecol. Evol. 9:639161. doi: 10.3389/fevo.2021.639161*

The invasive macroalga *Rugulopteryx okamurae* represents an unprecedented case of bioinvasion by marine macroalgae facing the European coasts. Since the first apparition of the species in the Strait of Gibraltar in 2015, its fast dispersion along the introduced habitats constitutes a real challenge to develop monitoring strategies that ahead of its impacts. The present study uses three different approaches to address impacts on the benthic ecosystems, at the same time offers relevant data for future management actions in El Estrecho Natural Park (PNE). Information obtained by monitoring permanent sentinel stations revealed a significant loss in resident species coverage after the moment of maximum growth in 2017. Thus, despite coverage of *R. okamurae* did not strongly varied in the latter years, impacts generated remain high in the habitats studied. Estimations of the invasive species coverage by combining cartographic image analysis and *in situ* data predicted a major occupation (over 85% coverage) between 10 and 30 m, coinciding with the maximum rocky surface areas ($m^2$) mapped on the PNE. Furthermore, a Citizen Science research collaboration evidenced impacts on the benthic seascape through an *ad hoc* exploration of images that allowed a "before" and "after" comparison of the invasion process in the same geographic locations. This has made it possible to graphically demonstrate severe changes in the underwater seascape and, therefore, the general impact of this new biological invasion. The spatial colonization estimations combined with the impacts reported by both scientific [Sessile Bioindicators in Permanent Quadrats (SBPQ) sentinel stations] and civilian (Citizen Science) monitoring methodologies claim the urgent development of further studies that allow the design of monitoring strategies against *R. okamurae* expansion across the Mediterranean and Atlantic waters.

**Keywords: *Rugulopteryx okamurae*, Citizen Science, benthic biota, monitoring, invasive species, invasive macroalgae, El Estrecho Natural Park, Strait of Gibraltar**

## INTRODUCTION

The Strait of Gibraltar is a hot spot area for marine biodiversity in the Atlantic-Mediterranean waters with great biogeographic importance due the coalesce of the Lusitanian, Mediterranean and Mauritanian regions (Ekman, 1953; Briggs, 1974; García-Gómez, 2002). Together with the Alboran Sea, the Strait coasts harbor species from the northern Atlantic, subtropical waters of the northwestern of Africa and the Mediterranean Sea (Templado, 2011; Mannino et al., 2017; Urra et al., 2017). Its species richness and habitat diversity is influenced by the littoral physiographic complexity, which has led to the co-occurrence and dominance of different biological strategies and thus affecting the composition of benthic communities (Zabala and Ballesteros, 1989). The biodiversity of this area has been largely assessed by a list of references in terms of foundation species [macroalgae (Flores-Moya et al., 1995a,b; Conde et al., 1996; Adama et al., 2021) and sessile macroinvertebrates as ascidians (Carballo et al., 1997) or molluscs (García-Gómez, 2002; Gofas et al., 2011)] and associated fauna (e.g., García-Raso, 1993; Conradi et al., 2000; Castello and Carballo, 2001; Guerra-García et al., 2009; García-Raso et al., 2011).

However, the benthic systems have changed over time according to different biotic and abiotic factors (see Gallardo et al., 2021). The biodiversity and species richness have been threatened by several anthropogenic pressures for many years, mainly due to the proximity to pollution resources (e.g., chemical industries, thermal plants, oil slick) (Morales, 2007; Soussi et al., 2020), artificial infrastructures (Sánchez-Moyano et al., 2000; Sedano et al., 2020) or maritime shipping and human activities (Bianchi et al., 2013; Nachite et al., 2020). Indeed, the Strait of Gibraltar supports the highest density of maritime traffic in the Western Mediterranean (Abdulla and Linden, 2008; Endrina et al., 2018). This implies a threat due to marine bioinvasions since ballast waters and boat hulls fouling are recognized as potential transport vectors for non-indigenous species (NIS) (Ribera-Siguan, 2003).

Favorable environmental conditions increase the settlement success of invaders (Villèle and Verlaque, 1995), which in turn compromise the survival of surface-dependent organisms by changing the physical characteristics and available substrata (Mannino et al., 2017). Macrophytes (macroalgae and seagrases) constitute the dominant group of invasive species in the Western Mediterranean (Zenetos et al., 2010, 2012). In the recent years, a number of studies have been performed on invasive macroalgae that have interacted the resident sessile communities promoting also cascading influence on associated fauna in the Strait waters. Some examples are *Asparagopsis armata* Harvey (Boudouresque and Verlaque, 2002; Guerra-García et al., 2012), *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon (Altamirano et al., 2008; Navarro-Barranco et al., 2018), *Caulerpa cylindracea* Sonder (Altamirano et al., 2014); *Womersleyella setacea* (Hollenberg) R. E. Norris (Bedini et al., 2015), or *Lophocladia lallemandii* (Montagne) F. Schmitz (Ballesteros et al., 2007). Despite positive and neutral effects may also occur [e.g., *Caulerpa racemosa* (Forsskål) J. Agardh may maintain caprellid populations in shallow Mediterranean habitats (Vázquez-Luis et al., 2009)], these species have displayed pronounced and drastic effects on the underwater seascape making it difficult the implement success of strategies to mitigate their impacts (Anderson, 2007; Klein and Verlaque, 2008).

The last notorious case of macroalga colonizing the Western Mediterranean littorals is the species *Rugulopteryx okamurae* (E. Y. Dawson) I.K. Hwang, W.J. Lee, and H.S. Kim. This brown macroalga, originated from the northwest of Asia (Hwang et al., 2009), has been systematically reported on the coasts of the Strait of Gibraltar since 2015 (see Altamirano-Jeschke et al., 2016), when more than 5,000 tons of wracks were extracted from the beaches of its south coasts, in the city of Ceuta (North-Africa) (Ocaña et al., 2016). The rocky bottoms of The Jbel Moussa Site of Biological and Ecological Interest (SIBE) (El Aamri et al., 2018) and the eastern littoral of El Estrecho Natural Park (PNE) (García-Gómez et al., 2018) firstly represented the northern and southern scenarios of *R. okamurae* expansion in the Strait of Gibraltar. Until date, these areas constitute the most intensely affected by the brown alga, which continues its westward and eastward directionality of expansion (Altamirano et al., 2019; Figueroa et al., 2020) with trend to monopolize the sea rocky bottom in detriment of the photophilous resident biota (García-Gómez et al., 2020b). In the introduced areas, the species is present throughout the year and is dispersed mainly due to asexual and vegetative strategies by propagules and monospores (Altamirano-Jeschke et al., 2017; Altamirano et al., 2019). Although it has not been possible to assess if the species is able to complete its entire life cycle in the Atlantic and Mediterranean waters (Verlaque et al., 2009; Altamirano-Jeschke et al., 2016, 2017), the fast expansion and massive occupation potential since its first detection in 2015 reflects that this bioinvasion case is one of the most serious and threatening caused by marine macroalgae in the European waters (García-Gómez et al., 2018, 2020b).

It is urgent to carry out studies on the distribution, ecology and impacts of *R. okamurae* in the Mediterranean and the Atlantic coasts, as well as the implementation of management measures. However, few studies have been carried out on *R. okamurae* distribution (e.g., Altamirano-Jeschke et al., 2016; Ocaña et al., 2016; El Aamri et al., 2018; Altamirano et al., 2019) and its derived impacts on the recipient sessile (García-Gómez et al., 2018, 2020b; Sempere-Valverde et al., 2020) and mobile associated biota (Navarro-Barranco et al., 2019). In this regard, there is only one published study monitoring the temporal dynamic of the invasion since the first apparition of the species in the Strait waters (see García-Gómez et al., 2020b) by the utilization of Sessile Bioindicators in Permanent Quadrats (SBPQ). The SBPQ is part of a monitoring of sessile sentinel species which has been carried out since 2013 to detect early impacts on the littoral environment, including changes in the benthic system related to global warming (García-Gómez, 2015). Thus, this methodology has allowed to document not only the establishment of *R. okamurae* but also the disappearance of target species which become displaced in the absence of environmental stability.

Long-term monitorings, as observational studies that obtain full ecological characterizations in environmental evaluations

(Moschella et al., 2005), are essential for the management of invasive species, their early detection and the implementation of a rapid response (Lodge et al., 2006; Williams and Smith, 2007; García-Gómez, 2015). In this sense, Citizen Science is a research collaboration strategy involving members of the public in scientific research projects to address real-world problems (Wiggins and Crowston, 2011). This constitutes an emerging movement of citizen participation given the breakdown or reduction of barriers caused by advances in communication technologies. Although there are challenges to effectively use citizen-generated data to monitor invasive species on a global scale (Earp and Liconti, 2020; Johnson et al., 2020), it can be a useful tool to detect and monitoring the bioinvasion processes (present study). In this sense, special emphasis has been placed on the underwater seascape, as highlighted in previous works performed in other research fields (Pittman et al., 2011; Gobert et al., 2014; Cheminée et al., 2016; Schejter et al., 2017; Ceraulo et al., 2018). The monitoring of an area by comparative images reflecting "before" and "after" scenarios due to bioinvasion processes as a proxy of BACI analyses (Before After Control Impact) (Underwood, 1994; Montefalcone et al., 2008; Conner et al., 2015; Donázar-Aramendía et al., 2018, 2020), may offer key information on the degree of affection that the local ecosystem has suffered and the risk of its prevalence in the area. Among other aspects, the comparative analysis of images can allow inferences regarding the behavior of biota and ecological connectivity, since the underwater seascape can have a great influence on it (Grober-Dunsmore et al., 2009).

The overall aim of this study was to advance our knowledge on the *R. okamurae* bioinvasion case targeting efforts on different monitoring approaches. Thus, objectives were threefold: (1) to provide updated data about the evolution of *R. okamurae* and key resident taxa in pre-coralligenous habitats and to test better designs for future monitoring programs; (2) to estimate the coverage of the invasive species on the rocky surface areas of the PNE, providing mapping areas of suitable rocky substrata to host the invasive species; and (3) to offer graphical evidences of radical changes before and after the spatial establishment of *R. okamurae* along the PNE littoral through Citizen Science collaborations.

# MATERIALS AND METHODS

## Study Area

The present study is focused on the northern coastline of the Strait of Gibraltar. Concretely, the PNE, which is located in the southern Iberian Peninsula and included within the Marine Protected Areas (MPAs) of the Andalusian Intercontinental Biosphere Reserve (Spain-Morocco). Situated between the Atlantic Ocean (western coasts) and the Mediterranean Sea (eastern coasts), the PNE extends from southern Spain to northern Morocco, separating Europe and Africa by 14 km distance. The study area includes the eastern littoral of the PNE coastline, between Tarifa Island (36°05′20.38″N, 5°48′45.34″O) and Punta Carnero (Algeciras) (36°4′30.18″N, 5°25′11.16″O) (**Figure 1**).

## Monitoring of the Submarine SBPQ Station of Tarifa Island

The sessile community at the SBPQ station of Tarifa Island (**Figure 1**) was seasonally sampled on partially shaded vertical walls of the pre-coralligenous habitats (15 m depth) during 2013–2017 by García-Gómez et al. (2020b). The SBPQ methodology is specifically designed to assess impacts on sensitive species characterized by long-life cycles, thus providing evidences in any period of the year. This methodology has been designed as a simple, non-invasive, underwater environmental alert tool for the potential early detection of environmental impacts of anthropic origin in the sublittoral system: in the short term (local alterations derived from pollutants, coastal dredging or civil engineering works, early detection of exotic species with invasive potential, etc.), and in the medium or long term (global warming) (García-Gómez, 2015; García-Gómez et al., 2020a). Because *R. okamurae* is present all-year round in the Strait of Gibraltar (pers. obs.) and most of target species from the sentinel station of Tarifa showed at least 10% of coverage in all seasons (see García-Gómez et al., 2020b), it could be expected that this long-term technique based on permanent quadrats will allow the detection of changes in the coverage of the invasive and the target species only considering one sampling season. In this study, the monitoring activities started in 2013 were temporally continued until 2020 and only considering winters (no data are available from 2018, when sampling was missed because of technical issues).

The monitoring station of Tarifa Island is composed of three 1 × 1 m fixed quadrats separated 5–10 m from each other. Within each fixed quadrat, four photo-quadrats of 50 × 50 cm were collected using *in situ* photographs via scuba diving. Following the methodology proposed by García-Gómez (2015), García-Gómez et al. (2020a) and the monitoring study performed for 2013–2017 (García-Gómez et al., 2020b), species coverage (percent) was obtained by superposing 10 × 10 grid over each photo-quadrat obtained for each fixed quadrat. Since the methodology overestimates the species-cover, the total percentage coverage in each photo-quadrat exceeded 100%.

To visualize the spatial distribution of replicates (quadrats) among years, a non-metric multidimensional scaling (nmMDS) based on a Bray–Curtis similarity matrix was performed on the square root transformed coverage data considering all the data pool since 2013. Differences in the sessile community structure over the sampling years were analyzed using PERMANOVA analysis under a nested design (sampling times were defined as random factor, "Season," nested within "Year," fixed factor with seven levels: 2013–2020). P-values were obtained through a Monte Carlo test when small number of unique permutations were obtained (Anderson et al., 2008). Also, the homogeneity of the data dispersion among samples was tested for the fixed factor "Year," using a permutational analysis of multivariate dispersions (PERMDISP) (Anderson, 2006). The contribution of each species to the Bray–Curtis similarity was obtained using a SIMPER (SiMilarity PERcentages) analysis. After performing analyses considering the whole data base, we wanted to test if the methodology was functional only sampling once a year considering the community present in this sentinel station. We

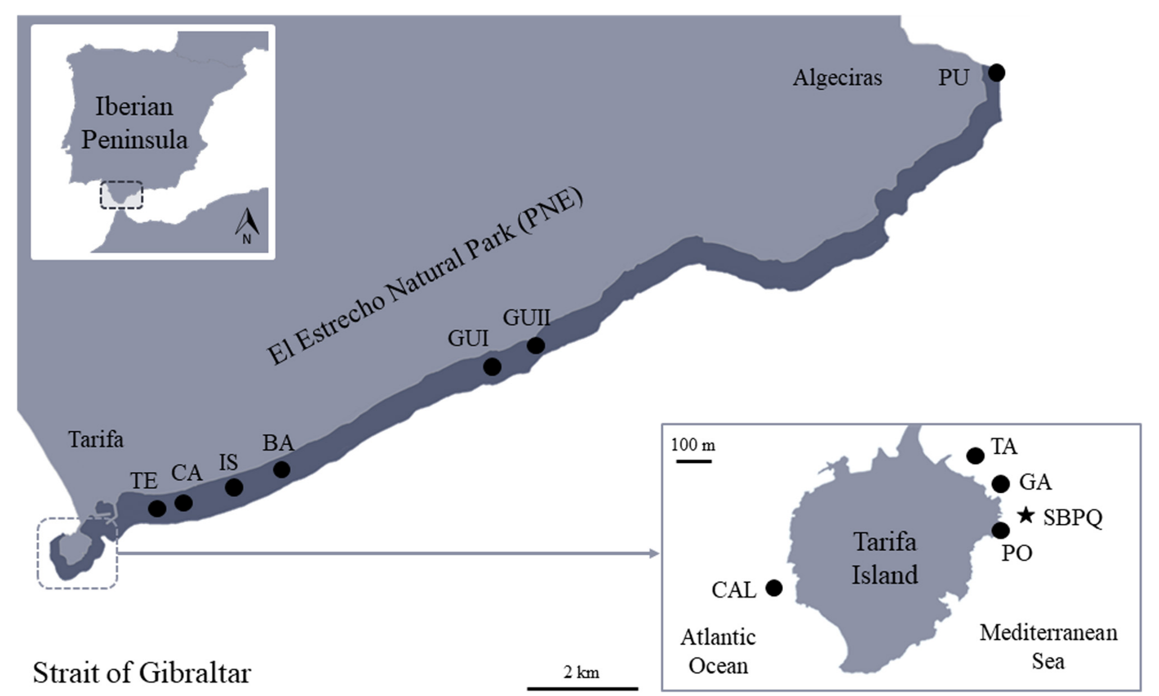


**FIGURE 1 |** Location of the study area in the Strait of Gibraltar showing the different sampling stations for each research objective. Star: location of the SBPQ station in the Tarifa Island; Dark band: eastern littoral of El Estrecho Natural Park (PNE) subjected to estimations of *R. okamurae* coverage-affections; Black points: sampling stations for Citizen Science collaborations. CAL = Caldera Profunda; TA = Tanque Gasoil; GA = La Garita; PO = Pozas Intermareales; TE = El Tejar; CA = La Caleta; IS = La Isleta; BA = Barranco Hondo; GUI = Guadalmesí I; GUII = Guadalmesí II; PU = Punta Carnero.

considered winters as the season of the year most appropriate to test whether the SBPQ methodology is minimally robust, since it is the time when it is expected (for middle latitudes) that the development and growth of the invasive macroalga is lower (this has been supported by pers. obs. and growth data for *R. okamurae* in Japan (Agatsuma et al., 2005), with similar north latitude to Spain: between 20° and 40°). Thus, the sensitivity of the SBPQ methodology was tested repeating all the analyses but only considering the data from the winter of each year (i.e., factor "Year," with seven levels: 2013–2020). Overall multivariate analyses were carried out using PRIMER-e v6 PERMANOVA + software (Clarke and Gorley, 2006; Anderson et al., 2008).

## Estimations of *Rugulopteryx okamurae* Coverage in the PNE

The sublittoral physical cartography of the Strait of Gibraltar (0–1 nautical mile zone) (García-Gómez et al., 2003; see also CMAyOT Consejería de Medio Ambiente y Ordenacion del Teritorio, 2008; MITECO Ministerio para la Transición Ecológica, 2012) was used to estimate the geographical and bathymetric expansion of *R. okamurae* along the sublittoral coastline of the PNE (**Figure 1**). Thus, *R. okamurae* coverage data were estimated and applied to bathymetric intervals of rocky sublittoral habitats (0–5, 5–10, 10–20, 20–30, and 30–40 m) by averaging coverage data obtained at the horizontal illuminated rocky surfaces of the southern coasts of the Strait (summer 2018, at 14 km from the study area; data previously published in García-Gómez et al., 2020b). Thus, the degree of coverage of the rocky bottoms were mapped using a polygon methodology for each bathymetric interval considered as follow: (1) A digital bathymetry model (DTM) was made in the PNE area and a 3-m orthogonal mesh was generated (surfer application from Golden Software, LLC was used). (2) The polygons of the outcropping rocks were extracted from the GIS database and (3) an intersection operation was performed between the DTM and the outcropping rock polygons. For this, the geo-processing tools of the Qgis application with the GNU general public license was used. (4) Once the DTM of the bathymetry was obtained, surface of the outcropping rock in each bathymetric interval was automatically calculated using a basic scripting language code from Golden Software, LLC (Contarea2.bas, 2000). The planar area (projected surface in the horizontal plane) and the real surface were calculated. (5). Finally, to generate a mapping of the rocky areas, the bathymetric DTM was divided in the ranges described above, so percentage coverages per bathymetric interval considered were displayed.

## "Before-After" Underwater Seascape Approximation by Citizen Science Initiative

With the aid of local scuba divers and citizen scientists, the research group of this study often obtains useful information in environmental assessments on the Strait coasts and Algeciras bay. In this regard, occasional observational surveys of the benthic communities have been performing on the subtidal coastline of the PNE for more than 10 years, providing valuable evidences of the underwater seascape dynamic over time. In this study, 11 video graphically monitored sites between Tarifa and Punta Carnero (Algeciras) (**Figure 1**) have been selected to compare environmental scenarios before and after the first establishment of *R. okamurae* on the northern Strait of Gibraltar (2015). Citizen participants were constituted by experienced local divers, that carefully recorded the underwater seascape every time they performed their activities in the sites indicated. With the attempt to combine minimal diving efforts with the widest relevant information obtained (and thus, an optimal collaboration), data was recorded by video graphic instead of photographic methods (Cabatain et al., 2006). Thus, citizen and scientific collaborators provided a large number of video graphic data, of which individual video frames were selected and analyzed in the laboratory.

Data from videos recorded between Tarifa Island and Punta Carnero (i.e., El Tejar, La Caleta, La Isleta, Barranco Hondo, Guadalmesí I, Guadalmesí II and Punta Carnero) yielded information on the whole natural rocky area between 3 and 10 m depth, while videos from Tarifa Island offered data on artificial substrata (i.e., Tanque Gasoil and Caldera Profunda; 7–10 m depth) and natural sublittoral (i.e., La Garita; 10–14 m depth) and intertidal habitats (i.e., Pozas Intermareales). Images taken before and after the first citation of *R. okamurae* in the Strait coasts (2015) were then selected and compared providing different scenarios of the underwater seascape and bioinvasion consequences.

## RESULTS

### Sessile Communities at the SBPQ Monitoring Station of Tarifa (2013–2020)

Results obtained showed that the percentage coverage of the sessile species at the SBPQ sentinel station located on vertical surfaces of shady pre-coralligenous habitats in Tarifa Island suffered a decrement in terms of species percent coverage until 2020, excepting *R. okamurae* and the coral *Astroides calycularis* (Pallas, 1766), which slightly increased after 2019 (**Figure 2**). PERMANOVA results revealed no evidences of significant differences in the community structure between 2019 and 2020. However, it significantly differed from previous years (2013–2017) (**Table 1A** and **Figure 3A**). The same pattern was observed when the community from 2017 was compared with the rest of sampling years. SIMPER analysis revealed that dissimilarities with previous years were mainly given by *R. okamurae* mean coverage values, which highly increased until 2017 (**Supplementary Table 1**). Instead, *R. okamurae* coverage decreased after 2017, and only contributed to differences with most recent data (2019–2020) in 13 and 15%, respectively. In this case, it was the native community which mainly contributed to dissimilarities, with an accumulative contribution up to 60% in both cases and lower average values.

Results obtained only considering samplings from winters are shown in **Supplementary Figure 1** and **Table 1B**. Comparisons revealed a hindrance of the exponential growth of *R. okamurae* from 2016 (**Supplementary Figure 1**). In 2019 and 2020, a slightly coverage enhancement was observed, but these values only contributed to dissimilarities against previous winters in a 16% (2019) and 17% (2020) (**Supplementary Table 2**). Overall, species coverage did not significantly differ between 2019 and 2020 (**Table 1B**). In fact, ordination analyses (nmMDS) revealed similar patterns to those obtained when including all the seasons form the period 2013–2017 (**Figure 3B**). Communities in 2020 significatively differed from winters before 2017 (included) and 2019 significantly differed from winters before 2016 (included). Despite the high coverages reached in 2019 and 2020 contributed to main differences against 2016 in both cases, when comparing with 2017, the loss of autochthonous brown algae and *A. calycularis* contributed up to 50% of dissimilarities in both cases.

### *Rugulopteryx okamurae* Coverage Estimations on the Sublittoral Areas of the PNE

Coverage values registered at the bathymetric range of distribution of *R. okamurae* in 2018 on horizontal illuminated surfaces (García-Gómez et al., 2020b) (**Figure 4A**) allowed the estimation of the species coverage for the different bathymetric intervals (**Figure 4B**). *R. okamurae* percentage coverages were mapped for all the PNE coastline (**Figure 5**) and rocky surface areas and corresponding estimated percent coverages were obtained for the eastern littoral of the PNE (**Figures 6**, **7**). The highest percentage coverages (85–96%) were obtained between 5 and 30 m depth. Over 10 m, these values coincided with the less extensive (565,469 $m^2$ between 5 and 10 m) and the most extensive rocky surfaces registered along the PNE (more than 3,000,000 $m^2$) (**Figure 7**). Thus, 96% of total coverage values were reached at the bathymetric interval of 10–20 m depth, estimated for a total rocky surface of 3,141,476 $m^2$. Estimated percentages of *R. okamurae* cover remained high (85%) until −30 m. The lowest percentage coverages (42 and 45%) occupied the deepest and the shallowest habitats (30–40 m and 0–5 m, respectively). No coverage data deeper than 40 m were obtained since no measurements were performed at such depth in studies performed in 2018 (see García-Gómez et al., 2020b).

### "Before-After" Underwater Seascape Approximation by Citizen Science Initiatives

The monitoring activities performed under the Citizen Science approach leaded to identify radical changes in the underwater seascape along the PNE littoral. Graphical data before and after the first establishment of *R. okamurae* revealed visual changes in the benthic community composition where the invasive species was represented as a dominant component by most of image data taken after 2015. The selection of visual data and concerning results at each sampling station and time is presented in the **Table 2**.

## DISCUSSION

Results obtained by the different objectives prospected in this study evidenced the extreme effects of *R. okamurae* on the benthic

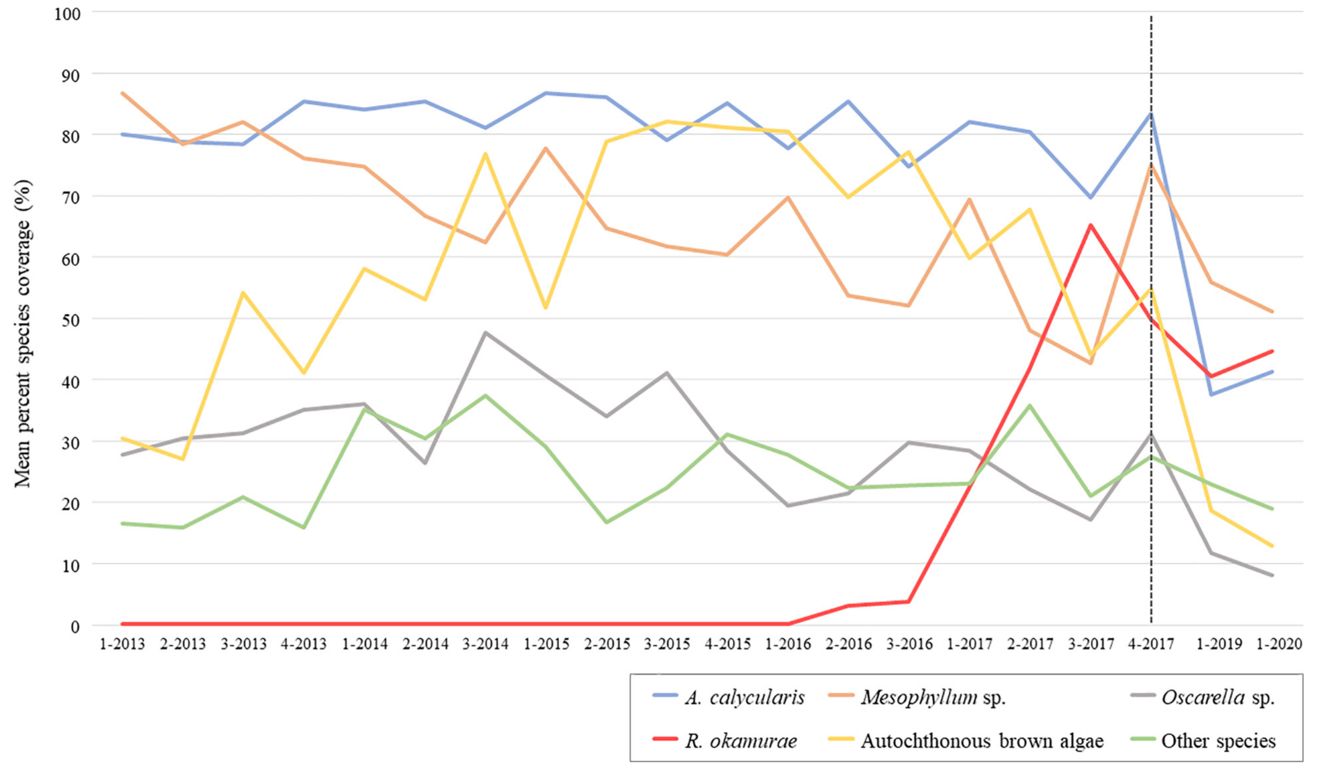


**FIGURE 2 |** Temporal variation of benthic mean species percent coverage at the SBPQ station in Tarifa Island from years 2013 to 2020 (2018 data is missed). The dotted line locates, at the right side of the graph, the species fluctuations recorded after the last monitoring in 2017. Species with less than 10% coverage (*Alcyonium* sp., *Aplidium* sp., *A. armata*, *Crambe* sp., *Ircinia* sp., and *Polycitor adriaticum*) were grouped under "Other species." 1 = winter; 2 = spring; 3 = summer; 4 = autumn.

ecosystems of the northern coasts of the Strait of Gibraltar, both by scientific (SBPQ alert method) and citizen (Citizen Science) monitoring methodologies. This, together with the high coverage levels estimated along the PNE coastline, illustrates the potential risk that the species represents to the benthic ecosystems in the Strait waters.

## Updated Fluctuations of *Rugulopteryx okamurae* by Monitoring Sessile Bioindicators in Permanent Quadrats

The application of the SBPQ methodology has allowed the continuity of monitoring activities from 2017 to 2020 at the shady vertical surfaces of the pre-coralligenous habitats from the submarine sentinel station of Tarifa Island. Results showed that the benthic community structure differed between 2016 and 2017 due the high coverage levels of *R. okamurae* reached in that year. This pattern reflects the high spatial growth of the invasive species and, potentially, the ability to efficient using resources in the recipient habitats (Vaz-Pinto et al., 2014), which could results in the stronger and faster growth in detriment of the resident community, as is observed later in 2019 and 2020.

Until our study, few data have been offered about dominance-dynamics of *R. okamurae* after the huge coverages reached in 2017. Using the same methodology, Sempere-Valverde et al. (2020) registered coverage increments of the invasive species in most of monitored sites of coralligenous habitats after 2017. Our results showed a decrease in percent coverage, slightly increasing in 2020. Changes in shape and size of the macroalgal beds can be modified by a variety of abiotic factors as temperature, salinity or turbidity (Glasby et al., 2005a). In fact, according to bloom-bust dynamic theories, a drastic decline in the invasive populations can occur after an initial rapid increase of the abundances, without implying recoveries in the macroalgal resident communities [e.g., *Caulerpa taxifolia* (M.Vahl) C.Agardh (Glasby et al., 2005a,b)]. This has been further combined with other works that assume that impacts on the resident biota cannot be assessed only considering species gain and loss without including mechanisms involved (Chapin et al., 2000). According to our results, differences in the community structure between the last 2 years and 2017 were due to an effective loss of resident biota, instead of fluctuations in *R. okamurae* presence. This is in line with results from Sempere-Valverde et al. (2020), who also found changes in the community structure and the regression of bioindicator species. Thus, despite certain coverage stabilization could have been raised in the last years, impacts generated by *R. okamurae* remains high in the habitat studied, and therefore it can be assumed that no signs of decline in its invasive potential have been perceived. However, longer-scale monitorings are needed in order to totally stablish the strength of the bioinvasion, so

**TABLE 1 |** PERMANOVA and PERMDISP (for the factor "Year") results for SBPQ station coverage data (2013–2020) **(A)** considering intra-annual variability (i.e., all seasons) and **(B)** only winter seasons.

| | df | SS | MS | Pseudo-F | P(MC) |
|---|---|---|---|---|---|
| **(A)** | | | | | |
| Year | 6 | 5,329.8 | 888.3 | 18.673 | <0.001 |
| Time (year) | 13 | 618.43 | 47.571 | 0.97385 | 0.5173 |
| Res | 40 | 1,954 | 48.849 | | |
| Total | 59 | 7,902.2 | | | |
| P (PERMDISP): | 0.6006 | | | | |
| Pair-wise test for years 2019 and 2020 | 2019 = 2020 ≠ 2017 ≠ (2016, 2015, 2014, 2013) | | | | |
| | 2020 = 2019 ≠ 2017 ≠ (2016, 2015, 2014, 2013) | | | | |
| **(B)** | | | | | |
| Year | 6 | 2,995.1 | 499.18 | 8.2181 | <0.001 |
| Res | 14 | 850.38 | 60.741 | | |
| Total | 20 | 3,845.5 | | | |
| P (PERMDISP) | 0.4237 | | | | |
| Pair-wise test for years 2019 and 2020 | 2019 = 2020; = 2017; ≠ (2016, 2015, 2014, 2013) | | | | |
| | 2020 = 2019; ≠ 2017; ≠ (2016, 2015, 2014, 2013) | | | | |

*Pair-wise comparisons are based in Monte-Carlo P values. Summary results of Pair-Wise tests are showed only for comparisons between 2019–2020 and the series 2013–2017 (evidences of significative differences are referred as ≠ [i.e., P(MC) < 0.05] while "=" is used when no evidences were obtained).*

monitoring efforts should be continued in the future to full characterize dynamics observed here.

Sessile Bioindicators in Permanent Quadrats focuses on monitoring information in substrata colonized by colonial species with long life cycle [i.e., pre-corallingenous (García-Gómez et al., 2020a) and coralligenous rocky bottoms (Sempere-Valverde et al., 2020)], so changes due to long established species can be easily perceived. In this study, the data available in winter revealed similar patterns while more progressive changes across years than when considering the whole intra-annual variability from 2013 to 2017. Thus, although the larger information obtained the higher characterization of the species dynamic can be ensured, the high similarity between ordination analyses performed in this study, reinforce the utility of the SBPQ methodology even with one sampling per year. Moreover, taking into account that at least in introduced habitats the species is also present in winter, cold seasons could be especially interesting because smaller coverages of the species may allow to reflect competitive processes missed in those periods where huge biomass led the substrata overgrowth.

## Implications of Coverage Estimations of *Rugulopteryx okamurae* Within the PNE

Coverage results obtained in 2018 by García-Gómez et al. (2020b) on horizontal illuminated rocky surfaces, extrapolated here for a larger-scale approximation, suggest a high impact on sublittoral habitats due to the massive occupation of the generalized conquest of rocky areas by *R. okamurae*. In general, the coverage data obtained were very high, especially if compared with the biomass data observed in native habitats (Japan) by Agatsuma et al. (2005) (with similar north latitude to Spain, between 20° and 40°). Results obtained for coverage extrapolation coincide with those obtained in 2019–2020 by CAGPyDS (2020) for the bathymetric intervals between 0 and 20 m (80–100% *R. okamurae* coverage). However, the same results were not found for the intervals between 20 and 30 m (10–50%), so it could be interpreted a possible decline between 2018 and 2020 in the depth ranges where the illumination exposition is lower, so the competitive interactions with the resident macrobiota have not been able to be maintained after the initial stages of strong expansion after 2016.

Following the favorability models (Real et al., 2006), *R. okamurae* could proliferate within the ecological environments within the Atlantic coasts of Andalusia and Morocco, the Mediterranean Sea and the Black Sea (Muñoz et al., 2019). In fact, it has been confirmed the fast progress of the species toward the Mediterranean and Atlantic waters, and the recent arrival by wrack deposits at the nearby coasts of Granada and Almería (Altamirano et al., 2019; CAGPyDS, 2020; Figueroa et al., 2020). The nature of the ecosystem implications by *R. okamurae* establishment in the recipient ecosystems have been previously exposed in García-Gómez et al. (2018); Altamirano et al. (2019) and García-Gómez et al. (2020b). Results obtained in these experiences and the spread dynamic of the species alarm the rate of recorded invasions by marine macroalgae that have taken the place of target resident species becoming dominant in the last years (Boudouresque and Verlaque, 2002). This makes the geographic expansion along the rocky surfaces of the PNE littoral worrying and stress the detriment of the benthic biota already attributed to the establishment of *R. okamurae* in the area. In the southern coasts of the Strait, habitat changes derived from *R. okamurae* establishment have proved to have implications in endangered coralligenous species (Sempere-Valverde et al., 2020) and associated fauna to resident macroalgae (Navarro-Barranco et al., 2019), so it could be also expected that effects on sessile communities can be also translated to other ecosystem components. As Levine et al. (2004) propose, recognizing that biotic containment can occur through species interactions, it could be expected that ecosystem components interacting with *R. okamurae* could regulate the invasive populations dominance. In this sense, more efforts are needed studying interspecific interactions involving the invasive species and the incipient role of co-occurring specific resident taxa taking advantage of the spatial colonization [e.g., *A. armata* has been observed on dense populations of *R. okamurae* (unpublished data)].

Moreover, the high coverage estimations challenge the ecosystem and socio-economic services in the area. The PNE is an integral part of the Mediterranean Intercontinental Biosphere Reserve. It is frequented by tourists and scuba divers, while receives a high influence from both commercial and recreational traffic from areas as Algeciras Bay (Bermejo et al., 2014). Although impacts on socio-economic services have not being investigated, the excess of biomass shortly after *R. okamurae* establishment reported substantial impacts in the area, both in tourism and fisheries (e.g., the trap of

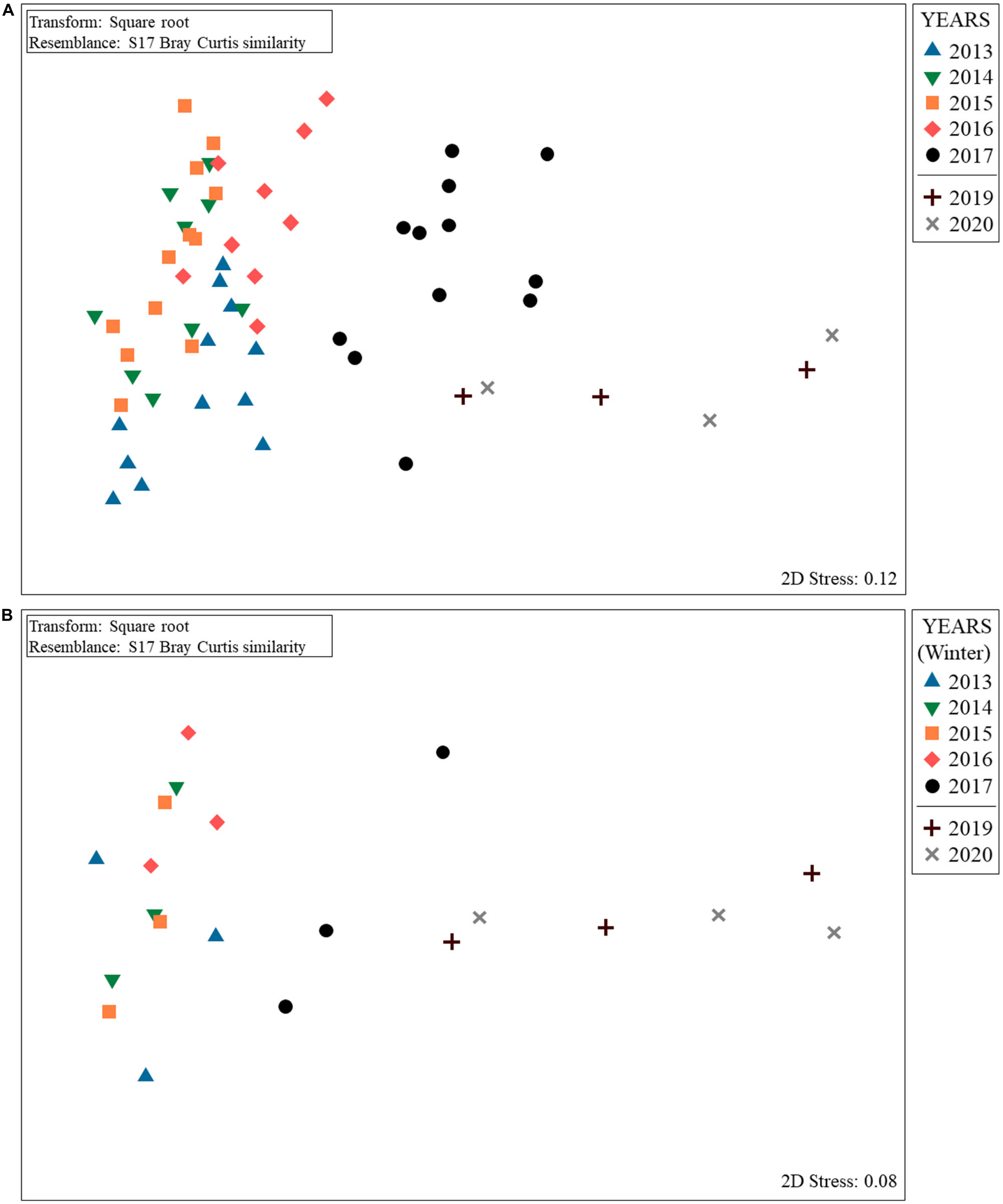


**FIGURE 3 |** nmMDS ordination for Tarifa Island SBPQ station showing the evolution of sessile communities from 2013 to 2020 (2018 data is missed) taking into account **(A)** intra-annual variability (i.e., seasons within each year) until 2017 and **(B)** only winter seasons.

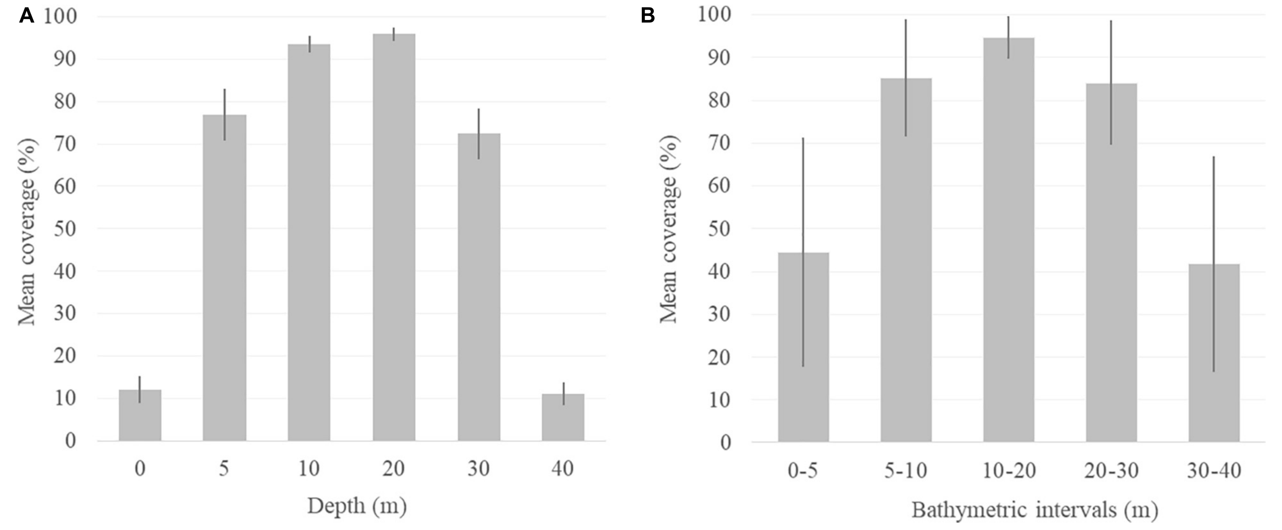


**FIGURE 4 |** Mean percentage coverage of *R. okamurae* in the **(A)** bathymetric range obtained from the southern coasts of the Strait of Gibraltar (Ceuta) in summer 2018 (García-Gómez et al., 2020b) and **(B)** average mean percent coverage estimated for the bathymetric intervals of the sublittoral PNE rocky areas. Standard deviation error bars are included in both cases.

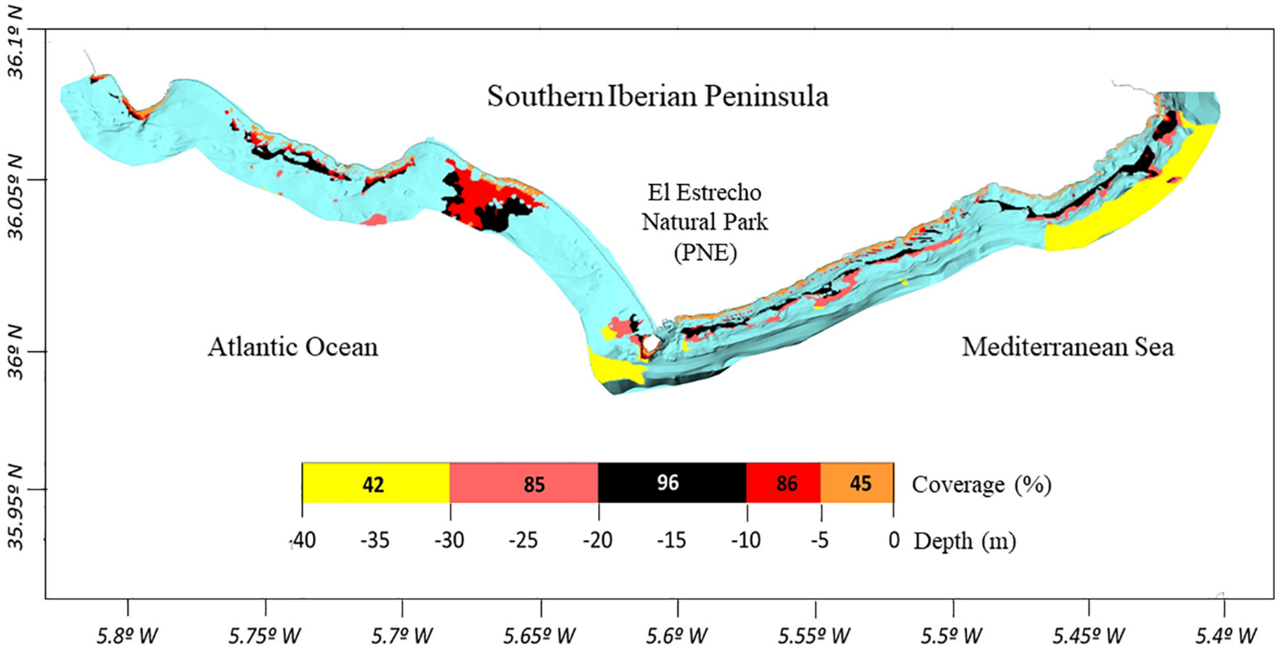


**FIGURE 5 |** Distribution map of estimated *R. okamurae* coverage along the rocky coastline of the PNE. Color scale represents coverage percentages per bathymetric intervals. Blue colors are referred to the total area considered within the cartography (i.e., 1 mile from the coast).

Tarifa) (García-Gómez et al., 2018; Altamirano et al., 2019). If we consider the ability of the species to easily remain attached on nets and other artificial materials (García-Gómez et al., 2018), results obtained for estimations at 1 mile from the coastline enhance the attention on potential impacts in practices developed in the area. Moreover, taking into account that the species was inadvertently introduced via marine aquaculture within the European waters (Thau Lagoon) (Verlaque et al., 2009), preventive strategies for secondary spread pathways across the Mediterranean and the Atlantic waters must be strongly considered.

Facing with the arduous challenge to strategies applied in advanced invasion stages, mitigation efforts could be essential to protect similar areas not yet impacted but susceptible to be invaded. It is as this point that monitor/modeling techniques play a key role, since estimations based on cartographies can

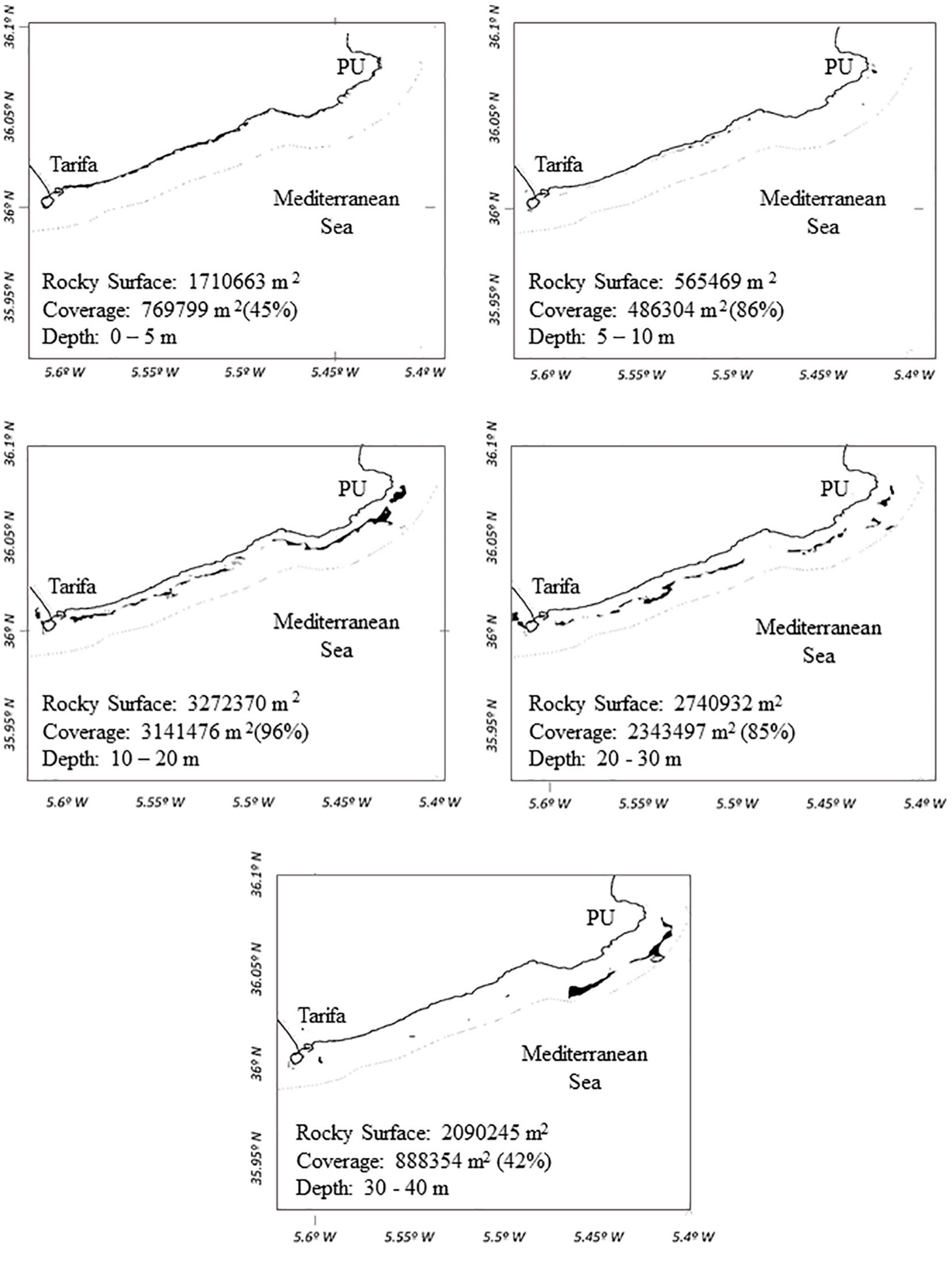


**FIGURE 6 |** Rocky surface areas ($m^2$) (black patches) mapped for the eastern sublittoral of the PNE (1 mile from the coast). Percentage coverages of *R. okamurae* at the different bathymetric intervals are represented (0–5, 5–10, 10–20, 20–30, and 30–40 m). PU = Punta Carnero.

result useful to identificate areas not yet colonized. Moreover, existing precedents of successful actions against invasive marine macroalgae establishment and propagation have revealed that monitoring strategies are not effective unless applied in early stages of colonization, when the species has a limited spatial distribution (Anderson, 2007). In fact, according to Ojaveer et al. (2015), if the species has already managed to establish in large areas, eradication is unlikely. In this sense, it is worth highlighting the case of *C. taxifolia* as a precedent of marine bioinvasion which invasive process resulted impossible to be stopped by control efforts (Ruesink and Collado-Vides, 2006), becoming the most widespread invasive macroalga in the

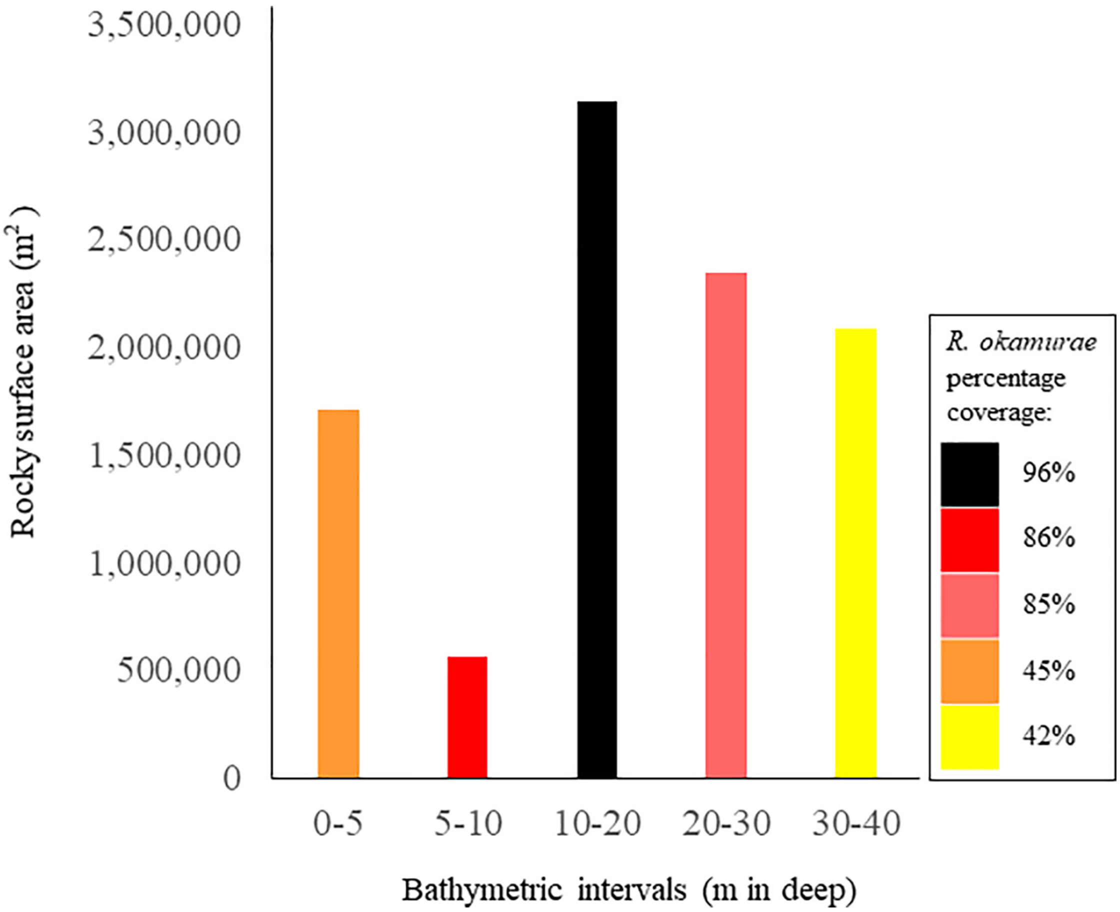


**FIGURE 7 |** Rocky surface areas (m$^2$) obtained for each bathymetrical interval (m) of the sublittoral coastline of the PNE. Colors legend represent the different percentage coverage values obtained for each bathymetrical interval mapped for the northern Strait of Gibraltar coastline (see **Figure 5**).

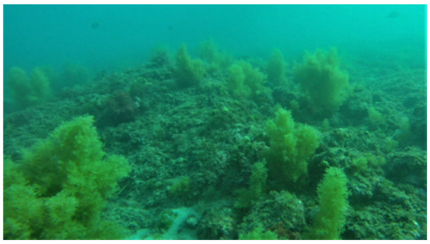
Mediterranean waters, occupying 20,000 Ha of sublittoral areas (Anderson, 2007).

## Before-After Seascape Scenarios Reflecting Extreme Changes Due *Rugulopteryx okamurae* Invasiveness

The comparative analyses of images can make it possible to obtain inferences about the behavior of the biota and the ecological connectivity, since the underwater seascape can have a great influence (Grober-Dunsmore et al., 2009). In this regard, the Citizen Science initiative developed in this study allowed a large spatial and temporal dataset to visualize impacts related with *R. okamurae* establishment, providing an accurate underwater seascape of the bioinvasion consequences. The seascape sampling provided an adequate approach for monitoring developments and it was useful for describing and categorizing some benthic communities that interact with the brown macroalga in the PNE littoral. Comparisons before and after *R. okamurae* establishment revealed an overall substitution of the benthic seascapes by the invasive species, but also effectively evidenced negative impacts on particular resident species. For example, the disappearance of sea urchin species [*Arbacia lixula* (Linnaeus, 1758) and *Paracentrotus lividus* (Lamarck, 1816)] from different shallow rocky bottoms could be inferred by comparing pairs of images examined. Indeed, in most of the cases, signs of total colonization were observed only 3 years after its establishment in the Strait of Gibraltar and thus, impacts by the generalized substitution of the resident macroalgae at illuminated and shaded habitats (i.e., native and invasive species already established in the area, as those from the genus *Asparagopsis*) were particularly visible.

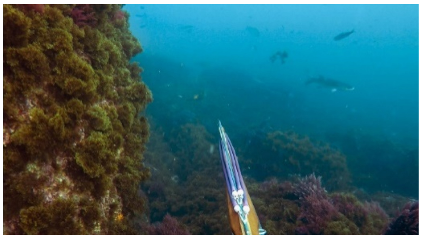
*In situ* observational data also increased the quantity of *R. okamurae* observations available for ecological researches (as it has previously been pointed out by Crall et al., 2015). Image data from 2016 at Tarifa Island revealed that *R. okamurae* monopolized more than 80% of highly illuminated horizontal surfaces at hard bottoms between 5 and 10 m depth, which contrast with results obtained at partially shaded vertical substrata sampled in the SBPQ station in the same year, where <10% mean coverage was estimated by photoquadrat analyses. In the latter habitats, *R. okamurae* coverage increased later, in 2017 (<60% coverage) (García-Gómez et al., 2020b), and thus revealing habitat-dependent patterns not previously perceived.

**TABLE 2 |** Comparisons before and after *R. okamurae* first apparition in the Strait of Gibraltar coasts (2015) in locations surveyed in the study area.

| Before 2015 | After 2015 |
|---|---|
| **Caldera Profunda** | |
| <br>May 2011<br>Bare horizontal and vertical metallic surfaces (artificial substrata) with associated coverage of photophilic crustose macroalgae | <br>September 2018<br>Horizontal and vertical metallic surfaces highly colonized by *R. okamurae* |
| **Tanque Gasoil** | |
| <br>September 2006<br>Bare horizontal and vertical metallic surfaces constituting the artificial substrata with associated populations of *Treptacantha usneoides* (Linnaeus) Orellana & Sansón (arboresecent talli of large size) | <br>September 2016<br>Horizontal and vertical metallic surfaces constituting the artificial substrata highly coated by *R. okamurae*. Populations of *T. usneoides* were not observed |
| **La Garita** | |
| <br>September 2006<br>Horizontal illuminated natural habitats colonized by *T. usneoides* (arborescents thalli), *Halopteris scoparia* (Linnaeus) Sauvageau, *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier and crustose macroalgae of the genus *Lithophyllum* | <br>September 2016<br>Horizontal illuminated natural habitats monopolized by *R. okamurae* |
| **Pozas Intermareales** | |
| <br>February 2006<br>Intertidal pool walls subjected to long shadow periods along the day, with no signals of *R. okamurae* presence | <br>May 2019<br>Overall presence of *R. okamurae* (discontinuous circle) closed to the vertical walls of the intertidal pools |

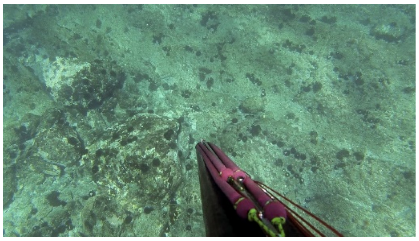
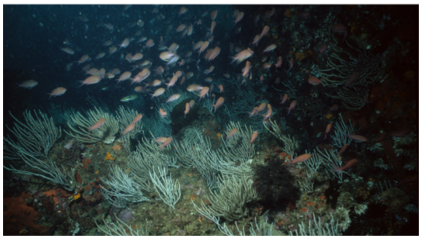
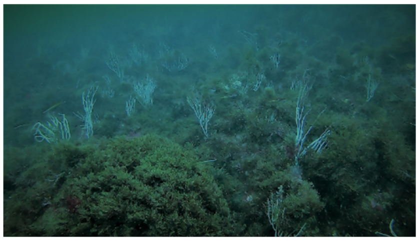
*(Continued)*

**TABLE 2 |** Continued

| Before 2015 | After 2015 |
|---|---|
| **El Tejar** | |
|  |  |
| October 2012.<br>Natural rocky substrata scarcely colonized by resident macroalgae while significant coverages of photophilic crustose macroalgae | October 2018<br>Natural rocky substrata totally coated by *R. okamurae* and detached mats floating on the water column |
| **La Caleta** | |
|  |  |
| July 2012<br>The seascape was characterized by the high presence of the invasive resident species *A. armata* and the sympatric native macroalga *H. scoparia* | July 2019<br>*R. okamurae* monopolized the rocky substrata. Affections by *R. okamurae* were observed on the photophilic crustose coralline communities |
| **La Isleta** | |
|  |  |
| August 2012<br>Natural rocky substrata where the sea urchin *A. lixula* is presented | August 2018<br>Surfaces totally coated by *R. okamurae*, while *A. lixula* was not detected |
| **Barranco Hondo** | |
|  |  |
| August 2012<br>Wide coverage of resident macroalgae (mainly native species) on natural rocky substrata | September 2018<br>Replacement scenarios of the benthic macrobenthos by *R. okamurae*, together with the presence of the previously established invasive macroalga *A. armata*. Affections by *R. okamurae* were also observed on the photophilic crustose coralline communities |

*(Continued)*

**TABLE 2 |** Continued

| Before 2015 | After 2015 |
|---|---|
| **Guadalmesí I** | |
| <br>May 2012<br>Natural rocky substrata with hardly any coverage of macroalgae and a generalized presence of the sea urchins *A. lixula* and, to a lesser extent, *P. lividus* | <br>May 2019<br>Apparent dominance of *R. okamurae* and disappearance of a large part of populations of the species *A. lixula* and *P. lividus* |
| **Guadalmesí II** | |
| <br>August 2015<br>Apparent high abundances of resident macroalgal species (e.g. *Dyctiota dichotoma var. intricata* (C. Agardh) Greville, *Dyctiota fasciola* (Roth) J. V. Lamouroux and *A. armata*) | <br>June 2017<br>Generalized presence of *R. okamurae* to the detriment of the previously established resident benthic biota. Affections by *R. okamurae* were also observed on photophilic crustose coralline communities |
| **Punta Carnero** | |
| <br>October 2016<br>The gorgonian colonies of *Eunicella singularis* (Esper, 1791) with resident macroalgal associated communities on rocky substrata (20–25 m depth) | <br>September 2019<br>The macroalgal community was replaced by the monopolized presence of *R. okamurae*. Adjunct substrata were practically colonized by the invasive macroalga (20–25 m depth) and the spatial pressure on gorgonians present was apparent |

## CONCLUSION

The present study determined that impacts derived from *R. okamurae* establishment remain high in the rocky habitats studied of the PNE. Monitoring studies on the SBPQ station of Tarifa Island revealed a high spatial establishment of the invasive species since its first detection in 2015 and an efficient loss in the sessile resident biota in the latter years, even in periods of minimum growth. In view of the ecosystem implications, coverage values estimated for rocky habitats (over 85% between 10 and 30 m depth) claim monitoring efforts focused in threatened habitats not yet colonized a remain step ahead of the drastic scenarios observed. In this regard, Citizen Science collaborations for the detection, evaluation and monitoring of impacts from *R. okamurae* resulted a useful and promising tool for further studies. We consider that these monitoring initiatives would be even more successful if combined with periodic monitoring methodologies under specific designs. Thus, monitoring stations located in areas coinciding with those where contributors act (e.g., SBPQ station in Tarifa Island), could allow citizen collaboration through the applicability of non-invasive tools for image analysis procedures easy to understand and apply.

Only if these tools are promoted within local networks (i.e., high anthropic pressure areas), they could help to early detect and monitor (e.g., "before-after" approximations) local (e.g., urban discharges, oil slicks) or global environmental impacts (e.g., global change), which would facilitate to act in time in the face of bioinvasion schemes.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

JG-G involved in investigation, writing – original draft, analysis data, supervision, validation, funding acquisition, and project administration. MF involved in investigation, writing – original draft, analysis data, and data curation. LO-P involved in investigation, special collaboration writing – original draft, and data curation. JRDdR involved in investigation and collaboration in cartography of coverage. ID-A involved in investigation, analysis data and special collaboration writing – original draft. MC, JQ, and SM collaboration underwater images "before-after" impact (Citizen Science). CM involved in investigation and supervision; JG-G, MF, LO-P, ID-A, and CM contributed substantially to revisions of manuscript. All authors contributed to the article and approved the submitted version.

## FUNDING

This study was funded by the CEPSA Foundation and Red Eléctrica de España (REE). Additional financial support was provided by the Organization of Fish Producers of Almadrabas (OPP-51), ENDESA, ACERINOX, and Diputación Provincial de Cádiz. This project has also benefited from scientific equipment and infrastructures financed by the AP of Seville and the Aquarium of Seville and by the VI Plan Propio Universidad de Sevilla via a post-doctoral grant (ID-A).

## ACKNOWLEDGMENTS

We are deeply grateful to Manuel Martínez Chacón, Juanjo Quintero, and Salvador Magariño for their selfless collaboration "Citizen Science" in the search, obtaining underwater images, and selection of graphic information, especially from documentary archives prior to 2015. We are also grateful to Red Eléctrica de España (REE) and CEPSA Foundation for mean financial support to scientific research related to the environmental impact of the invasive species *Rugulopteryx okamurae* on the marine autochthonous biodiversity of the Bay of Algeciras, Strait of Gibraltar, and nearby areas, and to Organization of Fish Producers of Almadrabas (OPP-51), ENDESA, ACERINOX, and Diputación Provincial de Cádiz for additional financial support, related with the presence of invasive algae in their artisanal fishing or industrial port infrastructures. We thank the Port Authority of Seville (APS) and Seville Aquarium for scientific infrastructure acquired in project number 1889 (FIUS), related to the estuary of the Guadalquivir River implied in environmental monitoring campaigns and controls in the areas near the mouth of the mentioned river. We thank ESGEMAR, S.A., for providing cartographic support and map delimitation and CIES (Algeciras) and Campo de Gibraltar (La Linea) diving clubs. We also thank Isabel Cárdenas, Curro Sánchez, Rocío Espada, Juan Miguel Recio, Antonio Vegara, José Fosela, and Candela Sánchez for their continued collaboration. This paper has been benefited in the city of La Línea by the logistical support of Puerto La Alcaidesa, the Yacht Club (RCNLL), and the Maritime Club, as well as by the town halls of this city and Tarifa.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.639161/full#supplementary-material

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**Conflict of Interest:** JRDdR was employed by the company Esgemar S.A.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 30 April 2021
doi: 10.3389/fevo.2021.631762

# Development and First Tests of a Lab-Scale Electric Field for Investigating Potential Effects of Electric Barriers on Aquatic Invasive Invertebrates

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Canals and other connected waterway systems, including the Chicago Area Waterway System (CAWS), have often facilitated the spread of non-native species. Electric barriers have recently emerged as a method for preventing this spread and protecting uninvaded ecosystems from new invaders. The largest system of electric barriers in the world is in the CAWS and is operated primarily to prevent the spread of invasive Asian carp. It is not known whether these barriers are effective for other species, particularly invasive invertebrates. Here, we provide data regarding the efficacy of an electric field that operates at the same parameters as the electric barrier in the CAWS in affecting behaviors of two invertebrate species, the red swamp crayfish *Procambarus clarkii* and the amphipod *Hyalella azteca*. We constructed an electric field within a tank that operates at the same parameters as the existing CAWS barriers and determined the effects of the electric field on our test species. At the electric field parameters of the CAWS barriers, the vast majority of *P. clarkii* individuals showed altered movement with maintained equilibrium. For *H. azteca*, behavioral responses were less extreme than for *P. clarkii*, with a majority of individuals experiencing altered movement. By measuring the orientation of organisms to the electric field, we determined that the test organisms are affected by the electric field, especially at lower field strengths where they exhibited no or little other behavioral response. At lower field strengths, *P. clarkii* exhibited changes in orientation, but at higher field strengths, individuals were less able to orient themselves. *H. azteca* exhibited changes in orientation to the electric field at all field strengths. The results of this study suggest that the existing electric barriers may not slow or prevent spread of invasive invertebrates—including amphipods and crayfish—through passive movement attached boats/barges or through downstream drift, but that the barriers may prevent spread by active upstream movement. Overall, our work gives new data regarding the efficacy of electric fields in preventing the spread of invasive invertebrates and can inform management decisions regarding current and future electric barriers in the CAWS.

**Keywords: invasive species, crayfish, *Procambarus clarkii*, *Apocorophium lacustre*, Chicago Sanitary and Ship Canal, amphipod**

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**Specialty section:**
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

**Received:** *20 November 2020*
**Accepted:** *22 March 2021*
**Published:** *30 April 2021*

**Citation:**
*Egly RM, Polak RD, Cook ZA, Moy HD, Staunton JT and Keller RP (2021) Development and First Tests of a Lab-Scale Electric Field for Investigating Potential Effects of Electric Barriers on Aquatic Invasive Invertebrates. Front. Ecol. Evol. 9:631762. doi: 10.3389/fevo.2021.631762*

## INTRODUCTION

Invasive freshwater species cause large ecological and economic impacts (Pimentel et al., 2005; Lodge et al., 2016). Preventing the spread of established invaders is a major goal for conservation and management but can be particularly difficult in connected freshwater ecosystems (Strayer, 2010). Whereas many terrestrial invasive organisms can be managed with herbicides, pesticides, and mechanical means, the available technologies for managing freshwater invasive species are more limited because of the difficulty of directly targeting a given species (Manfrin et al., 2019). Recently, there has been the development and limited deployment of novel technologies for controlling invasive species and restricting their spread through freshwater ecosystems. These include bio-bullets (BioBullets[1]), which target filter-feeding biofouling organisms in industrial settings, electric barriers to deter spread of aquatic organisms (Sparks et al., 2010; Benejam et al., 2015; Kim and Mandrak, 2017), and more recently the suggestion that water saturated with carbon dioxide could be used to inhibit the spread of invasive organisms (Kates et al., 2012; Treanor et al., 2017; Suski, 2020). While these technologies each offer promise, more research is needed to understand how effective they are at deterring spread of a range of non-native species.

The Mississippi River and Laurentian Great Lakes basins have been invaded by many non-native aquatic species, including bighead and silver carp (*Hypophthalmichthys nobilis* and *Hypophthalmichthys molitrix*; Kolar et al., 2005), round goby (*Neogobius melanostomus*; Kornis et al., 2012), rusty crayfish (*Faxonius rusticus*; Peters et al., 2014), and numerous amphipods (Grigorovich et al., 2005, 2008). These basins were ecologically separated until the 19th century when canals were built to facilitate transport and wastewater disposal. The major connection between them is the Chicago Sanitary and Ship Canal (CSSC), which forms part of the Chicago Area Waterway System (CAWS). The CSSC was opened in 1900 and created the first large permanent waterway connecting the Mississippi and Great Lakes basins. Subsequent canal building has expanded the CAWS, and there are now three harbors in Lake Michigan from which water flows through the CAWS and eventually into the Mississippi River. This connection has allowed several non-native freshwater species to move from the Great Lakes to the Mississippi River and vice versa. Some of these species are presumed to have moved with the aid of boats *via* hull-fouling (e.g., *Dreissenid* mussels), while others (e.g., round goby) have presumably been able to transit the system unaided (Holeck et al., 2004; Keller et al., 2011).

Electric barriers are an emerging technology for preventing the spread of invasive aquatic species through waterways and canals (Sparks et al., 2010; Benejam et al., 2015; Kim and Mandrak, 2017). These barriers offer the promise of addressing invasive species threats without affecting the flow of water or the passage of recreational and commercial boats. The largest electric barriers in operation are in the CSSC where they have been developed and parameterized to prevent the upstream spread of Asian carp species from the Mississippi River into the Great Lakes (Holliman et al., 2015; Parker et al., 2015). Although the electric barriers may prevent spread of these large fishes, the CSSC remains a potential route for spread of many other taxa, which pose risks of moving through both upstream and downstream and which may be transported on the hulls of boats. Little information has previously been available about the effect of electric barriers on these other species or modes of transport.

The CAWS remains a major risk for spread of damaging invasive species, and much effort has been expended to understand how species move through it, which species pose a large risk for future spread, and how that spread can be prevented (Veraldi et al., 2011). After round goby became established in the Great Lakes, there was sufficient concern about its potential to spread into the Mississippi River Basin that the construction of electric barriers in the CSSC was proposed and approved (Sparks et al., 2010). Unfortunately, by the time the first barrier (known as the Demonstration Barrier) was operational in 2002, round goby was already established in the Mississippi River Basin (Kornis et al., 2012). Subsequent barriers (Barrier IIA and IIB) were constructed in 2009, and all three barriers now operate to deter the spread of bighead and silver carp (these species are often collectively referred to as Asian carp) from the Mississippi River Basin to the Great Lakes (Veraldi et al., 2011; Parker et al., 2015). The barriers consist of steel cable electrodes that create direct current (DC) pulses in the CSSC at an electric field strength of 2.3 V/in, a frequency of 34 Hz, and a pulse length of 2.3 ms (USACE, 2011). These parameters were established based on tests with bighead and silver carp (Holliman et al., 2015). A further barrier (Permanent Barrier I) is planned to be operational by 2021 and will be the first barrier with flexibility to adjust settings for electric field strength, frequency, and pulse duration (Charles Shea, USACE, personal communication). Testing is currently being conducted by the United States Army Corps of Engineers to determine the parameters at which Permanent Barrier I will be operated. Although the electric barriers in the CAWS are operated to prevent the spread of invasive silver and bighead carp, many other non-native species present risks of moving through this system, and it is unknown whether the barriers could effectively prevent their spread. Previous studies have found that electric fields can alter the behavior of crustaceans including fright or anxiety-like responses, attempted escape from the field, and involuntary restless movement, but the effect of electric fields on mobility and mortality in invertebrates is largely unknown (Biswas, 1971, 2008; Vannini and Insom, 1976; Fossat et al., 2014; Perrot-Minnot et al., 2017). If the barriers are not effective, then greater resources and actions may be necessary to prevent the spread of these species. In this study, we have tested the effect of different electric field strengths on two aquatic invertebrate species: *Hyalella azteca*, a small invertebrate amphipod that is native to the region, and *Procambarus clarkii* (red swamp crayfish), a large invasive crayfish that is currently of great concern due to its recent arrival and spread in the Great Lakes region.

These species were chosen for two reasons. First, electric fields are known to affect different sized organisms in different ways, and the two species used in our experiment measured are of quite different sizes (*H. azteca* average size of 4.6 mm; *P. clarkii*

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[1] http://biobullets.com

average size of 20.2 mm). Second, these species either are already of invasion concern in the region or are taxonomically and morphologically similar to species of concern. *P. clarkii* is an invasion concern as a crayfish with recently detected established populations in inland and Great Lakes-adjacent waters in Illinois, Ohio, Michigan, and Wisconsin (Ellison, 2015; Bunk and Van Egeren, 2016; Jacobs and Keller, 2017; Donato et al., 2018; Smith et al., 2018; Egly et al., 2019; Oficialdegui et al., 2019). Native to the south-central United States and northern Mexico, *P. clarkii* is a generalist species that can survive in a wide range of freshwater habitats and is already globally widely established (USGS; Cruz and Rebelo, 2007; Larson and Olden, 2012). Invasive populations of *P. clarkii* can reduce biomass and species richness of macrophytes, leading to stable state shifts, reduced abundance of macroinvertebrates, and displaced native crayfishes through mechanisms such as competition for food and shelter (Rodríguez et al., 2003; Paglianti and Gherardi, 2004; Gherardi and Acquistapace, 2007; Matsuzaki et al., 2009; Twardochleb et al., 2013). We used juvenile *P. clarkii* since the effect of the electric field on an organism is directly proportional to organism size (Sternin et al., 1976; Miranda, 2009), so juveniles are likely to be less affected by the electric field than adults and thus more likely to pass through the barrier unhindered.

We chose *H. azteca* as a proxy for the amphipod *Apocorophium lacustre* (scud), a filter-feeding amphipod native to estuaries on the Atlantic coasts of North America and Europe (Shoemaker, 1934; Bousefield, 1973; Faasse and van Moorsel, 2003). *A. lacustre* has not previously been reared in any lab and is difficult to maintain. *H. azteca* is similar in size and has similar habitat preferences to *A. lacustre*, is readily available from biological supplies houses, and has well-established protocols for care (Grigorovich et al., 2008). *A. lacustre* was first recorded as established in the lower Mississippi River in 1987 (Payne et al., 1989) and has since spread extensively within the Mississippi River basin to occupy the Ohio River, upper Mississippi River, and the Illinois River. Its current known distribution extends to within 100 river kilometers of Lake Michigan (Heard, 1982; Payne et al., 1989; Grigorovich et al., 2008; Keller et al., 2017).

Our work investigates the effects of electric fields on these two invertebrates. We created an electric field contained within a tank which operates at the same parameters as the existing electric barriers in the CAWS. We are among the first to develop a relatively straightforward system using inexpensive materials for testing the effects of electric fields on smaller organisms. After constructing our electric field, we conducted experiments to determine the effects of the electric field on our test species and classified organism behavior and used order parameter analysis to quantify amphipod and crayfish response to the electric field. Although our study focuses on static electric fields rather than the experience of an organism approaching and moving through an electric field, the behavior and orientation of organisms within an electric field are critical to understanding potential effects of electric barriers on organisms. Based on our initial results, we conducted experiments with higher electric field strengths than are produced in the CSSC to determine whether realistic increases could produce a viable barrier to the spread of invertebrate invaders.

# MATERIALS AND METHODS

## Organisms

Juvenile *P. clarkii* were reared in lab from adult females that were caught in the North Branch of the Chicago River in October 2018 and October 2019. Juvenile *P. clarkii* were kept in aerated tanks with dechlorinated water and fed every 3–5 days. *Hyalella azteca* specimens were purchased from an online vendor and maintained in the lab in aerated tanks with dechlorinated water and fed every 3–5 days.

## Electric Field Setup and Testing

We constructed an electric field within a rectangular glass tank (122 cm long, 32 cm wide, and 34 cm deep) and calibrated it to produce the same electric field strength and waveform as the electric barriers in the CAWS. Our equipment consisted of three elements: a modified backpack electrofishing unit (ETS PK-C[2]); a power supply (Volteq HY3010EX), which supplies a DC to the electrofishing unit and replaces its battery; and two Type 316 stainless steel plate electrodes (38 cm × 27 cm) placed at opposite ends of the tank (**Figure 1**). The electrofishing unit was rewired so that the anode and cathode lines were attached with jumper cables to the electrodes. These were placed at each end of the tank and produced a uniform electric field throughout the tank.

To confirm that our system produced the desired electric field, we compared the true output of the electric field with the expected output based on the backpack readings (**Supplementary Material 3**). In particular, we measured the voltage, current, frequency, duty cycle, and waveform integrity in the tank using a Fluke 87V Industrial Multimeter, Fluke 124B Industrial Scopemeter, and Fluke 80i-119s AC/DC Current Clamp (US Fish and Wildlife Service, 2017). We used both the multimeter and the scopemeter to test voltage. The average difference of the true output voltage compared with the expected output was 1.2% as measured by the multimeter and 3.3% as measured by the scopemeter. The multimeter measured current between 0.04 and 0.10 A, higher than the expected output when measuring a range of currents from 0 to 1.1 A. We also used the scopemeter to measure frequency and duty cycle. The scopemeter confirmed that the waveform of the output was as expected. The average difference was 2.1% for frequency and 6.4% for duty cycle. These differences are minor considering the range over which we ran the electric field (see below) and confirm that the electric field produced was similar to that of the barrier in the CAWS.

## Experimental Protocols

All experiments were conducted using lab water at both ambient water temperature (mean ± standard deviation = 20.3 ± 1.4°C) and ambient specific conductivity (mean ± standard deviation = 321.6 ± 56.8 μS/cm). To recreate the parameters of the electric barrier in the CAWS, the initial settings on the

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[2] https://www.ets.org

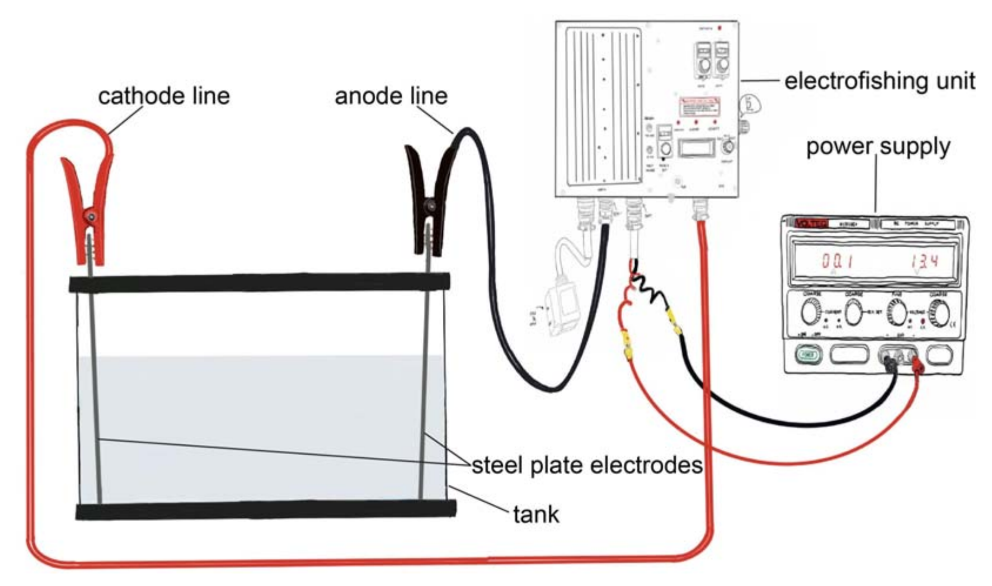

**FIGURE 1 |** Diagram of experimental electric barrier setup, including power supply, electrofishing unit, tank, steel plate electrodes, and cathode and anode lines.

electrofishing unit were 106 V, 34 Hz, pulse length = 2.3 ms, and duty cycle = 7.2%, creating an electric field of 2.3 V/in (USACE, 2011).

Each trial began with five individual organisms (haphazardly selected from a tank containing the available pool of individuals) placed in a non-conductive nylon mesh container in the center of the tank. Trials consisted of three consecutive phases of 5 min: pre-stimulus, stimulus, and post-stimulus (following Kim and Mandrak, 2017). The electric field was off for the pre-stimulus phase, on for the stimulus phase, and off again for the post-stimulus phase. Trials were recorded with a video recorder (GoPro, HERO4) placed overhead at the center of the tank. During each trial, we recorded the behavior at the end of each minute and response to a physical prodding with non-conductive rod every 2.5 min. All organisms were kept for 24 h after each trial to check for delayed mortality. It was not possible to record the behavior of each individual organism over time. Instead, we recorded the number of organisms in each behavioral state at each time. All personnel who recorded behaviors were trained by the lead author and frequently coordinated with each other in an effort to limit observer bias (e.g., two observers viewing the same organism but describing the behavior differently). Our study included distinct behavior categories, which made it difficult to make a mistake in classification, and we often had multiple observers recording results independently, which when compared always displayed >90% agreement between observers. We were not able to make the observers "blind" to whether the barrier was on or off due to safety issues that could arise (Holman et al., 2015). We acknowledge that having different observers and not knowing whether the barrier was on/off may have led to some bias, but for the reasons described, we believe this would have been minimal.

Using the video recordings and SolidWorks software (BIOVIA, 2018; **Supplementary Material 4**), we later determined the orientation of each individual to the electric field every minute during the pre- and post-stimulus phases and approximately every 30 s during the stimulus phase. Initial trials were conducted at the field strength currently produced in the CSSC. Based on results in these trials, we tested the effects on crayfish at 25%, 50%, 200%, 300%, and 400% of the electric barrier's field strength by changing voltage to 26, 53, 212, 318, and 424 V, respectively, while leaving all other parameters constant. We did the same for *H. azteca* except that we did not test at 25 and 50% because of the minimal response observed during the initial (100%) trials for this species.

Three trials were conducted for each combination of field strength and species, and each trial included five individuals. For juvenile crayfish, 18 trials were conducted using a total of 90 individuals (mean carapace length ± standard deviation = 20.2 ± 7.2 mm, $n$ = 90; **Supplementary Table 1**). There were inevitable differences in sizes of individuals available for the different trials. The only trial where this may have been important is the 25% trial, which had somewhat smaller organisms than the other trials (see section "Results"). For amphipods, 12 trials were conducted using a total of 60 individuals (mean length ± standard deviation = 4.6 ± 1.0 mm, $n$ = 60; **Supplementary Table 2**). Individual organisms were not reused in any trials.

## Behavioral Analysis

Observations and video were used to score behaviors during each trial. During the 5-min stimulus phase, organism behavior was recorded and classified every minute for each individual as one of five categories: *no change in behavior*, individual exhibits normal behavior; *altered movement*, individual exhibits difficulty in moving or swimming; *rigid and maintaining equilibrium*, body is rigid but stays upright and organism maintains equilibrium; *rigid and lost equilibrium*, body is rigid with no motor functions and organism is not maintaining itself in upright position; and *mortality*, a loss of equilibrium and motor functions with no recovery, death.

## Order Parameter Analysis

We recorded the influence of the electric field on organism orientation by determining the order parameters and director angles of organisms when the barrier was off (pre- and post-stimulus phases) and on (stimulus phase). For a system of rods or rod-like objects, the order parameter and director angle can be used to describe how well the objects align and in what direction, respectively. Aquatic species such as fish will often orient themselves in a preferred direction relative to a pulsed electric field. In some cases, the fish may swim toward the anode with their bodies oriented parallel to the electric field (Halsband, 1967; Lamarque, 1967). In others, fish will orient themselves perpendicular to the electric field to minimize the electric potential across their bodies, which in turn minimizes the discomfort experienced (Burger et al., 2015). If the long axis of an organism is oriented parallel to the electric field (in our case, this would be an organism oriented with its posterior end pointed at one electrode and the anterior end pointed at the other), the angle would be measured as 0°. If the long axis is perpendicular, it would be measured as 90°.

The orientation of each individual to the electric field was measured five times each during the pre- and post-stimulus phases (every 1 min) and 10 times during the stimulus phase (every 30 s) for a total of 100 measurements per trial. These values were used to determine the average orientation of the organisms to the electric field, called the director angle, and how well the organisms line up with one other, called the order parameter (Andrienko, 2018). When examining the director angle, we are looking to see if the organisms are aligning themselves either parallel (0°) or perpendicular (90°) to the electric field or are oriented in some other direction. If the director angle is close to 0° or 90°, then organisms are likely responding the electric field. The order parameter S, is given by the following equation,

$$S = \left\langle 2\cos^2\theta - 1 \right\rangle \tag{1}$$

where θ is the angle of orientation measured relative to the average orientation and the angle brackets indicate that we are averaging over all measurements. *S* ranges in value from 1, which indicates that all objects in a system are perfectly aligned, to 0, which indicates that objects in a system are randomly oriented. An order parameter of 0.5 would indicate that the organisms are somewhat aligned but have a typical deviation from the director angle of 30°. In this work, we used an increase in order parameter to indicate that the organisms were reacting to the electric field and attempting to align in a preferred direction.

# RESULTS

## Behavioral Analysis

At 100% of the existing electric barrier field strength, most *P. clarkii* individuals experienced altered movement (46%) or rigidity with maintained equilibrium (36%; **Figure 2A**). Fewer *P. clarkii* experienced rigidity and lost equilibrium (10%), and none died either during the experiment or the 24 h following. For *H. azteca*, behavioral responses at 100% of the existing barrier strength were similar (**Figure 2B**), with a majority of individuals (57%) remaining responsive but experiencing altered movement. *H. azteca* individuals also displayed rigidity with maintained equilibrium (31%) and rigidity with lost equilibrium (12%). No *H. azteca* died during the experiment at 100% of existing barrier field strength or during the 24 h following. Results in **Figure 2** are aggregated across time to show overall behavior during the stimulus phase at different electric field strengths because reactions across the five organisms in each trial did not change consistently throughout the 5-min stimulus phase for either species (see **Supplementary Figures 1**, **2** for full time series data).

At electric field strengths ≥200% of the existing electric barrier field strength, the number of strong behavioral responses increased for *P. clarkii*, with the majority of individuals experiencing rigidity and lost equilibrium (64% at 200% barrier strength, 77% at 300% barrier strength, 91% at 400% barrier strength; **Figure 2A**). Again, none were killed during the experiments, and all recovered within 24 h after the experiments. At electric barrier strengths lower than the existing barrier (25 and 50%), behavioral effects on *P. clarkii* were less extreme. At 25% of the existing barrier's electric field strength, *P. clarkii* did not exhibit any behavioral response; but at 50% of the existing barrier's electric field strength, a majority of individuals displayed altered movement (72%). We note that juvenile crayfish used in the trials for 25% of the existing barrier's strength were slightly smaller (average size = 12.7 mm vs. average size for all juveniles tested of 20.2 mm). This was due to the availability of individuals and may have affected the behavioral response seen in the 25% trial.

For the amphipod *H. azteca*, an increasing number of individuals experienced rigidity and lost equilibrium at electric field strengths ≥200% of the existing barrier, with 51% of individuals experiencing rigidity and lost equilibrium at 400% (**Figure 2B**). None were killed during the experiments, and all except three individuals survived for 24 h after the experiment. Two *H. azteca* from the 200% trial died, and one from the 400% trial.

## Order Parameter Analysis

For every trial, we calculated director angle and order parameter when the electric field was on (stimulus phase) and off (pre- and post-stimulus phases). At 25% of the existing electric barrier's electric field strength, *P. clarkii* did not exhibit a behavioral response recorded on our five-point scale (see above) but did exhibit changes in orientation. These changes in orientation are characterized by an increase in the order parameter (**Figure 3A**) and a director angle close to 90° (i.e., perpendicular alignment to the electric field) when the electric field was on (**Figure 4**). At 50% and 100% of the existing barrier's field strength, we observed a larger increase in the order parameter when the electric field was turned on and a director angle close to 90°. However, at electric field strengths ≥200% of the existing electric barrier, the increases in order parameter were smaller, and the director

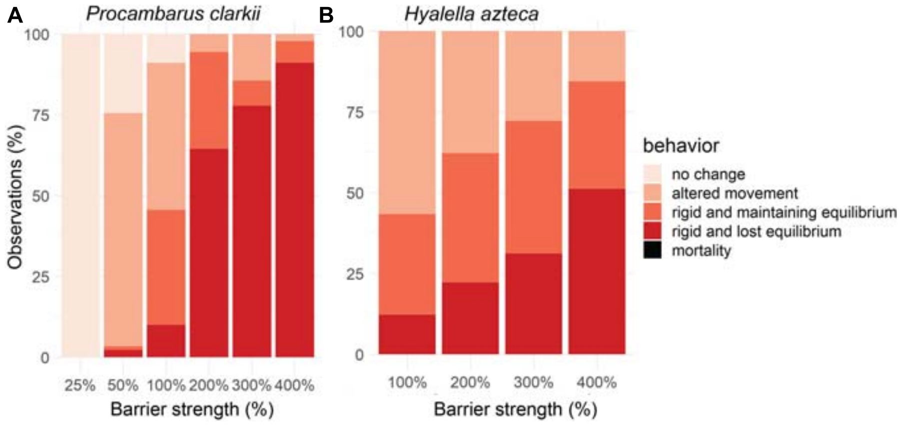

**FIGURE 2 |** Aggregated behavior across time during 5 min of stimulus phase for **(A)** juvenile *Procambarus clarkii* (*n* = 15 for each barrier strength) for 25%, 50%, 100%, 200%, 300%, and 400% of existing barrier strength; and **(B)** *Hyalella azteca* (*n* = 15 for each barrier strength) for 100%, 200%, 300%, and 400% of existing barrier strength.

angle when the electric field was turned on was not close to 0° or 90°.

*Hyalella azteca* exhibited changes in orientation to the electric field at all electric field strengths, characterized by an increase in the order parameter and a director angle close to 90° (perpendicular alignment) when the electric field was turned on (**Figure 4**). At 200% of the existing barrier's electric field strength, we observed a larger increase in the order parameter when the electric field was turned on than other voltages (**Figure 3B**). At 400% of the existing barrier's electric field strength, order parameter values and director angles indicate that organisms were still capable of responding to the electric field. At all electric field strengths, individuals were able to maintain equilibrium, and order parameter values and director angles can be inferred to be a response to the discomfort of the electric field.

## DISCUSSION

It is unknown whether the existing barrier in the CSSC would deter the passage of invertebrates such as our study species. Based on our results, it appears that the electric field created by the existing barriers would affect behavior of organisms similar to those used in our study when they were within the barriers. Our results indicate that invertebrates similar in size to our two study species may be less affected by electric fields than Asian carp (Holliman et al., 2015; Parker et al., 2015). When exposed to an electric field identical to that in the CSSC, many *P. clarkii* and *H. azteca* were able to maintain equilibrium, many remained mobile, and none were killed. This indicates that individuals of either species could survive transit through the barrier at its existing strength. Transit could occur attached to the hull of a boat or in downstream drift (i.e., from the Great Lakes to the Mississippi basin). Our work did not directly address whether either of these species would be deterred from independent movement upstream through the barrier at its current strength.

Our constructed electric field is flexible in its parameters, and this allowed us to test the effects of lower electric field strengths on *P. clarkii* and higher electric field strengths on both *P. clarkii* and *H. azteca*. For *P. clarkii*, at ≥50% of the existing barrier's electric field strength, some individuals exhibited altered movement and rigidity, but there was only a consistent loss of equilibrium at ≥200% of the existing barrier's electric field strength. Similarly, at ≥100% of the existing barrier's electric field strength, *H. azteca* individuals exhibited altered movement and rigidity but did not consistently experience loss of equilibrium even at 400% of the existing barrier's electric field strength. Few individuals of either species died during the experiments, and this was only at very high electric field strengths.

The order parameter and director angle analysis offer complementary metrics for investigating the effects of electric fields on invertebrates. At 25% of the existing barriers' field strength, there was no apparent change in *P. clarkii* behavior, but this species was clearly orienting itself to reduce exposure to the electric field. As described in the section "Materials and Methods", this may have been influenced by the smaller size of the organisms used in this trial, which we would expect to make them less susceptible to the effects of the electric field (see section "Results"). This effect was also apparent at 50% and 100% of the barrier strength, but at 200% and above, *P. clarkii* individuals were less able to orient themselves. This is consistent with most individuals being rigid at and above this field strength and presumably unable to orient themselves in relation to the electric field. This effect was not observed for *H. azteca*, which were still able to orient themselves at 90° to the electric field at the maximum field strength of 400%. These results show that invertebrates are sensitive to electric fields even at low strengths relative to the existing CSSC barrier, and it is plausible that this sensitivity may provide a deterrent to active upstream movement.

Previous results from the CSSC show that the electric field weakens near the hulls of metal boats (Dettmers et al., 2005). Dettmers et al. (2005) confined fish to non-conductive cages attached to both non-conductive and steel-hulled boats traveling

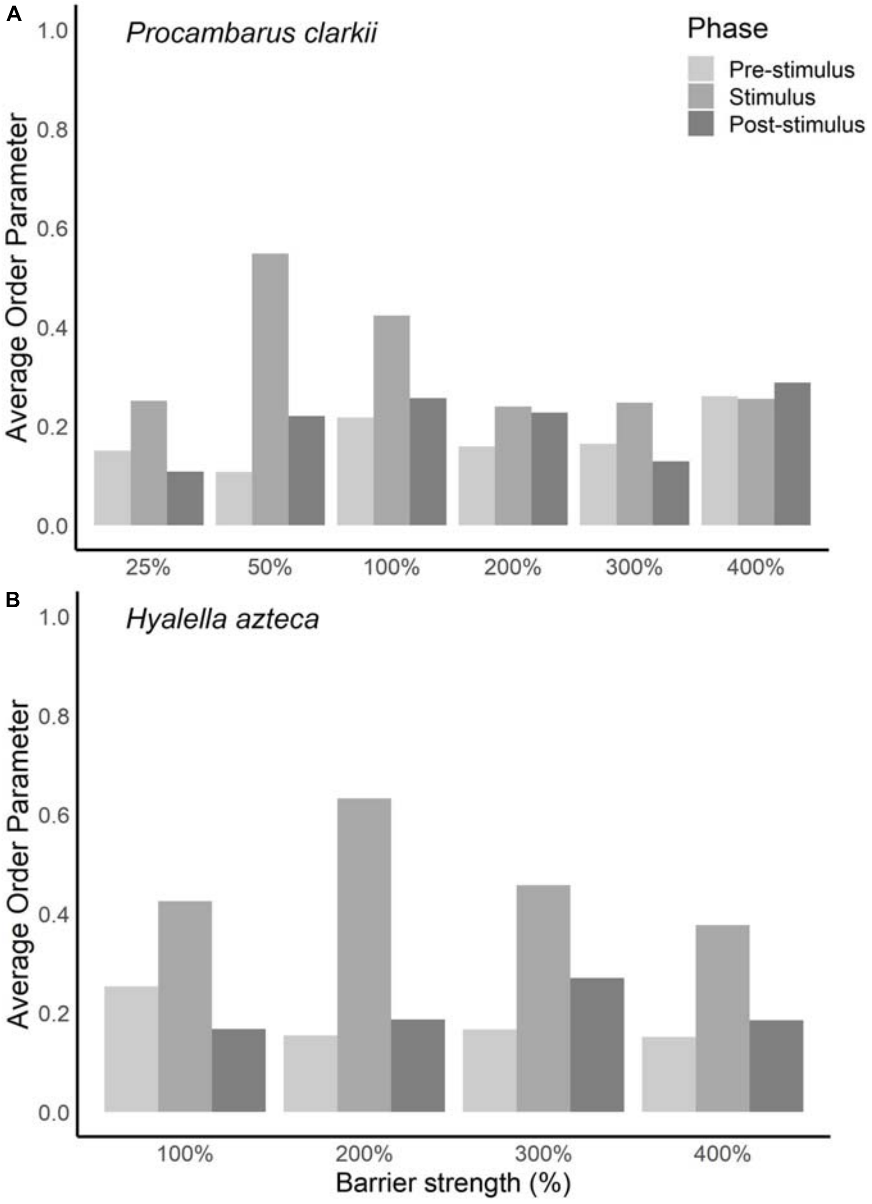

**FIGURE 3 |** Average order parameter values while barrier was turned off (pre- and post-stimulus phases) and while barrier was turned on (stimulus phase) for different barrier strengths for **(A)** *Procambarus clarkii* and **(B)** *Hyalella azteca*.

through the electric barrier to determine whether steel-hulled barges reduce the electric field immediately around their hulls, potentially allowing fish to move through the electric barriers. They found that fish swimming alongside steel-hulled boats took about three times longer to become immobilized than those swimming alongside non-conductive boats. Although measurements have not been taken at the interface of the boat and water, this suggests that fouling organisms would experience a far lower strength of electric field than a barrier puts into the water column. Fouling organisms, which are similar in size to *H. azteca*—such as the invasive *Apocorophium lacustre*—may have a similar response. For these organisms, our behavioral results suggest that even at full strength, the existing barriers are unlikely to cause dislodgement of fouling organisms from boats. While further studies investigating how metal barges affect the electric field would be helpful, the available evidence suggests that the existing barriers are unlikely to prevent the spread of organisms that move attached to hulls. Additionally, crayfish species such as *P. clarkii* have the ability to spread to new waterbodies through overland dispersal (Ramalho and Anastácio, 2014). Although our study does not address this method of spread, the existing electric barriers in the CAWS would be ineffective in preventing overland dispersal of *P. clarkii*.

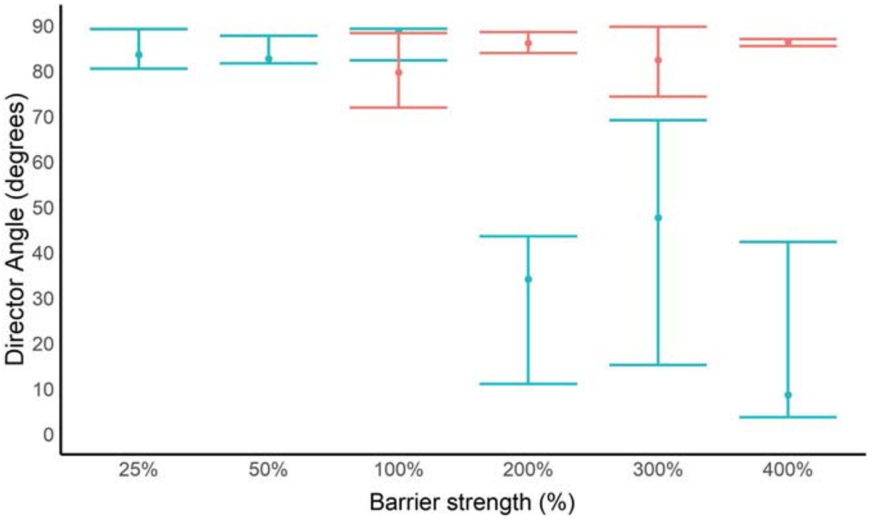

**FIGURE 4 |** Average and range of director angle values for *Procambarus clarkii* and *Hyalella azteca* during stimulus phase for different barrier strengths. Juvenile *P. clarkii* is displayed in blue, and *H. azteca* is displayed in red.

The additional electric barrier being designed for the CAWS will be capable of flexible operating parameters (Charles Shea, USACE, personal communication). Our results show that very large increases in field strength would be required to appreciably change the effect on invertebrates. It is possible, however, that changes to waveform, pulse duration, and/or pulse length may make the barrier more effective for addressing the risks from invasive invertebrates. We did not experiment across changes in these parameters, but we urge that more research on this be conducted because it is possible that parameters exist, which better balance prevention of movement for fishes and invertebrates without simply increasing the strength of the electric field.

The two invertebrate species that we tested measured an average of 4.6 mm for *H. azteca* and 20.2 mm for juvenile *P. clarkii*. Previous studies have shown that organism size is an important determinant of the effects of electric fields, with larger organisms generally being more affected (Sternin et al., 1976; Miranda, 2009). Although we tested two invertebrates of varying average size, there are taxonomic and morphological differences among invertebrates that likely also affect organism response. For example, mollusks have shells and are most likely to transit the barriers attached to boats. We thus consider it unlikely that they would be strongly affected by the barriers, although this should be tested. Zooplankton, on the other hand, is most likely to drift through the barrier in the water column. Based on our results, we would not expect such organisms to be killed, and downstream drift is presumably a feasible mode of spread through the barrier. Further data on the electric barrier's effects on a larger taxonomic range would be useful in determining parameters for future electric barriers.

A species of particular and immediate concern for spread through the CSSC and into Lake Michigan is the amphipod *A. lacustre*. This species is morphologically similar to *H. azteca* and has a distribution in the CAWS up to the Dresden Island Pool, 40 river kilometers from the existing electric barrier (Grigorovich et al., 2008; Keller et al., 2017; Egly et al., 2021) and within 100 river kilometers of Lake Michigan. Due to its proximity to the Great Lakes, its ability to withstand a wide range of environmental conditions (Szöcs et al., 2014), and the high abundances it reaches in its invasive range, which may alter food webs by displacing native amphipods (Heard, 1982; Grigorovich et al., 2005, 2008), *A. lacustre* is listed in the United States Army Corps of Engineers' Great Lakes and Mississippi River Interbasin Study as a High Risk Aquatic Invasive Species (Veraldi et al., 2011). This species is known to be transported as a fouling organism on boats (Power et al., 2006). Our results indicate that the existing electric barriers are unlikely to prevent its spread, and thus that additional management will be necessary if the species is to be prevented from entering the Great Lakes.

Previous studies of electric barriers have largely focused on fishes. These have found that electric barriers can restrict movement of sea lamprey (Swink, 1999), common carp (Verrill and Berry, 1995), and Asian carps (Sparks et al., 2010; Parker et al., 2015), but there are large gaps in information regarding effectiveness of electric barriers, particularly concerning operating parameters, effects on non-target species, and how effects depend on organism size. Our study is the first of which we are aware that begins to fill gaps in the research by providing methods for construction of an electric field contained in a tank using inexpensive materials and providing data on the response of invertebrates to electric fields. Results suggest that electric barriers may deter the spread of invasive invertebrates similar to our study organisms but only if those organisms pose a risk of spreading upstream by their own locomotion. Further research into electric barriers operating with different parameters may find parameters that have stronger effects.

## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

RE, RP, ZC, HM, and JS constructed the experimental electric barrier. RE and RK designed the experiments. RE, RP, ZC, HM, and JS conducted the experiments and analyzed the data. RE and RK wrote the manuscript with assistance from all co-authors.

## FUNDING

Sampling was conducted under Illinois Department of Natural Resources Permit Number A18.6222. This research was financially supported by the Illinois Department of Natural Resources Grant Number RC20FW144B and Illinois Indiana Sea Grant Number F0008309702040.

## ACKNOWLEDGMENTS

Jonathan Cirone, Liz Chaparro, and Andrew Fischer aided with construction of the barrier and experiments. Colette Copic aided with field sampling. Kannon Larison, Justin Hameline, and Sarah Sukanen aided with editing the manuscript. Julia Egly and Jonathan Cirone created diagram of the barrier setup.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.631762/full#supplementary-material

**Supplementary Figure 1 |** Behavior of juvenile *Procambarus clarkii* during stimulus (barrier on) and post-stimulus (barrier off) phases for **(A)** 25%, **(B)** 50%, **(C)** 100%, **(D)** 200%, **(E)** 300%, and **(F)** 400% of existing barrier strengths.

**Supplementary Figure 2 |** Behavior of *Hyalella azteca* during stimulus (barrier on) and post-stimulus (barrier off) phases for **(A)** 100%, **(B)** 200%, **(C)** 300%, and **(D)** 400% of existing barrier strengths.

**Supplementary Table 1 |** Size of *Procambarus clarkii* individuals used in experiments for different electric field strengths.

**Supplementary Table 2 |** Size of *Hyallela azteca* individuals used in experiments for different electric field strengths.

**Supplementary Material 3 |** Electric barrier calibration report.

**Supplementary Material 4 |** Order Parameter Data Collection/SolidWorks.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

REVIEW
published: 26 May 2021
doi: 10.3389/fevo.2021.629756

# Plastic as a Vector of Dispersion for Marine Species With Invasive Potential. A Review

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Plastic debris constitutes up to 87% of marine litter and represents one of the most frequently studied vectors for marine alien species with invasive potential in the last 15 years. This review addresses an integrated analysis of the different factors involved in the impact of plastic as a vector for the dispersal of marine species. The sources of entry of plastic materials into the ocean are identified as well as how they move between different habitats affecting each trophic level and producing hot spots of plastic accumulation in the ocean. The characterization of plastic as a dispersal vector for marine species has provided information about the inherent properties of plastics which have led to its impact on the ocean: persistence, buoyancy, and variety in terms of chemical composition, all of which facilitate colonization by macro and microscopic species along with its dispersion throughout different oceans and ecosystems. The study of the differences in the biocolonization of plastic debris according to its chemical composition provided fundamental information regarding the invasion process mediated by plastic, and highlighted gaps of knowledge about this process. A wide range of species attached to plastic materials has been documented and the most recurrent phyla found on plastic have been identified from potentially invasive macrofauna to toxic microorganisms, which are capable of causing great damage in places far away from their origin. Plastic seems to be more efficient than the natural oceanic rafts carrying taxa such as Arthropoda, Annelida, and Mollusca. Although the differential colonization of different plastic polymers is not clear, the chemical composition might determine the community of microorganisms, where we can find both pathogens and virulent and antibiotic resistance genes. The properties of plastic allow it to be widely dispersed in practically all ocean compartments, making this material an effective means of transport for many species that could become invasive.

**Keywords: plastic debris, alien species, marine exotic species, plastic dispersion, marine ecosystem, non-indigenous species**

***Edited by:***
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*Institute of Botany (ASCR), Czechia*

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***Specialty section:***
*This article was submitted to*
*Biogeography and Macroecology,*
*a section of the journal*
*Frontiers in Ecology and Evolution*

***Received:*** *15 November 2020*
***Accepted:*** *18 March 2021*
***Published:*** *26 May 2021*

***Citation:***
*García-Gómez JC, Garrigós M and Garrigós J (2021) Plastic as a Vector of Dispersion for Marine Species With Invasive Potential. A Review.*
*Front. Ecol. Evol. 9:629756.*
*doi: 10.3389/fevo.2021.629756*

## INTRODUCTION

Marine ecosystems around the world are threatened by several factors related to human activity (Ibabe et al., 2020), such as biological invasions (Ojaveer et al., 2015). Invasive species generally have a strong influence on the invaded environment, altering the structure of the community and the functions of the ecosystem, through competition with native species (Bertness, 1984), introduction of pathogens (Rilov and Crooks, 2009b), or indirect changes in habitat conditions (Crooks, 2002).

The exponential increase in the rate of invasive alien species (IAS) over the last decades has stimulated the study of biological invasions (Seebens et al., 2017), especially in the marine environment, which has received less attention compared to the terrestrial one (Davis, 2000; Katsanevakis et al., 2014). In addition to traditional marine vectors (biofouling and ballast water), which gained importance with the development of commercial shipping (Carlton, 1987; Clarke Murray et al., 2014), new challenges were added to the study of dispersion factors, such as plastic materials (see Audrézet et al., 2020; previous and complementary article of this review, mainly focused on the biosecurity of marine plastic debris and the knowledge gaps and research priorities that exist on this topic), other materials derived from aquaculture or aquarium hobbies (Rilov and Crooks, 2009b; Walters et al., 2011).

Plastic is a potential dispersal vector of marine species (Rech et al., 2016). It is the most common marine debris, constituting 61–87% of all types of marine debris (Eriksen et al., 2014; Serra-Gonçalves et al., 2019), and is considered as one of the major threats to marine biodiversity (Avio et al., 2017). Plastic production has increased exponentially in the last 60 years, from 0.5 million tons in 1960, to almost 300 million tons in 2013 (PlasticsEurope, 2014) and 360 million tons in 2018 (PlasticsEurope, 2018). About 10% of plastic production has been introduced into marine ecosystems (Thompson, 2006) through land-based sources such as rivers, storm drains (Moore et al., 2011), urban runoff, sewage discharge, effluents from plastic manufacturing factories (Eerkes-Medrano et al., 2015), landfills or recycling points (Alomar et al., 2016), coastal areas due to the action of the wind, illegal dumping, fishing, and other human activities (Derraik, 2002). van Sebille et al. (2015) estimated that microplastics (MPs) in the oceans have reached $52.2 \times 10^{12}$ particles, 236,000 metric tons, mainly distributed in the centers of the subtropical gyres.

The global distribution, buoyancy, and high levels of colonization of plastic debris greatly facilitate the transport of microbial communities (Carson et al., 2013), algae, invertebrates, and fish (Goldstein et al., 2014) to non-native regions (Barnes, 2002). Marine plastic debris is not only a threat to marine wildlife, but also causes significant economic and ecological damage (Keswani et al., 2016) acting both as a vector for the primary introduction of alien species into remote regions, and as a secondary vector for the regional expansion of marine species (Rech et al., 2016; Audrézet et al., 2020).

Several gaps remain to be filled regarding the potential of plastic as a species vector. For example, the harmonization of methodological approaches to study marine litter in different environmental compartments (Galgani et al., 2019) or the impact caused by the secondary propagation, which is not yet sufficiently documented (National Oceanic and Atmospheric Administration Marine Debris Program, 2017). Also, understanding the biosecurity implications associated with plastics could be a vital step toward understanding, monitoring, and eventually mitigating its impacts on a global scale (Audrézet et al., 2020).

This work aims to identify the dispersal potential of plastic as a vector for alien species introductions and to compare it with other vectors, as well as to expose the qualitative composition of the communities that inhabit plastic debris. On the other hand, we attempt to synthesize the methodological aspects of the detection of AIS introduced through plastic debris and the prevention of their negative impacts.

## METHODOLOGY

Scientific literature published in the last 30 years (1990–2020) was collected from Science Direct, Scopus, Web of Science, and Google Scholar scientific databases, and the most widely consulted publishers and/or scientific internet networks were Elsevier, Springer, ResearchGate, Wiley Online Library, Dialnet, and Academia. The keywords related to invasive species in the ocean, especially those carried by plastic debris, were used in the title and keywords field: "Alien Species," "Ballast Water," "Biofouling," "Ecology," "Ecosystem," "Impact," "Invasive Species," "Marine," "Management," "Microplastics," "Ocean," "Plastic Debris," "Rafting," "Sea," "Threat," "Transport," "Vector," and "Waste." The searches were conducted mostly in March 2020 on the full range of articles or reviews available at that time. The last search was made on April 20, 2020.This initial search yielded a total of 447 articles which included information on invasive and potentially invasive species in the ocean and different dispersal vectors. In this preliminary library, a pre-selection step was carried out according to the presence of at least one of three criteria: (1) articles focused on the impact caused by one or more invasive marine species; (2) articles focused on the management of the invasion of one or more marine species; or (3) articles that include both concepts. After applying these selection criteria, 228 articles were obtained, of which 48 were discarded after analysis because they were not directly related to the topic with respect to the sections considered in the manuscript. Therefore, most of the information presented in this paper was extracted from 180 scientific publications. In addition, other articles named in the literature and previously known to the authors due to their high topic relevance were used for the review.

Selected articles were classified according to the dispersion vector(s) (Plastic Debris, Boat hulls (biofouling), Climatic Events, Ballast Water, Aquaculture, or General), their publication date (1990–2005 or 2006–2020), and the aspect addressed: Impact (I), Management (M) or Impact+Management (I+M). Impacts included articles focused on describing the impacts produced by alien species, and Management included articles focused on the management of these impacts. We separated the last 30 years into two bands to appreciate the differences in the efforts made by scientists regarding different topics in the near past and at present. On the other hand, the label "General" was included for those papers that covered more than one vector.

For the invasive or potentially invasive species listed in **Table 1**, it was specified whether they were sessile or no sessile, in order to draw conclusions about the biology of the species inhabiting plastic. Also, it was specified the transport vector for which they were identified (Plastic Debris, Boat hulls (biofouling), Climatic Events, Ballast Water, Aquaculture, Aquariums, or Transoceanic Channels/Swimming). The native

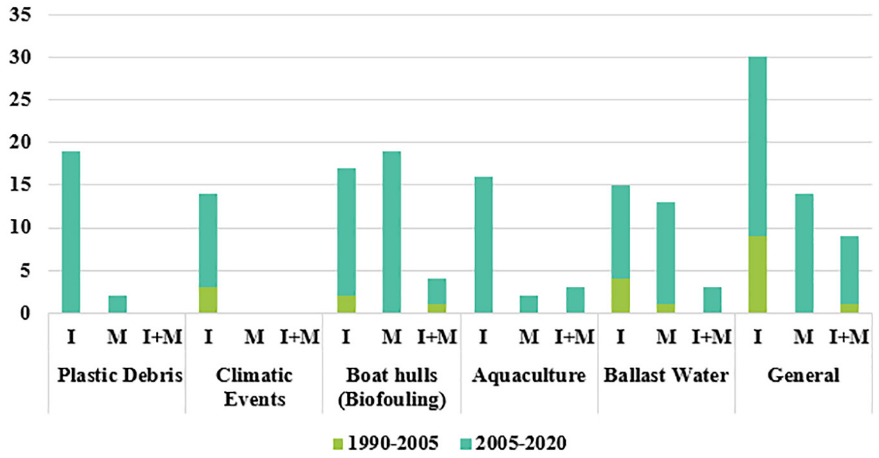

**FIGURE 1 |** Percentage of alien marine species introduced by different dispersal vectors on a global scale (see **Table 1** for details).

and non-native locations of the invasive and potentially invasive species were indicated.

Moreover, other relevant information was extracted from the selected and related articles such as plastic as a vector, different types of plastic and how their characteristics affect the colonization of macro and microscopic marine species, recurrent species transported by plastics, associated microorganisms dispersion and species and dispersal patterns of plastic in the ocean and how they can influence horizontal and vertical transport.

## PLASTIC DEBRIS COMPARED TO OTHER DISPERSAL VECTORS

With respect to the total number of articles, the labels that yielded the highest number of selected articles were "Boat hulls (biofouling) and Ballast Water" including I, M, and I + M, with 40 and 31 papers, respectively, followed by "Plastic Debris, Aquaculture and Climate Events" (21, 21, 15, respectively) (**Figure 1**).

In the last 15 years, the most frequent labels were "Plastic Debris-Impact," and "Biofouling – Management" with 19 articles each. No articles were selected between 1990 and 2005 for the labels "Plastic Debris" and "Aquaculture." There was also a great difference in the number of research papers on the management of invasive species from the dispersal vectors "Boat hulls (biofouling)" and "Ballast Water," and the vectors "Plastic Debris," "Aquaculture," and "Climatic Events."

Of the 216 exotic species identified in the present study (**Table 1**), 68% were considered to have been introduced through maritime transport, divided into the categories "Boat hulls (biofouling)" and "Ballast Water," followed by dispersal as a consequence of the "Aquaculture" (16%), and "Plastic debris" (5%) (**Figure 2**).

This result is to be expected, as commercial shipping as a cause of IAS dispersal has been cited long before other vectors such as plastic (e.g., Carlton, 1987). Although it is a more recent problem, we consider that the studies on plastics as an IAS vector were quite important between 2005 and 2020. Furthermore, it is expected that the number of papers on plastic as a vector of species will increase in the coming years, as its production increases every year and it is currently an emergent topic.

## CHARACTERIZATION OF PLASTIC AS A VECTOR

Plastic debris abundance (Winston et al., 1997), artificial origin (Glasby et al., 2007; Pinochet et al., 2020), and properties can affect its potential to act as a vector of IAS: durability, buoyancy (Schoener and Rowe, 1970), size, and structural complexity of the surface determine colonization by marine organisms and the succession of the community associated with plastic debris, with differences in the sessile and mobile organisms (Kiessling et al., 2015).

The increasing introduction of plastic pollution into the ocean increases the chances for alien species to become invasive. For example, the bryozoan *Electra tenella* [Hickins, 1880; this name is currently not accepted and it is *Arbopercula tenella* (Hickins, 1880)] previously identified on natural rafts, may be increasing in abundance and distribution due to the increasing amounts of plastic entering the Caribbean currents and the Gulf Stream (Winston et al., 1997). Natural rafts (eg, wood, pumice, and marine vegetation) are generally characterized by low or patchy abundance, limited longevity, and relatively high habitability, due to high surface roughness, structural complexity, and biodegradability (Gil and Pfaller, 2016). Compared to natural rafts, the abundance of plastic debris is increasing (Ebbesmeyer and Ingraham, 1992), and its longevity generally exceeds that of natural debris, taking decades or even centuries to be degraded (Gregory, 1999). The durability of plastic along with its buoyancy in comparison to organic materials (Schoener and Rowe, 1970) allows a greater dispersal potential for organisms that colonize plastic debris (Barnes, 2002; Barnes

**TABLE 1 |** Compilation of invasive and non-native species which have been introduced or transported into areas far from their origin by the following dispersal vectors: Plastic, boat hulls (biofouling), ballast water, aquaculture, aquarium, and transoceanic channel/swimming.

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| **Algae (34)** | | | | | | | | | | |
| ***Acrothamnion preissii*** E.M.Wollaston, 1968 | | X | | X | | X | | Indo-Pacific (Australia) | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Agardhiella subulata*** **(**C.Agardh) Kraft and M.J. Wynne, 1979 | | | | | X | | | Atlantic North America | United Kingdom | Eno et al., 1997 |
| ***Anotrichium yagii*** (Okamura) Baldock, 1976 | | X | | | | | | Japan | Argentina | Horta and Oliveira, 2000 |
| ***Antithamnionella spirographidis*** (Schiffner) E.M. Wollaston, 1968 | | X | | | | | | Mediterranean Sea | United Kingdom | Eno et al., 1997 |
| ***Antithamnionella ternifolia*** (J.D.Hooker and Harvey) Lyle, 1922 | | X | | | | | | Australia | United Kingdom | Eno et al., 1997 |
| ***Asparagopsis armata*** Harvey, 1855 | | X | | | | | | Western Australia New Zealand | European coasts Northeast Atlantic Mediterranean Sea South Africa Middle East Indo-Pacific | Pinteus et al., 2018 |
| ***Bonnemaisonia hamifera*** Hariot, 1891 | | X | | | | | | Northwest Pacific | Europe | Katsanevakis et al., 2014 |
| ***Caulerpa cylindracea*** Sonder, 1845 | | | | X | | X | | Indo Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Caulerpa ollivieri*** Dostál, 1929 | | X | | X | | | | Mediterranean Sea | Bahamas | Williams, 2007 |
| ***Caulerpa taxifolia*** (M.Vahl) C.Agardh, 1817 | | | | X | | X | | Pacific Ocean | Mediterranean Sea | Occhipinti-Ambrogi and Savini, 2003 |
| ***Codium fragile tomentosoides*** **(1)** (van Goor) P.C.Silva, 1955 | | X | | X | | X | | Japan | Northwest Atlantic | Williams, 2007 |
| ***Codium fragile atlanticum*** (A.D.Cotton) P.C.Silva, 1955 | | | | | X | | | Pacific coast of Japan | United Kingdom | Eno et al., 1997 |
| ***Colpomenia peregrina*** **(2)** (Sauvageau) Hamel, 1937 | | | | | X | | | Pacific coast of North America | United Kingdom | Eno et al., 1997 |
| ***Durvillaea antarctica*** (Chamisso) Hariot, 1892 | | | X | | | | | Chile Southern New Zealand South Atlantic | King George Island (Antarctica) | Fraser et al., 2018 |

*(Continued)*

**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Eucheuma denticulatum*** (N.L.Burman) Collins and Hervey, 1917 | | | | | X | | | Sulu Sea | Indian Ocean | Williams, 2007 |
| ***Grateloupia doryphora*** (Montagne) M.Howe, 1914 | | | | | X | | | Pacific North America | United Kingdom | Eno et al., 1997 |
| ***Grateloupia filicina* var. *luxurians* (3)** A.Gepp and E.S.Gepp, 1906 | | | | | X | | | Japan | United Kingdom | Eno et al., 1997 |
| ***Grateloupia imbricata*** Holmes, 1896 | | X | | | | | | Japan Korea | Portugal | Chainho et al., 2015 |
| ***Grateloupia lanceolata* (4)** (Okamura) Kawaguchi, 1997 | | X | | | | | | East of Asia | Portugal | Chainho et al., 2015 |
| ***Grateloupia turuturu*** Yamada, 1941 | | X | | | | | | Pacific ocean | Portugal | Chainho et al., 2015 |
| ***Halophila stipulacea*** (Forsskål) Ascherson, 1867 | | | X | | | | | Indo-Pacific | Mediterranean Sea | Hernández-Delgado et al., 2020 |
| ***Kappaphycus alvarezii*** (Doty) Doty ex P.C.Silva, 1996 | | | | | X | | | Sulu Sea (Philippines) | Southwest Pacific Indian Ocean | Williams, 2007 |
| ***Lomentaria clavellosa*** (Lightfoot ex Turner) Gaillon, 1828 | | X | | | | | | Northeast Atlantic | North America | Mathieson et al., 2008 |
| ***Lophocladia lallemandii*** (Montagne) F.Schmitz, 1893 | | | | | | | X | Indo-Pacific | Northern Coast Ibiza | García-Gómez et al., 2020b |
| ***Mastocarpus papillatus*** (C.Agardh) Kützing, 1843 | | X | | X | | | | North Pacific | Chile | Castilla and Neill, 2009 |
| ***Monostroma oxyspermum* (5)** (Kützing) Doty, 1947 | | X | | | | | | Northeast Atlantic Northwest Pacific | West coast of India | Anil et al., 2002 |
| ***Neosiphonia harveyi* (6)** (Bailey) M.-S.Kim, H.-G.Choi, Guiry and G.W. Saunders, 2001 ***Polysiphonia harveyi* (6)***Bailey, 1848* | | X | | X | X | | | Japan North-Pacific Pacific coast of Japan | Argentina United Kingdom | Eno et al., 1997; Schwindt et al., 2014 |
| ***Pikea californica*** Harvey, 1853 | | X | | | | | | North America | United Kingdom | Eno et al., 1997 |

*(Continued)*

**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Polysiphonia morrowii*** Harvey, 1857 | | X | | X | | | | Northeast Asia | Chile | Castilla and Neill, 2009 |
| ***Rugulopteryx okamurae**** (E.Y.Dawson) I.K.Hwang, W.J.Lee and H.S.Kim, 2009 | X | X | | | X | | | Pacífico noroccidental | Strait of Gibraltar (Cádiz, Spain) Thau Lagoon (France) Western Mediterranean | Huang, 1994; Verlaque et al., 2009; García-Gómez et al., 2018 |
| ***Sargassum filicinum* (7)** Harvey, 1860 | | X | | | | | | Japan and Korea | California (UNITED STATES) | Miller et al., 2006 |
| ***Solieria chordalis*** (C.Agardh) J. Agardh, 1842 | | X | | X | | | | Northern France | United Kingdom | Eno et al., 1997 |
| ***Undaria pinnatifida*** (Harvey) Suringar, 1873 | | X | | | X | | | Northwest Pacific | Spain France Unites Kingdom Belgium The Netherlands New Zealand Australia Argentina | Epstein and Smale, 2017 |
| ***Womersleyella setacea*** (Hollenberg) R.E.Norris, 1992 | | X | | X | | | | Pacific | Mediterranean Sea | Williams, 2007 |
| **Porifera (4)** | | | | | | | | | | |
| ***Crambe crambe*** (Schmidt, 1862) | | X | | X | | | | Mediterranean Sea | Portugal | Chainho et al., 2015 |
| ***Gelliodes fibrosa* (8)** (Wilson, 1925) | | X | | | | | | Philippines | Pearl Harbor (Oahu, Hawai) | Godwin, 2003; Therriault et al., 2018 |
| ***Paraleucilla magna*** Klautau, Monteiro and Borojevic, 2004 | | X | | | | | | Brazil | Portugal | Chainho et al., 2015 |
| ***Stelletta clarella*** de Laubenfels, 1930 | | X | | X | | | | North Pacific | Chile | Castilla and Neill, 2009 |
| **Cnidaria (16)** | | | | | | | | | | |
| ***Aiptasia diaphana* (9)** (Rapp, 1829) | | X | | | | | | Eastern Atlantic Mediterranean Sea | Portugal | Chainho et al., 2015 |
| ***Amelia aurita*** (Linnaeus, 1758) | | | | X | | | | Black Sea Norest Atlantic Chile | Caspian Sea | Korsun et al., 2012 |
| ***Blackfordia virginica*** Mayer, 1910 | | X | | X | | | | Baltic Sea | Portugal | Chainho et al., 2015 |
| ***Cladonema radiatum*** Dujardin, 1843 | | X | | X | | | | West Pacific | Northeast Pacific | Williams, 2007 |
| ***Clavularia viridis*** Quoy and Gaimard, 1833 | | | | | | X | | Indo-Pacific | Ilha Grande Bay (Brazil) | Mantelatto et al., 2018 |

*(Continued)*

**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Cordylophora caspia*** (Pallas, 1771) | | X | | | | | | Caspian Sea Black Sea | Portugal | Chainho et al., 2015 |
| ***Diadumene lineata*** (Verrill, 1869) | X | X | X | X | | | | Northwest Pacific (Japan) | Northwest Atlantic Northwestern Hawaii | Williams, 2007; Gregory, 2009; Miller et al., 2018 |
| ***Garveia franciscana* (10)** (Torrey, 1902) | | | | | X | | | Indo-Pacific | Mediterranean Sea | Marchini et al., 2015b |
| ***Gonionemus vertens*** A. Agassiz, 1862 | | X | | X | X | | | North Pacific Portugal | Northwest Atlantic United Kingdom | Eno et al., 1997; Williams, 2007 |
| ***Haliplanella lineata* (11)** (Verrill, 1869) | | X | | | | | | Pacific Japan | United Kingdom | Eno et al., 1997 |
| ***Oculina patagonica*** de Angelis, 1908 | | X | | | | | | South West Atlantic | Mediterranean Sea | Fine et al., 2001 |
| ***Rhizostoma pulmo*** (Macri, 1778) | | | | X | | | | Southern North Sea | Black Sea | Boran, 2017 |
| ***Rhopilema nomadica*** Galil, Spanier and Ferguson, 1990 | | | | | | | X | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| *Sansibia spp.* | | | | | | X | | Indo-Pacific | Ilha Grande Bay (Brazil) | Mantelatto et al., 2018 |
| ***Tubastraea coccinea*** (Ehrenberg, 1834) | | X | | | | | | Unknown (widespread distribution) | Southwest Atlantic | Creed et al., 2017 |
| ***Tubastraea tagusensis*** Wells, 1982 | | X | | | | | | Galapagos archipelago | Southwest Atlantic | Creed et al., 2017 |
| **Ctenophora (2)** | | | | | | | | | | |
| ***Beroe ovato*** Bruguière, 1789 | | X | | | | | | East Atlantic (North and South America) | Black Sea Denmark | Shiganova et al., 2014 |
| ***Mnemiopsis leidyi*** A. Agassiz, 1865 | | | | X | | | | West Atlantic | Black Sea | Shiganova et al., 2019 |
| **Platyhelminthes (1)** | | | | | | | | | | |
| ***Koinostylochus ostreophagus*** (Hyman, 1955) | | X | | | | | | Northwest Pacific | Strait of Georgia (Canada) | Gartner et al., 2016 |
| **Nematoda (1)** | | | | | | | | | | |
| ***Anguillicola crassus* (12)** Kuwahara, Niimi and Itagaki, 1974 | | | | X | | | | Taiwan | United Kingdom | Eno, 1996 |
| **Mollusca (44)** | | | | | | | | | | |
| ***Arcuatula senhousia*** (Benson, 1842) | | X | | X | | X | | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Batillaria attramentaria*** (G. B. Sowerby II, 1855) | | | | | X | | | Asia | California (UNITED STATES) | Grosholz et al., 2015 |

*(Continued)*

**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Chaetopleura angulata*** (Spengler, 1797) | | X | | X | X | | | Brazil | Portugal | Chainho et al., 2015 |
| ***Chama macerophylla*** Gmelin, 1791 | | X | | | | | | West Indies | Pearl Harbor (Oahu, Hawaii) | Godwin, 2003; Therriault et al., 2018 |
| ***Crassostrea gigas*** (Thunberg, 1793) | | X | | | X | | | Asian Pacific Ocean | New Zealand | Chainho et al., 2015 |
| ***Crassostrea virginica*** (Gmelin, 1791) | | X | | | X | | | Northeast America | North Sea | Gollasch, 2002 |
| ***Crepidula fornicata*** (Linnaeus, 1758) | | X | | | X | | | Atlantic coast of North America | Norway | Minchin and Gollasch, 2005 |
| ***Crepidula onyx*** G. B. Sowerby I, 1824 | | | X | | | | | Northwest Pacific | Northeast Pacific | Miller et al., 2018 |
| ***Dreissena polymorpha*** (Pallas, 1771) | | | | X | | | | Caspian Sea Black Sea | St Clair lake (North America) | Hebert et al., 1991 |
| ***Ensis americanus* (13)** (Gould, 1870) | | | | X | | | | Atlantic North America | United Kingdom | Eno et al., 1997 |
| ***Haliotis rufescens*** Swainson, 1822 | | | | | X | | | North Pacific | Chile Peru | Castilla and Neill, 2009 |
| ***Hexaplex trunculus*** (Linnaeus, 1758) | | X | | X | | | | Mediterranean Sea | Portugal | Chainho et al., 2015 |
| ***Lopha cristagalli*** (Linnaeus, 1758) | X | | | | | | | Indo-Pacific | Southwestern New Zealand | Gregory, 2009 |
| ***Lyrodus medilobata*** (Edmonson, 1942) | | | | X | | | | Indo-Pacific Ocean | West coast of India | Anil et al., 2002 |
| ***Lyrodus takanoshimensis*** (Roch, 1929) | | | X | | | | | Northwest Pacific | Northeast Pacific | Miller et al., 2018 |
| ***Mactra discors* (14)** J.E. Gray, 1837 | | X | | | | | | Pacific Ocean (New Zealand) | North Sea | Gollasch, 2002 |
| ***Magallana angulata*** (Lamarck, 1819) | | | | | X | | | Pacific Ocean | Southern Portuguese coast | Rech et al., 2018b |
| ***Magallana gigas*** (Thunberg, 1793) | X | | | | | X | | Indo-Pacific Ocean | Mediterranean Sea Cantabrian Coast | Miralles et al., 2018; Bonanno and Orlando-Bonaca, 2019 |
| ***Mercenaria mercenaria*** (Linnaeus, 1758) | | | | | X | | | West Atlantic | Great Britain | Williams, 2007 |

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**TABLE 1** | Continued

| **INVASIVE and potential invasive species** | **Plastics** | **Boat hulls (biofouling)** | **Climate events** | **Ballast water** | **Aquaculture** | **Aquariums** | **Transoceanic channels/ swimming** | **Native location** | **Non-native or invaded location** | **References** |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Musculista senhousia* (15)** (Benson, 1842) | | X | | X | | | | West Pacific | California | Williams, 2007 |
| ***Mya arenaria*** Linnaeus, 1758 | | | | X | | | | Northern Atlantic | Black Sea, Sea of Azov | Occhipinti-Ambrogi and Savini, 2003 |
| ***Mytella cnarruana* (16)** (d'Orbigny, 1846) | | | | X | | | | Atlantic South America Pacific Central South America | South-east North America | Spinuzzi et al., 2013 |
| ***Mytilopsis sallei*** (Récluz, 1849) | | X | | | | | | Central and South America | Australia | Minchin and Gollasch, 2005 |
| ***Mydlus galloprovincialis*** Lamarck, 1819 | | | X | | | | | Japan | Pearl Harbour (Hawaii) | Therriault et al., 2018 |
| ***Mydlus trossulus* Gould**, 1850 | X | | | | | | | North Atlantic North Pacific Baltic Sea | Cantabrian Coast | Miralles et al., 2018 |
| ***Nassarius costellifera* (17)** (A. Adams, 1853) | | X | | | | | | Atlantic Ocean | North Sea | Gollasch, 2002 |
| ***Nausitora dunlopei*** E. P. Wright, 1864 | | | | X | | | | Cochin (India) | Goa (India) | Anil et al., 2002 |
| ***Ocenebra inornata* (18)** (Récluz, 1851) | | | | | X | | | Japan Korea | Portugal | Chainho et al., 2015 |
| ***Ostrea lurida*** Carpenter, 1864 | | X | | | | | | Pacific North America | North Sea | Gollasch, 2002 |
| ***Perna viridis*** (Linnaeus, 1758) | X | | | X | X | | | Tropical Indo-Pacific | Florida Colombian Caribbean | Spinuzzi et al., 2013; Gracia and Rangel-Buitrago, 2020 |
| ***Philine auriformis*** Suter, 1909 | | X | | X | | | | New Zealand | California | Williams, 2007 |
| ***Potamocorbula amurensis*** (Schrenck, 1861) | | | | X | | | | Asia | San Francisco (UNITED STATES) | Godwin, 2003; Therriault et al., 2018 |
| ***Potamopyrgus antipodarum*** (Gray, 1843) | | X | | X | | | | New Zealand | Portugal Baltic Sea | Leppäkoski and Olenin, 2000; Chainho et al., 2015 |
| ***Rapana venosa*** (Valenciennes, 1846) | | | | X | | | | Sea of Japan | Black Sea Adriatic Sea | Occhipinti-Ambrogi and Savini, 2003 |
| ***Ruditapes philippinarum*** (A. Adams and Reeve, 1850) | | | | | X | | | Indo-Pacific | Portugal | Braga et al., 2017 |
| ***Saccostrea cucculata*** (Born, 1778) | | X | | X | X | | | Indo-Pacific | South Brazilian coast | do Amaral et al., 2020 |

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**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Scapharca inaequivalvis* (19)** (Bruguière, 1789) | | | | X | | | | Indo-Pacific | Black Sea Adriatic Sea | Occhipinti-Ambrogi and Savini, 2003 |
| ***Senilia senilis*** (Linnaeus, 1758) | | X | | | | | | North east Atlantic | North Sea | Gollasch, 2002 |
| ***Teredo fulleri*** *Clapp,* 1924 | | | | X | | | | Gulf of Mannar (Southeast India) | Okha (West India) | Anil et al., 2002 |
| ***Teredo navalis*** Linnaeus, 1758 | | | X | | | | | Northeast Atlantic | Florida (UNITED STATES) | Miller et al., 2018 |
| ***Theora lubrica*** Gould, 1861 | | | | X | | | | Inland Sea (Qatar) | San Francisco Bay (UNITED STATES) | Carlton, 1996 |
| ***Tonicia atrata* (20)** Hutton, 1880 | | X | | X | X | | | Europe | Portugal | Chainho et al., 2015 |
| ***Urosalpinx cinerea*** (Say, 1822) | | | | | X | | | North America | United Kingdom | Eno, 1996 |
| ***Xenostrobus securis*** (Lamarck, 1819) | | X | | | | | | Western Australia New Zealand | North Sea | Gollasch, 2002 |
| **Annelida (21)** | | | | | | | | | | |
| ***Branchiomma bairdi*** (McIntosh, 1885) | | X | | | | | | Caribbean Sea | Portugal | Chainho et al., 2015 |
| ***Clymenella torquata*** (Leidy, 1855) | | | | | X | | | Western Atlantic | United Kingdom | Eno et al., 1997 |
| ***Eulalia viridis*** (Linnaeus, 1767) | | X | | | | | | North Atlantic | Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Eumida sanguinea*** (Örsted, 1843) | | X | | | | | | Northeast Atlantic | Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Ficopomatus enigmaticus*** (Fauvel, 1923) | | X | | X | | | | Indian Ocean | Black Sea | Occhipinti-Ambrogi and Savini, 2003 |
| ***Goniadella gracilis*** (Verrill, 1873) | | X | | | | | | North America | United Kingdom | Eno et al., 1997 |
| ***Hydroides dianthus*** (Verrill, 1873) | | X | | | X | | | Atlantic North America | United Kingdom | Eno et al., 1997;<br>Katsanevakis et al., 2014 |
| ***Hydroides elegans*** (Haswell, 1883) [nomen protectum] | | | X | | | | | Indo-Pacific Northwest Pacific | Australia | Bryan et al., 2004 |
| ***Hydroides ezoensis*** Okuda, 1934 | | X | | X | | | | Japan | United Kingdom Tropical Northeast Pacific | Eno et al., 1997 |
| ***Hydroides sanctaecrucis*** Krøyer in Mörch, 1863 | | X | | | | | | Caribbean Sea | Northern Australia | Lewis et al., 2006 |
| ***Janua brasiliensis* (21)** (Grube, 1872) | | X | | | | | | Tropical areas (e.g., Brazil) | United Kingdom | Eno et al., 1997 |

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**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Marenzelleria viridis*** (Verrill, 1873) | | X | | X | | | | North America | Baltic Sea | Leppäkoski and Olenin, 2000 |
| ***Mercierella enigmatica*** **(22)** Fauvel, 1923 | | X | | | | | | Australia | Indian Ocean | Anil et al., 2002 |
| ***Neodexiospira brasiliensis*** (Grube, 1872) | | | | | X | | | South America | Northwest Atlantic Great Britain | Williams, 2007 |
| ***Parougia caeca*** (Webster and Benedict, 1884) | | X | | | | | | North America | Johnstone Strait (Canada) | Gartner et al., 2016 |
| ***Pileolaria berkeleyana*** (Rioja, 1942) | | X | | | | | | Japan | United Kingdom | Eno et al., 1997 |
| ***Polydora cornuta*** Bosc, 1802 | | X | | X | X | | | Unknown | Black Sea | Radashevsky and Selifonova, 2013 |
| ***Pseudopolydora kempi japonica*** Imajima and Hartman, 1964 | | | | | X | | | Japan | Northwest Pacific | Williams, 2007 |
| ***Sabaco elongatus*** (Verrill, 1873) | | | | | X | | | West Atlantic | Northwest Pacific | Williams, 2007 |
| ***Sabella spallanzanii*** (Gmelin, 1791) | X | | | | X | | | Mediterranean Sea | New Zealand | Campbell et al., 2017 |
| ***Streblospio benedicti*** Webster, 1879 | | | | | X | | | West Atlantic | Northwest Pacific | Williams, 2007 |
| **Arthropoda (51)** | | | | | | | | | | |
| ***Acaria (Acartiura) omori*** Bradford, 1976 | | | | X | | | | North Pacific | Chile | Castilla and Neill, 2009 |
| ***Acaria (Acanthacartia) tonsa*** Dana, 1849 | | | | X | | | | Indo-Pacific | Portugal | Sobral, 1985 |
| ***Ammothea hilgendorf*** (*Böhm,* 1879) | | X | | | | | | Japan | United Kingdom | Eno et al., 1997 |
| ***Amphibalanus amphitrite*** (Darwin, 1854) | X | | | | | | | Unknown | Cantabrian Coast | Miralles et al., 2018 |
| ***Amphibalanus improvisus*** (Darwin, 1854) | | X | | | | | | Western Atlantic | Strait of Georgia (Canada, Northwest Pacific) | Gartner et al., 2016 |

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**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Amphibalanus reticulatus*** (Utinomi, 1967) | | X | | | | | | Japan | Southern Brazil | Kauano et al., 2016 |
| ***Ampithoe valida*** Smith, 1873 | | X | | X | X | | | Japan | Strait of Georgia (Canada) | Williams, 2007 |
| ***Austrominius modestus*** (Darwin, 1854) | X | | | | | | | Australia New Zealand | North Spain Coast (Cantabria, Asturias, Biscay) | Miralles et al., 2018; Rech et al., 2018b |
| ***Balanus amphitrite* (23)** Darwin, 1854 | | X | | | | | | Japan Korea | North Sea | Gollasch, 2002 |
| ***Balanus campbelli* (24)** Filhol, 1886 | | X | | | | | | New Zealand | North Sea | Gollasch, 2002 |
| ***Balanus eburneus* (25)** Gould, 1841 | | X | | | | | | North America | North Sea | Gollasch, 2002 |
| ***Balanus perforatus* (26)** Bruguière, 1789 | | X | | | | | | Northeast Atlantic | North Sea | Gollasch, 2002 |
| ***Balanus variegatus* (27)** Darwin, 1854 | | X | | | | | | Fare East Australia India | North Sea | Gollasch, 2002 |
| ***Callinectes sapidus*** Rathbun, 1896 | | | | X | | | | Western Atlantic Ocean | Portugal | Chainho et al., 2015 |
| ***Caprella drepanochir*** Mayer, 1890 | | X | | | | | | North Pacific | Strait of Juan de Fuca (Canada)<br>Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Caprella mutica*** Schurin, 1935 | | X | X | X | | | | Northwestern Pacific Ocean (Japan) | Strait of Georgia (Canada) | Cook et al., 2007; Gartner et al., 2016 |
| ***Caprella scaura*** Templeton, 1836 | | X | | X | X | | | Indo Pacific | Girona (Spain) | Martínez and Adarraga, 2008 |
| ***Carcinus maenas*** (Linnaeus, 1758) | | X | | | | | | Northeast Atlantic | North America South Africa | Grosholz and Ruiz, 1995 |
| ***Centropages abdominalis*** Sato, 1913 | | X | | X | | | | North Pacific | Chile | Castilla and Neill, 2009 |
| ***Cercopagis pengoi*** (Ostroumov, 1891) | | | | X | | | | Caspian Sea | Baltic Sea | Leppäkoski and Olenin, 2000 |
| | | X | | | | | | Japan Korea | New Zealand | Brine et al., 2013 |
| ***Cilicaea latreillei*** Leach, 1818 | | X | | X | | | | Indonesia Philippines Sri Lanka South Africa Red Sea Australia | Arabian Sea | Anil et al., 2002 |
| ***Diamysis lagunaris*** Ariani and Wittmann, 2000 | | | | X | | | | Mediterranean Sea Black Sea | Portugal | Chainho et al., 2015 |

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**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Dynamene bidentata*** (Adams, 1800) | | X | | | | | | Northeast Atlantic | North Sea | Gollasch, 2002 |
| ***Elminius kingii*** Gray, 1831 | | X | | | | | | South America | North Sea East cost of Canada | Gollasch, 2002 |
| ***Elminius modestus* (28)** Darwin, 1854 | X | X | | X | | | | New Zealand | United Kingdom Shetland Islands | Eno et al., 1997; Barnes and Milner, 2004 |
| ***Elminius simplex*** Linzey (1942) | | X | | | | | | Indian Ocean Australia South America | North Sea East cost of Canada | Gollasch, 2002 |
| ***Endeis nodosa*** Hilton, 1942 | | | X | | | | | Northwest Pacific | Tropical Eastern Atlantic | Miller et al., 2018 |
| ***Eriocheir sinensis*** H. Milne Edwards, 1853 | | X | | X | | | | Japan China | United Kingdom | Eno et al., 1997 |
| ***Hemigrapsus penicillatus*** *(De Haan, 1835 [in De Haan, 1833-1850])* | | X | | | | | | Fare East (Japan, China, Korea) | North Sea French Atlantic coast | Gollasch, 2002 |
| ***Hemigrapsus sanguineus*** (De Haan, 1835 [in De Haan, 1833-1850]) | | | X | | | | | Japan | Hawaii Northeast Pacific | Therriault et al., 2018 |
| ***Hesperibalanus fallax*** (Broch, 1927) | X | | | | X | | | Atlantic Coast of tropical Africa | South Portugal | Rech et al., 2018b |
| ***Hyas araneus*** (Linnaeus, 1758) | | X | | X | | | | North Atlantic Arctic Ocean | Antarctic Peninsula | Tavares and De Melo, 2004 |
| ***Ianiropsis serricaudis*** Gurjanova, 1936 | | | X | | | | | Northwest Pacific | North America | Miller et al., 2018 |
| ***Incisocalliope derzhavini*** (Gurjanova, 1938) | | X | | | | | | Northeast Pacific | Strait of Juan de Fuca (Canada) Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Ligia oceanica*** (Linnaeus, 1767) | | X | | X | | | | Northeast Atlantic | Portugal | Chainho et al., 2015 |
| ***Liocarcinus navigator*** (Herbst, 1794) | X | | | | | | | Eastern Atlantic Mediterranean Sea | Adriatic Sea | Tutman et al., 2017 |

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**TABLE 1** | Continued

| **INVASIVE and potential invasive species** | **Plastics** | **Boat hulls (biofouling)** | **Climate events** | **Ballast water** | **Aquaculture** | **Aquariums** | **Transoceanic channels/ swimming** | **Native location** | **Non-native or invaded location** | **References** |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Megabalanus coccopoma*** (Darwin, 1854) | | X | | X | | | | Pacific Central South America | San Diego (California) | Spinuzzi et al., 2013 |
| ***Melita nitida*** S.I. Smith in Verrill, 1873 | | X | | | | | | North America | Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Metapenaeus monoceros*** (Fabricius, 1798) | | | | | X | | | Indo-Pacific Ocean | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Monocorophium acherusicum*** (Costa, 1853) | | X | | | | | | Eastern Atlantic | Strait of Juan de Fuca (Canada) Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Monocorophium insidiosum*** (Crawford, 1937) | | X | | | | | | Eastern Atlantic | Strait of Juan de Fuca (Canada) Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Oithona davisae*** Ferrari F.D. and Orsi, 1984 | | | | X | | | | North Pacific | Chile | Castilla and Neill, 2009 |
| ***Paracaprella pusilla*** *Mayer,* 1890 | | | | X | | | | Western Atlantic | Panama Mediterranean Sea | Ros et al., 2013 |
| ***Paracaprella tenuis*** Mayer, 1903 | | X | | | | | | Pacific North America Gulf of Mexico | North Sea | Gollasch, 2002 |
| ***Penaeus japonicus*** Spence Bate, 1888 | | | | | X | | | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Planes minutus*** (Linnaeus, 1758) | X | | | | | | | Indian ocean Atlantic ocean | Adriatic Sea | Tutman et al., 2017 |
| ***Pyromaia tuberculata*** (Lockington, 1877) | | | | X | | | | Southern California (UNITED STATES) | San Francisco (UNITED STATES) Japan Korea New Zealand | Carlton, 1996 |
| ***Rhithropanopeus harrisii*** (Gould, 1841) | | X | | X | X | | | West Atlantic | Portugal | Chainho et al., 2015 |
| ***Sphaeroma walkeri*** Stebbing, 1905 | | X | | | | | | Indian Ocean | Hong Kong | Lewis and Coutts, 2010 |
| ***Striatobalanus amaryllis*** (Darwin, 1854) | | X | | | | | | Indian Ocean West Pacific | West Africa | Kerckhof et al., 2010 |
| ***Temora turbinata*** (Dana, 1849) | | | | X | | | | Indian Ocean | Southwest Atlantic | Soares et al., 2018 |
| **Bryozoa (15)** | | | | | | | | | | |
| ***Bowerbankia gracilis* (16)** Leidy, 1855 | | X | | X | X | | | West Atlantic | California (UNITED STATES) | Williams, 2007 |
| ***Bugula flabellata* (17)** (Thompson in Gray, 1848) | | X | | X | | | | South Pacific South Atlantic | Chile | Castilla and Neill, 2009 |

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**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Bugula neritina*** (Linnaeus, 1758) | | X | | X | X | | | Pacific Ocean | Chile | Castilla and Neill, 2009 |
| ***Cryptosula pallasiana*** (Moll, 1803) | | | X | | | | | Northwest Pacific | Northeast Pacific | Miller et al., 2018 |
| ***Disporella novaehollandiae*** (d'Orbigny, 1853) | | | X | | | | | Northwest Pacific | Hawaiian Island | McCuller and Carlton, 2018 |
| ***Jellyella eburnea*** (Hincks, 1891) | X | | | | | | | Western Pacific | Central Pacific Eastern Pacific | McCuller and Carlton, 2018 |
| ***Jellyella tuberculata*** (Bosc, 1802) | X | | X | | | | | Western Pacific | Central Pacific Eastern Pacific | McCuller and Carlton, 2018 |
| ***Membranipora membranacea*** (Linnaeus, 1767) | X | | | | | | | Atlantic Ocean Pacific Ocean | Artic Ocean | Barnes and Milner, 2004 |
| ***Savignyella lafontii*** (Audouin, 1826) | | X | | | | | | Mediterranean Sea | North Sea | Gollasch, 2002 |
| ***Schizoporella japonica*** Ortmann, 1890 | | X | X | X | X | | | Japan | California (UNITED STATES)<br>Columbia (Canada)<br>Northeast Pacific | Williams, 2007; Gartner et al., 2016; Miller et al., 2018 |
| ***Thalamoporella evelinae*** Marcus, 1939 | X | | | | | | | Brazil | Florida (UNITED STATES) | Winston et al., 1997 |
| ***Tricellaria inopinata*** d'Hondt and Occhipinti Ambrogi, 1985 | | X | | | | | | Pacific ocean | Portugal | Chainho et al., 2015 |
| ***Watersipora cucullata*** (Busk, 1854) | | X | | | | | | Northeast Pacific | New Zealand | Lewis and Coutts, 2010 |
| ***Watersipora subtorquata*** (d'Orbigny, 1852) | | X | | | | | | Unknown | Portugal | Chainho et al., 2015 |
| ***Zoobotryon verticillatum* (18)** (Delle Chiaje, 1822) | | X | | X | | | | Caribbean Sea | California (UNITED STATES)<br>Portugal | Williams, 2007; Chainho et al., 2015 |
| **Entoprocta (2)** | | | | | | | | | | |
| ***Barentsia benedeni*** (Foettinger, 1887) | | | | X | | | | Northeast Atlantic | Black Sea | Rilov and Crooks, 2009a |
| ***Barentsia ramosa*** (Robertson, 1900) | | | | X | | | | California (UNITED STATES)<br>Belgium | Indian Ocean | Anil et al., 2002 |
| **Echinodermata (2)** | | | | | | | | | | |
| ***Asterias amurensis*** Lutken, 1871 | | X | X | | | | | Northern Pacific (Japan) | South Australia | Godwin, 2003; Therriault et al., 2018 |

*(Continued)*

**TABLE 1** | Continued

| INVASIVE and potential invasive species | Plastics | Boat hulls (biofouling) | Climate events | Ballast water | Aquaculture | Aquariums | Transoceanic channels/ swimming | Native location | Non-native or invaded location | References |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Ophiothela mirabilis*** Verrill, 1867 | | X | | X | | | | Indo-Pacific | Ilha Grande Bay (Brazil) | Mantelatto et al., 2018 |
| **S. Tunicata (16)** | | | | | | | | | | |
| ***Ascidiella aspersa*** (Müller, 1776) | | X | | X | X | | | Northeastern Atlantic | Atlantic coast of North America New Zealand Southern Australia India | Lynch et al., 2016 |
| ***Asterocarpa humilis*** (Heller, 1878) | | X | | | X | | | South Pacific | Chile | Pinochet et al., 2017 |
| ***Botrylloides violaceus*** Oka, 1927 | | X | | X | | | | West Pacific | Northwest Atlantic Columbia (Canada) | Williams, 2007; Gartner et al., 2016 |
| ***Botryllus schlosseri*** (Pallas, 1766) | | X | | X | | | | Northeast Atlantic | East Atlantic Columbia (Canada) | Williams, 2007; Gartner et al., 2016 |
| ***Ciona intestinalis*** (Linnaeus, 1767) | | X | | X | X | | | North Atlantic | Chile Iceland | Castilla and Neill, 2009; Micael et al., 2020 |
| ***Oavelina dellavalle*** (Zirpolo, 1925) | | X | | X | | | | Northeast Atlantic | Portugal | Chainho et al., 2015 |
| ***Corella eumyota*** Traustedt, 1882 | | | | X | X | | | Southern Ocean | Portugal | Chainho et al., 2015 |
| ***Didemnum vexillum*** Kott, 2002 | | | X | | | | | Japan | Northwest Pacific Ocean Hawaii | Therriault et al., 2018 |
| ***Distaplia corolla*** Monniot F, 1974 | | X | | X | | | | West Atlantic Ocean | Portugal | Chainho et al., 2015 |
| ***Herdmania momus*** (Savigny, 1816) | | X | | X | | | | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Molgula ficus*** (Macdonald, 1859) | | | | | X | | | South Pacific | Chile | Castilla and Neill, 2009 |
| ***Molgula manhattensis*** (De Kay, 1843) | | X | | | | | | North America | Strait of Juan de Fuca (Canada) Strait of Georgia (Canada) | Gartner et al., 2016 |
| ***Perophora viridis*** Verrill, 1871 | | X | | X | | | | Western-Atlantic | Portugal | Chainho et al., 2015 |
| ***Pycnoclavella taureanensis*** Brunetti, 1991 | | X | | | | | | Mediterranean Sea | Portugal | Chainho et al., 2015 |
| ***Styela canopus*** (Savigny, 1816) | | X | | X | | | | West Pacific | Northwest Atlantic | Williams, 2007 |

*(Continued)*

**TABLE 1** | Continued

| **INVASIVE and potential invasive species** | **Plastics** | **Boat hulls (biofouling)** | **Climate events** | **Ballast water** | **Aquaculture** | **Aquariums** | **Transoceanic channels/ swimming** | **Native location** | **Non-native or invaded location** | **References** |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Styela clava*** Herdman, 1881 | | X | | | | | | Asian Pacific Ocean | Great Britain | Davis and Davis, 2007 |
| **Vertebrates (7)** | | | | | | | | | | |
| ***Lagocephalus sceleratus*** (Gmelin, 1789) | | | | | | | X | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Mugil soiuy*** **(32)** Basilewsky, 1855 | | | | X | | | | Amur river Sea of Japan | Sea of Azov | Occhipinti-Ambrogi and Savini, 2003 |
| ***Neogobius melanostomus*** (Pallas, 1814) | | | | X | | | | Caspian Sea | Baltic Sea | Holmes et al., 2019 |
| ***Pterois miles*** (Bennett, 1828) | | | | | | | X | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Pterois volitans*** (Linnaeus, 1758) | | | | X | X | X | | Indian West Pacific | East coast of North America Caribbean | Padilla and Williams, 2004 |
| ***Sargocentron rubrum*** (Forsskål, 1775) | | | | | | | X | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| ***Siganus rivulatus*** Forsskål and Niebuhr, 1775 | | X | | | | | X | Indo-Pacific | Mediterranean Sea | Bonanno and Orlando-Bonaca, 2019 |
| **Total: 216** | **17** | **128** | **18** | **84** | **50** | **9** | **6** | | | |
| **Sessile species** | **112** | | | | | | | | | |
| **Mobile species** | **104** | | | | | | | | | |

*Plastic and boat hulls are highlighted because of their importance in our study. 216 species were included, classified as sessile (pink cells) and no sessile species (blue cells) and sorted mainly by phylum (except the group Algae, subphylum Tunicata and the group Vertebrates). Next to each group, the number of species in the group is indicated in parentheses. The species name coincides with the name used in the citation. Species whose currently accepted name has changed are indicated by numbers in parentheses, and the currently accepted name is clarified at the end of the table.* ***Accepted names: (1)*** *Codium fragile subsp. fragile (Suringar) Hariot, 1889* ***(2)*** *Colpomenia sinuosa var. peregrina Sauvageau, 1927* ***(3)*** *Grateloupia subpectinata Holmes, 1912* ***(4)*** *Pachymeniopsis lanceolata (K.Okamura) Y.Yamada ex S.Kawabata, 1954* ***(5)*** *Gayralia oxysperma (Kützing) K.L.Vinogradova ex Scagel et al., 1989* ***(6)*** *Melanothamnus harveyi (Bailey) Díaz-Tapia and Maggs, 2017* ***(7)*** *Sargassum horneri (Turner) C.Agardh, 1820* ***(8)*** *Gelliodes wilsoni Carballo, Aquilar-Camacho, Knapp and Bell, 2013* ***(9)*** *Exaiptasia diaphana (Rapp, 1829)* ***(10)*** *Calyptospadix cerulea Clarke, 1882* ***(11)*** *Diadumene lineata (Verrill, 1869)* ***(12)*** *Anguillicola (Anguillicoloides) crassus Kuwahara, Niimi and Itagaki, 1974* ***(13)*** *Ensis leei M. Huber, 2015* ***(14)*** *Spisula discors (Gray, 1837)* ***(15)*** *Arcuatula senhousia (Benson, 1842)* ***(16)*** *Mytella strigata (Hanley, 1843)* ***(17)*** *Nassarius margaritifer (Dunker, 1847)* ***(18)*** *Ocinebrellus inornatus (Récluz, 1851)* ***(19)*** *Anadara inaequivalvis (Bruguière, 1789)* ***(20)*** *Plaxiphora (Plaxiphora) aurata (Spalowsky, 1795)* ***(21)*** *Neodexiospira brasiliensis (Grube, 1872)* ***(22)*** *Ficopomatus enigmaticus (Fauvel, 1923)* ***(23)*** *Amphibalanus amphitrite (Darwin, 1854)* ***(24)*** *Notomegabalanus campbelli (Filhol, 1885)* ***(25)*** *Amphibalanus eburneus (Gould, 1841)* ***(26)*** *Perforatus perforatus (Bruguière, 1789)* ***(27)*** *Amphibalanus variegatus (Darwin, 1854)* ***(28)*** *Austrominius modestus (Darwin, 1854)* ***(29)*** *Amathia gracilis (Leidy, 1855)* ***(30)*** *Bugulina flabellata (Thompson in Gray, 1848)* ***(31)*** *Amathia verticillata (delle Chiaje, 1822)* ***(32)*** *Planiliza haematocheila (Temminck and Schlegel, 1845). *García-Gómez et al. (2018) cite and photograph the species on nets, and these nets are made of nylon, like the piece illustrated in* ***Figure 3D*** *of this work. After 2018, the species have been observed (pers. obs.) on sunken plastic bags and bottles.*

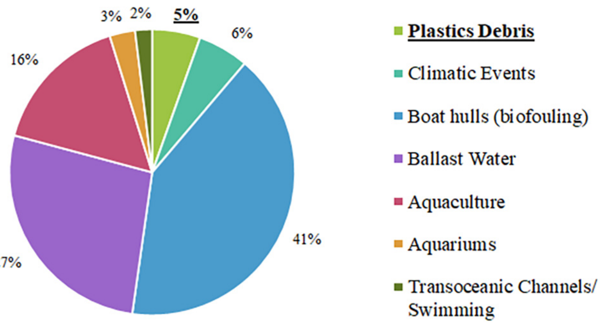

**FIGURE 2 |** Scientific publications on the vectors for the introduction of alien marine species (plastic, rafting, biofouling aquaculture, ballast water and general) over the last 30 years (1990-2020) and classified by Impact (I), Management (M) and Impact and Management (I+M).

and Milner, 2004), by increasing their potential travel distance (Thiel and Gutow, 2005).

Wasson et al. (2005) suggested that alien species preferred hard artificial materials (rip rap, gravel bars, pilings, and docks), while native species were found mainly on soft substrates. Pinochet et al. (2020) affirmed that native species are more commonly found on natural surfaces; for example, native algae such as *Sargassum* sp. and *Corallina* sp. are prevalent on natural reefs but not on artificial structures (Glasby et al., 2007). Pinochet et al. (2020) found that the settlement of the larvae of two invasive species of the genus *Bugula* on plastic surfaces was 70% higher than in cement or wood. Furthermore, settlement on plastic substrates was extremely rapid, with 50% of the larvae settling only after 5 min. For some species of invasive bryozoans, it has been suggested that their prevalence in artificial structures and settlement on plastic panels is explained by their ecology, since they are early successional species (Vail and Tranter, 1981), they show a faster growth, an early initiation of reproductive stages and have higher metabolic rates, allowing them to outgrow their competitors in the early successional stages of the developing community (Pettersen et al., 2016; Lagos et al., 2017). Astudillo et al. (2009) reported that approximately 60% of the fauna found on plastic buoys in Coquimbo Bay, a temperate zone of the Southeast Pacific Ocean, had direct development or short larval durations, so they were capable of maintaining persistent populations in floating elements, suggesting a high potential for long-distance dispersal of fauna on buoys.

Recent data suggest that larger pieces of plastic debris support greater biological diversity, which is consistent with the classic species-area relationships inherent in the biogeography of islands (Simberloff, 1976; Gil and Pfaller, 2016; Garcia-Vazquez et al., 2018). Debroas et al. (2017) observed a higher bacterial and eukaryotic richness in polyethylene (PE) of mesoplastic size (5 mm–20 cm) compared to MPs of 300 μm–5 mm, mainly PE. However, it is necessary to consider the complexity of the debris materials, since those with greater structural complexity (for example, groups of tangled ropes) support greater diversity (Goldstein et al., 2014). Plastic debris of all sizes often has limited structural complexity and smooth, rigid surfaces (e.g., buoys, containers, balls, liners). These characteristics can limit the habitability of plastic waste for many species, since a wide variety of organisms require shelter to persist (Gil and Pfaller, 2016). Even floating harbor pontoons, which carry well-established biofouling communities, can be an important vector for the massive expansion of native species in the face of extreme events that destroy them, such as tsunamis (Wang et al., 2016), displacing them thousands of kilometers away (**Figures 3A–D**).

Gil and Pfaller (2016) studied the relationship between the area and the structural complexity of marine plastic debris and the colonization of species. The study revealed contrasting patterns for the richness of sessile and mobile taxa. Regarding the number of sessile taxa on debris, the increase in surface had a significant positive effect, while the cover of barnacles of the genus *Lepas* had a significant negative effect. However, regarding the number of mobile taxa on the debris, the increase in surface area had a trivial positive effect, while the number of barnacles had a significant positive effect. These results suggest that barnacles of the genus *Lepas* act as base species in communities on plastic debris, providing a complex structural habitat on otherwise structurally limited plastic debris. In agreement with these data, Astudillo et al. (2009) carried out a study on biota inhabiting buoys in the sea and observed that the number of mobile species on buoys was positively related to the number and biomass of sessile species. Thus, benthic species which colonize plastic surfaces are considered eco-engineers, since they provide a habitat for mobile species that otherwise would not be able to colonize these surfaces (Astudillo et al., 2009).

## Differential Colonization in the Different Types of Plastic Polymers

The five main classes of plastic polymers, which comprise about 90% of polymer production, are polyethylene (PE), polypropylene (PP), polyvinyl chloride (PVC), polystyrene (PS), and polyethylene terephthalate (PET), with the latter being the most abundant in the ocean (Andrady and Neal, 2009).

While many authors have observed no evidence that the type of polymer is relevant for the composition of the macrobiota associated with plastics, Gündoğdu (2017) have found that the type of plastic (PE, PET, and PP) shows significant differences with respect to the diversity and abundance of species. On the other hand, it is commonly accepted that the difference in structural and/or chemical properties (plasticizers and colorants) observed among polymer families influences bacterial communities and dynamics (De Tender et al., 2015). Pinochet et al. (2020) observed that the bryozoan larvae of two invasive species of the genus *Bugula* showed preferences for colonizing PS and polycarbonate (PC) substrates within the polymer possibilities (PP, PVC, PET, and PC). Furthermore, antifouling treatments applied to different plastic materials, such as nylon fishing nets, could influence the community of organisms adhering to them (Núñez et al., 2006).

Although the reason for association with certain polymers is not clear, some authors have indicated that it might be due to the biofilm that develops on each polymer (Shin et al., 2013; Lagos et al., 2016; Morohoshi et al., 2018). According to

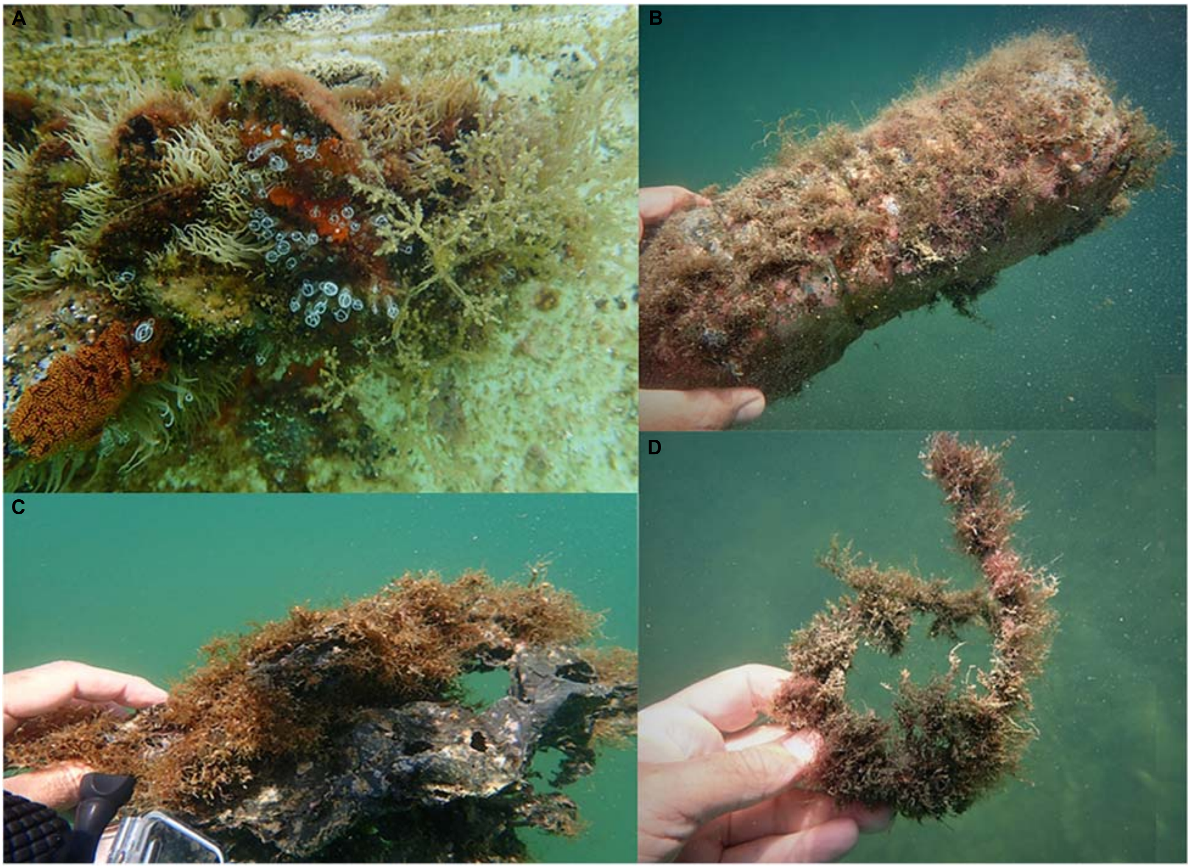

**FIGURE 3 |** Plastic fouling examples: **(A)** in floating boxes of polystyrene docks covered with pvc carrying fauna such us the invasive species *Amathia verticillata* (their breakage, due to a storm or tsunami (see text) can lead to their dispersion in the sea over great distances); **(B,C)** plastic bottle and plastic bag taken from the bottom of a port, with incipient cauloids of the possible fine morphotype of the Asian invasive algae, *Rugulopteryx okamurae*; **(D)** loose end nylon net, extracted from the bottom of a port, completely covered with biofouling. Pictures were taken at Leisure port La Alcaidesa (La Línea), Bay of Algeciras.

Oberbeckmann et al. (2014) the composition of the polymer not only influences the abundance of microorganisms associated with polymers, but also shapes the structure of the biofilm community, which could play a role in the establishment of other species associated with the biofilm (Shin et al., 2013; Lagos et al., 2016; Morohoshi et al., 2018).

## Macrobiota Transported by Plastics

Barnes (2002) highlighted the importance of marine debris as a distribution vector for marine species and estimated that it doubled the probability of transport of the species. After analyzing more than 200 pieces of debris from 30 different islands, he concluded that the most abundant groups were bryozoans, barnacles, polychaetes, hydroids and molluscs. Astudillo et al. (2009) found in the Southeastern Pacific 134 species in a total of 40 sampled buoys, mostly belonging to the Arthropoda, Annelida, and Mollusca phyla, 4 of them classified as invasive on the Chilean coast (Castilla et al., 2005): *Ciona intestinalis (Linnaeus, 1767), Bugula neritina (Linnaeus, 1758), B. flabellata* [Thompson in Gray, 1848; this name is currently not accepted and it is *Bugulina flabellata* (Thompson in Gray, 1848)] and the macroalgae *Codium fragile* (Suringar) Hariot, 1889 (frequencies of 73, 82, 59 and 9%, respectively). Later, in 2014, Goldstein et al. (2014) found 95 taxa in 242 pieces of plastic debris, most of them from the phylum Arthropoda, followed by Mollusca and Cnidaria. These data are consistent with the results obtained in our study (**Table 1**), as the phylum observed on plastic were Arthropoda (6), Bryozoa (4), Mollusca (4), Annelida (1) and Cnidaria (1), and the group Algae (1).

Some recurrent characteristics have been noted in the biology and ecology of species associated with plastic debris in the sea, such as cosmopolitan distributions, suspensivorous feeding (Astudillo et al., 2009) and sessile with short-lived larval development without natural potential means of dispersal (Barnes, 2002).

Kiessling et al. (2015) found 335 taxa associated with plastic garbage items in the ocean and stranded on the coast. In a study in the Atlantic Ocean, Barnes and Milner (2004) found several species of barnacles with a high incidence; the balanomorph *Semibalanus balanoides (Linnaeus, 1767)* were present in marine debris at all arctic and subarctic study sites; the invasive species *Elminius modestus* Darwin, 1854 [this name is currently not accepted and it is *Austrominius modestus* (Darwin, 1854)] was also found on plastic items in the Shetland Islands. The genus *Lepas* (one of the most common colonizers of plastic litter) (Miralles et al., 2018) shows a wide distribution associated with debris: from high latitudes in the Shetland Islands [*Lepas (Anatifa) anatifera Linnaeus, 1758*] *to* the Malvinas Islands [*L. (Anatifa) australis Linnaeus, 1758*], including locations closer to the equator such as the Ligurian Sea [*L. (Anatifa) pectinata* Spengler, 1793] (Aliani and Molcard, 2003). Other plastic colonizers include several species of hydroids and bryozoans (Aliani and Molcard, 2003; Barnes and Milner, 2004). The suspensivorous bivalve family Mytilidae form dense aggregations (Mikkelsen and Bieler, 2008) in specific vectors (e.g., marine debris, artificial substrates, ship hulls, and ballast water). This family includes invasive species carried by plastic debris such as *Perna viridis* (*Linnaeus, 1758*) (Gracia and Rangel-Buitrago, 2020).

Nikula et al. (2013) documented the transport of algae in debris, mostly plastic, between islands separated by more than 500 km. After a 30-year examination of the impact of the invasion of *Undaria pinnatifida* (Harvey) Suringar, 1873 in Australasia, South et al. (2017) indicated that its ability to settle and develop on any hard substrate until it reaches reproductive maturity, among those who frequented plastic products such as buoys, could be a key factor toin the initial success of its invasion. Recently, a study of the distribution and impact of *Rugulopteryx okamurae* in the Strait of Gibraltar also showed the highly competitive capacity of the algae to settle onto hard substrates, describing its ability to adhere to nets and ropes (made of nylon), and hooks of nets, constituting a problem for the fishing sector, and showing the potential of polyamides for the dispersal of species (García-Gómez et al., 2018).

### Plastic as a Vector for the Dispersal of Microorganisms and Associated Diseases

Plastics, including MPs and NPs, adsorb organic and inorganic nutrients from water (Frère et al., 2018), which, along with its physical properties and widespread distribution provides a unique and stable habitat (Zettler et al., 2013; Oberbeckmann et al., 2015; Keswani et al., 2016), thus attracting bacteria, viruses, plankton, and other microorganisms which adhere to its surface (Frère et al., 2018), and enhancing their dispersion to different oceanic regions (Zettler et al., 2013; Oberbeckmann et al., 2015; Keswani et al., 2016). This adhesion is facilitated by the complexity of plastic surfaces, such as roughness and braiding (Núñez et al., 2006).

Zettler et al. (2013) introduced the term "plastisphere" to define a community of microorganisms associated with marine plastic debris found on the surface of seawater. "Plastisphere" differs from the bacterial populations found in other marine ecosystems, both in the water column and in other natural substrates (Zettler et al., 2013; Harrison et al., 2014; Dussud et al., 2018; Curren and Leong, 2019) and host a diverse community, including heterotrophs, autotrophs, predators, and symbionts, which generally begin with microbial colonization and biofilm conformation, which at the same time facilitate the settlement of other species, for example bryozoans (Bryant et al., 2016). Oberbeckmann et al. (2014) show that microbial communities in plastic change in structure and composition with respect to geographic location, season and type of polymer, but that there are also similarities between these plastic communities, such as the predominance of the phyla Proteobacteria and Bacteroidetes (Zettler et al., 2013; Oberbeckmann et al., 2014; Frère et al., 2018; Curren and Leong, 2019) and some microalgal species such as diatoms and dinoflagellates (Carson et al., 2013).

Different cases of dissemination of potentially toxic species have been documented, including pathogens and invasive algae, which can invade new habitats and modify their structure, becoming a threat to the ecosystem (Zettler et al., 2013; Kirstein et al., 2016). The toxic bacterial genus *Vibrio* has been commonly detected in MPs (Zettler et al., 2013; Frère et al., 2018; Curren and Leong, 2019); Kirstein et al. (2016) confirmed the presence of *Vibrio spp*. in 13% of all MP particles collected in the sea, identifying the potentially pathogenic species *V. parahaemolyticus* (Fujino et al., 1974) Sakazaki et al., 1963 and *V. fluvialis* Lee et al., 1981. Masó et al. (2003) detected members of the potentially harmful dinoflagellate genera *Ostreopsis, Coolia,* and *Alexandrium* in plastic debris floating in Mediterranean coastal waters. These infectious organisms can reach their hosts through the ingestion of plastic (Harrison et al., 2011; Zettler et al., 2013).

Several authors found antibiotic resistance genes (ARG; Miller et al., 2009; Laganà et al., 2019), metal resistance genes (MRG; Yang et al., 2019) and virulence genes (Radisic et al., 2020) in different species of bacteria in marine environments. Radisic et al. (2020) findings of virulence genes and new ARG variants in the fish pathogen *Aeromonas salmonicida* (Lehmann and Neumann, 1896; Griffin et al. 1953) isolated from plastic debris in Norway showed their potential for causing infections.

Audrézet et al. (2020) highlight the importance of the study of the succession of plastiphere communities and the different factors that influence the transmission of microorganisms mediated by plastic through the combination of molecular and microscopic approaches, and the use of genetic markers.

Therefore, there is concern that MP pollution, which is increasing in the marine environment, may cause serious marine ecological effects, influence the dynamics of its population and, ultimately, the emergence of pathogens (Frère et al., 2018; Shen et al., 2019). The introduction of MPs colonized by non-native microbial communities is likely to alter microbial communities and genetic exchange in natural water and consequently affect the ecological function of microbial communities (Miao et al., 2019).

## SPATIOTEMPORAL DISPERSION PATTERNS OF PLASTIC DEBRIS IN THE MARINE ENVIRONMENT AND VULNERABLE AREAS

Plastic horizontal dispersion in the ocean is driven by different large-scale processes, such as the action of ocean currents, wind, tides (**Figure 4**; Law et al., 2010; Kim et al., 2015) and extreme meteorological events, such as hurricanes (Wang et al., 2019; Lo et al., 2020) and tsunamis (Wang et al., 2016). Sea state, wind (Astudillo et al., 2009; Thiel et al., 2011), and particle size and type (Reisser et al., 2015) influence the duration of transport. A Plastic particle from the east coast of the United States may reach the subtropical gyre of the Atlantic North in less than 60 days (Law et al., 2010). Six years after the 2011 tsunami in Japan, Carlton et al. (2017) documented 289 living species on the coasts of North America and Hawaii in marine debris originating after the catastrophe, among which plastic debris was abundant. On the ocean surface, downwind and slow current habitats are potential sinks for plastic debris (Browne et al., 2010). Currently, 5 ocean gyres have been identified, located in the North Atlantic, South Atlantic, South Indian, South Pacific, and North Pacific (Eriksen et al., 2014), which accumulate on their surfaces at least 79 thousand tons of plastic (Lebreton et al., 2018). Moreover, the appearance of another patch in the Barents Sea has been predicted (van Sebille et al., 2012). These areas can accommodate quantities of up to 21,290 tons of plastic in the North Pacific gyre (Law et al., 2010). In addition, in the convergence regions, surface water is pumped down to depths of a few hundred meters (van Sebille et al., 2020).

The vertical transport of plastic is both size- and density-dependent. MPs are more abundant than larger plastic debris, both on the sea's surface and in the water column (Kooi et al., 2017). On the other hand, plastic materials with a density lower than water (LD) (1.02 g/cm$^3$) are usually found on the surface and in neustonic environment (Moore et al., 2011), while those with a higher density (HD) reach the marine benthic environments (Moret-Ferguson et al., 2010; Ballent et al., 2012).

During plastic debris stay in the marine environment, their density can change over time due to the physical/chemical/biological degradation or biofouling attachment **Figure 4**) (Moret-Ferguson et al., 2010) of suspended matter, contamination by epiphytes or the formation of microbial biofilms (Lobelle and Cunliffe, 2011; Collignon et al., 2014; Bagaev et al., 2017). Increased density could cause the debris to sink, to be transported by underlying currents (Engler, 2012), trapped by turbulent currents of the benthic boundary layer, resuspended by deep currents, or finally to settle onto the seafloor (Bagaev et al., 2017; **Figure 4**). In many cases, sedimentation is facilitated by oceanographic processes (Wang et al., 2016) such as dense shelf water cascading (Canals et al., 2006), severe coastal storms (Sanchez-Vidal et al., 2012), offshore convection (Durrieu de Madron et al., 2013), and saline subduction (Talley, 2002). Predicting this vertical mixing could be essential, as it affects the horizontal drifting patterns and ecological impacts of plastic pollution (Reisser et al., 2015). Plastic concentrations have been shown to decrease exponentially with depth (Reisser et al., 2015). However, Woodall et al. (2014) reported an abundance of MPs on the seafloor four orders of magnitude greater than in surface water gyres, while Peng et al. (2018) reported abundant MP particles in the Mariana Trench, the deepest part of the world's ocean.

Plastic debris is widely distributed throughout our oceans and colonize from latitudes near the equator to the poles (Obbard et al., 2014), with the tropical regions being the areas where it is most frequent and predominant (Barboza et al., 2019). Regardless of the geographical region, the most vulnerable areas with respect to the colonization of exotic species transported by this debris are those where endemisms abound and endangered species are present (Gregory, 2009; Thevenon et al., 2014).

Therefore, given the spatial "cosmopolitanism" of plastic materials and their increasing abundance in the marine environment, generalist invasive species (or with invasive potential) in the surface waters of all oceans which can be transported by this vector, constitute an increasing threat—within the bathymetric range to which they are adaptive—especially to pristine and highly biodiverse ecosystems, with particular relevance to Marine Protected Areas.

## EARLY DETECTION AND SURVEILLANCE OF AIS IN MARINE PLASTIC DEBRIS

Rech et al. (2018a) found that the frequency of a specific taxon attached to plastic litter in a coastal area can be predicted based on the characteristics of biological communities associated with each litter material and the composition of beach litter. This approach, after being tested in other regions, may contribute as a simple and cost-effective tool for risk assessment in the future (Rech et al., 2018a). On the other hand, Fazey and Ryan (2016a,b) showed that small samples of plastic litter lost buoyancy due to biofouling much faster than larger ones, providing the first estimates of the longevity of different sizes of plastic debris at the surface of the ocean. This finding could be used to improve model predictions of the distribution and abundance of floating plastic debris globally.

Ports are often export areas for native generalist species and entry areas for alien species (Mineur et al., 2006; Keller et al., 2010; Airoldi et al., 2015; López-Legentil et al., 2015; Ferrario et al., 2017). A sport or recreational vessel whose hull is made of fiberglass-reinforced polyester can import or export native and alien species. But also, by accumulation and subsequent sinking, ports and marinas can import and export plastic trash with alien species. In many cases the plastic sinks (especially bags), because of the weight of the biofouling, remain at shallow depths (especially in ports and marinas, which tend to accumulate plastic garbage on their bottoms). For their control and environmental monitoring, a modification of the SBPQ (Sessile Bioindicators Permanent Quadrats) method could be applied, as recently proposed by García-Gómez (2015) and García-Gómez et al. (2020a) for the early detection of alien species and environmental impacts of a local nature (e.g., urban discharges) or global (climate change) in rocky natural habitats. It is a non-invasive method focuses on the monitoring of preselected sensitive (indicators) sessile target species associated with rocky coralligenous habitats using permanent quadrats in underwater sentinel stations. It could be adapted to plastic panels (completed with other types of non-plastic panels) which are susceptible to colonization by opportunistic sessile species that could become invasive, and act as "traps" for the early

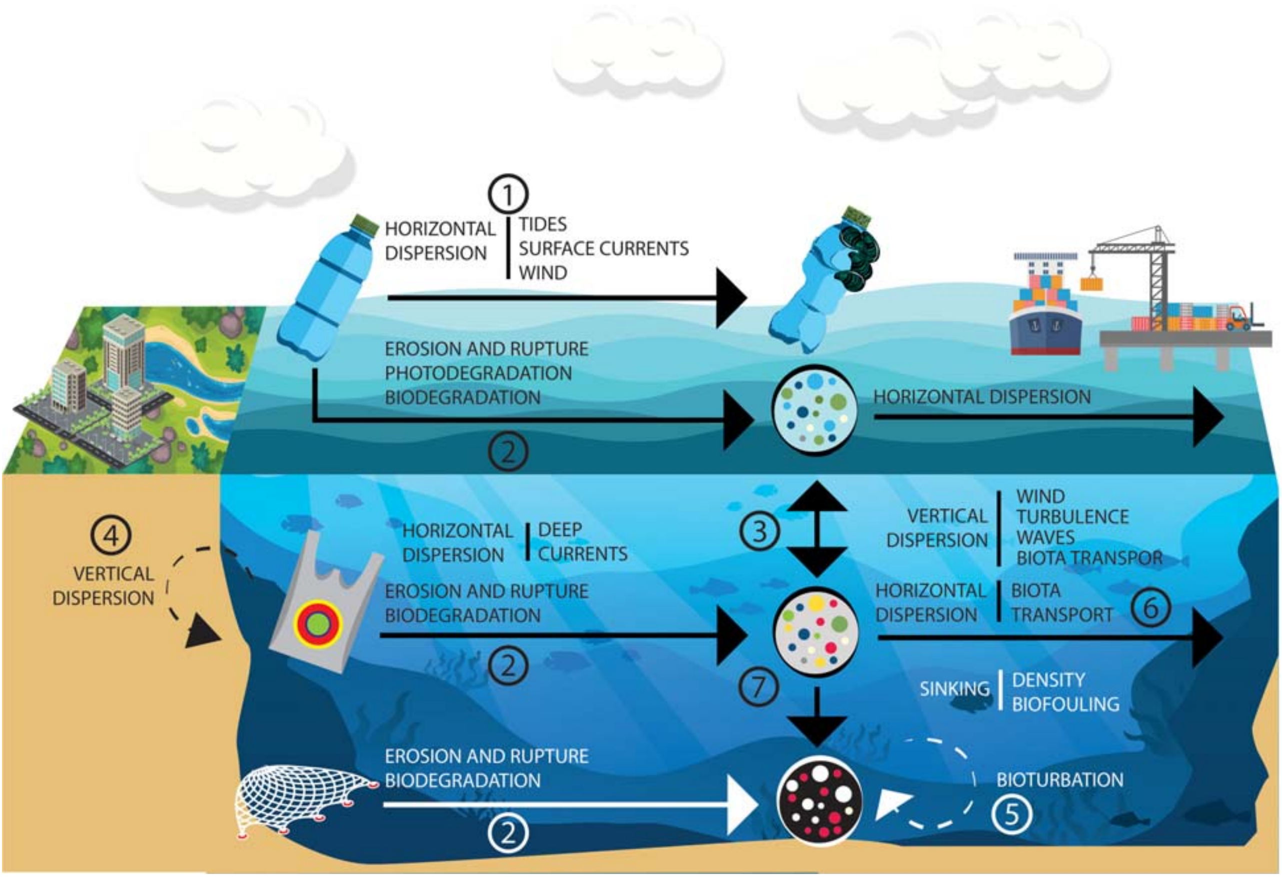

**FIGURE 4 |** Debris made of high-density polyethylene (HDPE), such as plastic bottles which could be transported through large areas and be vectors for potentially invasive marine species **(1)** or result in micro and nanoplastic material through physical degradation, photodegradation, or biodegradation **(2).** Plastic bags composed of low-density polyethylene (LDPE) which usually settle in the water column, while plastic fishing nets, in many cases constituted by nylon, tend to sink and settle on the seabed. Both plastic bags and fishing nets are susceptible to physical degradation and biodegradation. Plastic particles which could succumb to bioturbation **(5),** describe vertical movements **(3,4)** and be simultaneously ingested by animals from all oceanic stratum being dispersed by them **(6)**, as well as sink and stay at the seafloor due to their original density or to increase by processes such as biofouling **(7)**. Steps 1, 2, and 3 of "Horizontal Dispersion," which are the most frequently involved in biological invasions. To a lesser degree, steps 3 and 4 involve "Vertical Dispersion."

detection of alien species. In this regard, the installation of underwater sentinel stations should be tested at various inland points of ports, with plastic panels of at least five panels per point, of 25 cm × 25 cm, with different roughness and nature (e.g., polyamide or nylon, polyester, polyethylene, high density polyethylene and polypropylene), which serve to recognize the species which establish easily on this type of material and those which are more frequent and with a structural and adaptive profile of higher risk for invasion. This method could contribute to the early detection of alien species with invasive potential, and to the implementation of immediate mitigation and/or eradication measures.

## ADDITIONAL CONSIDERATIONS

From the foregoing, it can be deduced that plastic debris represents a ubiquitous vector with great potential for transporting both sessile and mobile species associated with it, capable of traveling long distances because plastic, due to its composition, is not biodegradable and, therefore, very durable over time.

We could ask ourselves which species of those transported by plastic (or that could be transported by this type of substrata) may have a greater risk of invasion. They would be sessile generalist arborescent species (e.g., seaweeds, hydrozoans, bryozoans) that, according to Bradshaw et al. (2003), are common components of fouling communities. So, they can provide food, shelter or hiding conditions for other mobile species that can travel with them (both non-native and native). About this, Marchini et al. (2015a) reported three mobile NIS associated with the introduced sessile species *Amathia verticillata* ( = *Zoobotrion verticillatum*) (Bryozoa) and suggested this species as substrate for transport between ports, facilitating its distribution. Also, Gavira-O'Neill et al. (2018) found 19 species associated with the invasive bryozoan *Tricellaria inopinata*—in list of "100 Worst Invasives" in the Mediterranean (Streftaris and Zenetos, 2006)—between them the three mobile introduced species *Caprella scaura*, *Monocorophium sextonae* (Amphipoda), and the *Paracerceis sculpta*, adding that these species represented over half of the quantified individuals and discussing the possibility of a potential case of "invasional meltdown"—expression by Simberloff and Von Holle (1999)—during which introduced species provide suitable habitat for other non-native species, favoring their establishment. Other studies also support this hypothesis for *T. inopinata* as a host for other mobile species introduced from other zoological groups, such as isopods and nudibranchs (Keppel et al., 2012; Hobbs et al., 2015). So, such arborescent sessile species (hosts of mobile fauna) are those that need to occupy the substrate surfaces of the bottom (even as epibionts) and, therefore, those that can generate the greatest environmental impact on the native sessile biota.

In order to improve biosecurity, the best mechanism is prevention and, in this sense, it is important to start acting against this ongoing problem; for example, through protocols for the sighting (from small boats and large ships) of accumulations of plastic adrift within 20 miles off the coasts, where the presence of accumulations of floating with well-established biofouling is detected. In the same way, ports and marinas must be involved in environmental surveillance for the early detection of alien species before they can become widespread.

Actions to manage the problem should be put into place, such as the collection of floating plastic by cleaning boats employed in coastal areas at risk of the entry of plastic accumulations due to winds and/or currents. International regulations or legal provisions must be implemented in this regard. Collaboration on the part of society must also be encouraged. Environmental education and the emerging "Citizen Science" movement (Wiggins and Crowston, 2011) should be stimulated and coordinated from public administrations, as well as large industries, companies or institutions that have large coastal infrastructures. In addition, large industries and companies should also participate in mitigating the problem under the influence of the emerging philosophy of "Working with nature" (PIANC, 2014; Martin et al., 2017; Nebot et al., 2017). which has generated an awareness of respect for nature, by which it is intended to act with it and not against it, collaborating in environmental monitoring and surveillance studies of threatened species naturally established in port breakwaters (García-Gómez et al., 2010, 2014) and, in the present case, for the early detection of alien species with invasive potential.

## CONCLUSION

1. The number of articles published of plastic debris as a vector for the introduction of alien species has increased enormously in recent years. This increase could be related to the increase in annual plastic production, which results in a greater threat, in addition to a growing interest in the problem on the part of the scientific community and, therefore, the greater number of research papers related to it.
2. Several of the biological characteristics of marine species commonly associated with plastic, such as the short life cycle and larval development, are also characteristics of a large portion of the known invasive species; so these species that travel on plastic debris across the ocean could generally be perceived as a major threat to their destination.
3. A wide variety of organisms colonize plastic materials, both microorganisms (e.g., species of the genus *Vibrio* or different species carrying virulent and antibiotic resistance genes) and macrofauna species (e.g., algae or bryozoan species). This fact increases the threat to ocean life caused by plastic and turns it into a means for spreading disease.
4. There are large gaps in knowledge about the functioning of plastic objects as vectors and the lack of studies on colonization processes on different plastic polymers by marine species generate contradictions between different authors. Despite the great advances produced today in the knowledge of plastic debris in the ocean, greater research are necessary to mitigate the threat of biological invasions linked to this type of pollutant.

## AUTHOR CONTRIBUTIONS

MG and JG made **Figures 1**, **2**, and **4**. JG-G provided the photographs of **Figure 3**. All authors decided the consensus on the structure of the manuscript and accomplished the literature search, and participated for the conclusion and formal aspects.

## ACKNOWLEDGMENTS

We are deeply grateful to the CEPSA Foundation and Red Eléctrica from Spain (REE) for its initiative to support and finance scientific research. Secondly, we are grateful to OBIMASA, ACERINOX, ENDESA, OPP-51 (Almadrabas) and Diputación de Cádiz. Additionally, this work has benefitted from the scientific projects financed by the Port Authority of Seville. We express our gratitude for the collaboration provided to the Seville Aquarium, the Town Halls of Tarifa and La Línea as well as the Puerto Deportivo La Alcaidesa, Club Marítimo and Real Club Náutico (RCN) de La Línea. From the Marine Biology Station of the Strait (Ceuta) we would also like to thank Watergames Gran Azul diving club, Marina Hércules S.A. and Consejería de Medio Ambiente y Sostenibilidad, Autonomous City of Ceuta.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers
in Ecology and Evolution

ORIGINAL RESEARCH
published: 08 June 2021
doi: 10.3389/fevo.2021.631754

# The Invasive Macroalga *Rugulopteryx okamurae*: Substrata Plasticity and Spatial Colonization Pressure on Resident Macroalgae

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**Specialty section:**
*This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution*

***Received:*** *20 November 2020*
***Accepted:*** *09 April 2021*
***Published:*** *08 June 2021*

**Citation:**
*García-Gómez JC, Florido M, Olaya-Ponzone L, Sempere-Valverde J and Megina C (2021) The Invasive Macroalga Rugulopteryx okamurae: Substrata Plasticity and Spatial Colonization Pressure on Resident Macroalgae. Front. Ecol. Evol. 9:631754. doi: 10.3389/fevo.2021.631754*

The present study constitutes the first evaluation of the space colonization strategies performed by *Rugulopteryx okamurae* when co-occurring with the resident macroalgal community in the introduced areas. Since the first apparition of the nonindigenous macroalga in the Strait of Gibraltar, its high propagation capacity together with its colonization ability has enhanced the establishment success of the species in detriment of the resident biota. In this study, we carried out observational surveys during 2017–2020 in order to assess the coverage levels of *R. okamurae* on different lighting conditions, surface orientations, and substrata types (artificial and natural). Results revealed that, beyond the high percent coverages already reported at illuminated and semi-illuminated natural rocky habitats, *R. okamurae* is able to settle on a wide variety of artificial substrata. The settlement performance of the species was also investigated and different mechanisms underlying the space colonization were proposed. Thus, *R. okamurae* was observed interacting with 43 resident macroalgal species at generally illuminated rocky habitats of the northern Strait coasts. Six colonization mechanisms were proposed for spatial growth scenarios. Overall, results pointed out that, in most of the cases where the invasive species co-occur with the resident community, *R. okamurae* would be favored as regards spatial growth success. Competitive interactions and environmental factors which influence results obtained must be addressed in order to fully predict impacts on resident communities. Moreover, together with previous scientific works, overall data provided in this study highlight the need to urgent implement management measures focused on habitats susceptible to be invaded, as well as studies on the ecology and dispersal vectors of *R. okamurae* in the Strait of Gibraltar and adjacent areas.

**Keywords: *Rugulopteryx okamurae*, macroalgae, biological invasions, invasive macroalga, space colonization, Strait of Gibraltar**

# INTRODUCTION

The introduction and spread of nonindigenous marine species (NIS) are within the major threats to global biodiversity, natural resources, and human health and constitute a priority for the protection and management of coastal areas (Bax et al., 2003; Galil et al., 2018). When an introduced NIS acclimates and expresses an aggressive ecological behavior, its status progresses from established NIS to invasive NIS. In such cases, NIS competes with the resident community for resources like space, so the ecosystem and its services can be altered. In the case of macroalgae, the establishment of the introduced species may lead to competitive interactions with the resident macroalgal community through lateral and epiphytic growth, which can be facilitated by a higher thermal tolerance than its competitors and the production of secondary metabolites for allelopathic defense (Tronholm et al., 2012). Secondary metabolites can ease lateral competition but also impede predation by native consumers, thus increasing the ecological competitiveness of the species in the introduced environments (Pereira and Da Gama, 2008). Consequently, NIS may severely affect the marine ecosystems by modifying the local habitats, community structure, and food webs (Viard and Comtet, 2015; Marks et al., 2018). To meet EU regulation on the prevention and management of NIS, it is highly necessary to establish standard methodologies and monitoring plans in sensitive and little-studied areas (Galil et al., 2018).

The Strait of Gibraltar is a biodiversity hotspot located in the convergence of three biogeographic provinces within the Atlantic–Mediterranean subregion (Ekman, 1953). This area is highly sensitive to environmental changes (Coll et al., 2010), and it experiences an intense maritime traffic, which is a major vector for the introduction of NIS (Papacostas et al., 2017). The benthic communities of the Strait of Gibraltar may have already suffered the cumulative impacts from the invasive NIS *Asparagopsis armata*, *Asparagopsis taxiformis*, and *Caulerpa cylindracea* (Boudouresque and Verlaque, 2002; Andreakis et al., 2004; Rivera-Ingraham et al., 2010). In such vulnerable geographical area, the detection and monitoring of potential invasive species can provide valuable information. Mechanisms that can influence the invasion success of marine macroalgae remain misunderstood, even though they are critical for the successful mitigation and conservation of the ecosystems affected (Noè et al., 2018).

In 2015, the brown macroalga *Rugulopteryx okamurae*, native to the Northwestern Pacific (Hwang, 1994), was detected for the first time on both shores of the Strait of Gibraltar (Altamirano-Jeschke et al., 2016; Ocaña et al., 2016). In the Mediterranean Sea, this species was previously recorded on the coastal lagoon of Thau (French Mediterranean coast), presumably introduced through the commerce of Japanese oysters for aquaculture (Verlaque et al., 2009). Nevertheless, in Thau lagoon, this species did not show a critical invasive behavior as it happened in the Strait coasts (Verlaque et al., 2009; García-Gómez et al., 2018). During 2015–2016, *R. okamurae* quickly colonized most of the shoreline of this Strait, requiring municipal cleaning machines to remove more than 5,000 tons of detached biomass from the touristic beaches of Ceuta, North Africa (Ocaña et al., 2016; El Aamri et al., 2018). The massive algal wracks detected (**Supplementary Figure 1**), together with the huge coverages identified when the species is attached to the rocky bottoms (García-Gómez et al., 2018, 2020), suggest that this case is worryingly unusual because of the large amounts of biomass produced in such a small geographical area. Beyond the ecological impacts, social and economic consequences of the invasive behavior of *R. okamurae* can be also assumed (e.g., the massive biomass released on the coasts threats the tourist inflow and the fishing sector as it becomes entangled in nets, hindering the fish extraction).

On its native distributional range, *R. okamurae* is abundant throughout the year. The maximum growth and reproductive development occurs above 15°C, while the thallus is reduced to a basal system of perennial rhizoids in winter (Kajimura, 1992; Hwang et al., 2009). Agatsuma et al. (2005) suggests that the biological cycle of the species in the pacific waters is completed in 2 years, but it is still unknown if the species is able to complete its life cycle in the Mediterranean and Atlantic waters (Verlaque et al., 2009; Altamirano-Jeschke et al., 2016, 2017). Despite that sexual reproduction is still unperceived in the introduced habitats, the vegetative and asexual strategies of the established populations (propagules and monospores) have led to the massive occupation of most of the rocky bottoms (Altamirano-Jeschke et al., 2017 and Altamirano et al., 2019), becoming present all-year round in the southern and northern coasts of the Strait of Gibraltar.

The extreme propagation capacity of the species, combined with a high survival capability, would make the impact magnitude high and any secondary spread events worrisome. In fact, shortly after delimiting the distributional range of *R. okamurae* in 2017 (see García-Gómez et al., 2020), massive wrack deposits of the species were sighted at points beyond its eastern and western limits along the northern coasts of the Strait of Gibraltar, in Granada and Almeria (Altamirano et al., 2019; Figueroa et al., 2020). Moreover, preliminary models predicting suitable areas for the incoming establishment of *R. okamurae* populations have evidenced the risk of nearby areas along the entire southern and eastern Iberian Peninsula, where protected areas and others of great conservation interest are included (Muñoz et al., 2019).

This study aims to perform a preliminary evaluation of the establishment potential of *R. okamurae* in the introduced habitats, as well as the vulnerability of the resident benthic macroalgae facing its spatial growth and propagation through the coasts of the Strait of Gibraltar. Specifically, the following objectives were raised (1) to estimate the coverage of *R. okamurae* on different substrata, orientations, and lighting conditions and (2) to assess the implications on the resident macroalgal community when *R. okamurae* is established in the same substrata, highlighting apparent colonization strategies underlying the spatial growth of the invasive species.

# MATERIALS AND METHODS

## Sampling Locations

Observational studies were performed in 12 surveys (period from June to September, during 2017–2020), comprehending all the ranges of distribution of *R. okamurae* on the northern coasts of the Strait of Gibraltar and adjacent areas. Each survey corresponded to one sampling site where the invasive species was present and attached to the rocky bottom and located less than 20 km from each other (**Figure 1**). This area hosts the Marine Protected Area "El Estrecho Natural Park," included within The Intercontinental Biosphere Reserve of the Mediterranean. The study sites were the following: Barbate, Punta Camarinal, Bolonia, Isla de Tarifa Oeste, Isla de Tarifa Este, Torre del Guadalmesí, Faro de Punta Carnero, La Ballenera, Punta de San García, Crinavis, Puerto de La Alcaidesa, and Playa de La Alcaidesa.

## Coverage of *R. okamurae* on Different Substrata and Lighting Conditions

In each sampled site, an estimation of *R. okamurae* coverage was carried out by direct visual observations in three 50-m-long and 4-m-wide transects. When necessary, *in situ* observations were supported by video- and photographic data taken in the same survey. Transects were located parallel to the shoreline between 0 and 10 m depth. In the case of sites where the considered substrata limited the sampling area (i.e., artificial structures at Puerto de La Alcaidesa and Crinavis), transects were located parallel to the shoreline but distributed along the horizontal plane. Thus, the coverage of *R. okamurae* was assessed considering the following substrata conditions: inclination (i.e., vertical and horizontal), lighting conditions (i.e., highly illuminated, moderately illuminated, poorly illuminated and unlit areas), and substrata nature (i.e., natural and artificial substrata). Natural substrata were represented by maërls and pebbles, limestone, sandstone, slate, and wood. Meanwhile, artificial substrata considered were breakwater boulders near sandy bottoms, cement and concrete, ceramics, breakwater limestone boulders, abandoned fishing nets and ropes, glass bottles, metallic surfaces, metallic surfaces on boats and ships, plastics, and car tires.

The total percent cover of *R. okamurae* per substratum was estimated as the overall coverage occupied at each abovementioned condition within the 200 square meters of each transect. Because some anomalous artificial substrata are not frequently found while crucial considering space availability in marine habitats, a selective exploration was carried near the limits of the sampling transects when considering components of the marine debris (i.e., plastics, ceramics, abandoned fishing nets and ropes, glass bottles, and car tires). Overall *R. okamurae* coverage values were included within a 0 to 3 scale attending to different ranges. Thus, if the coverage ranged between 1 and 30% for all aforementioned transects at one specific substratum, the

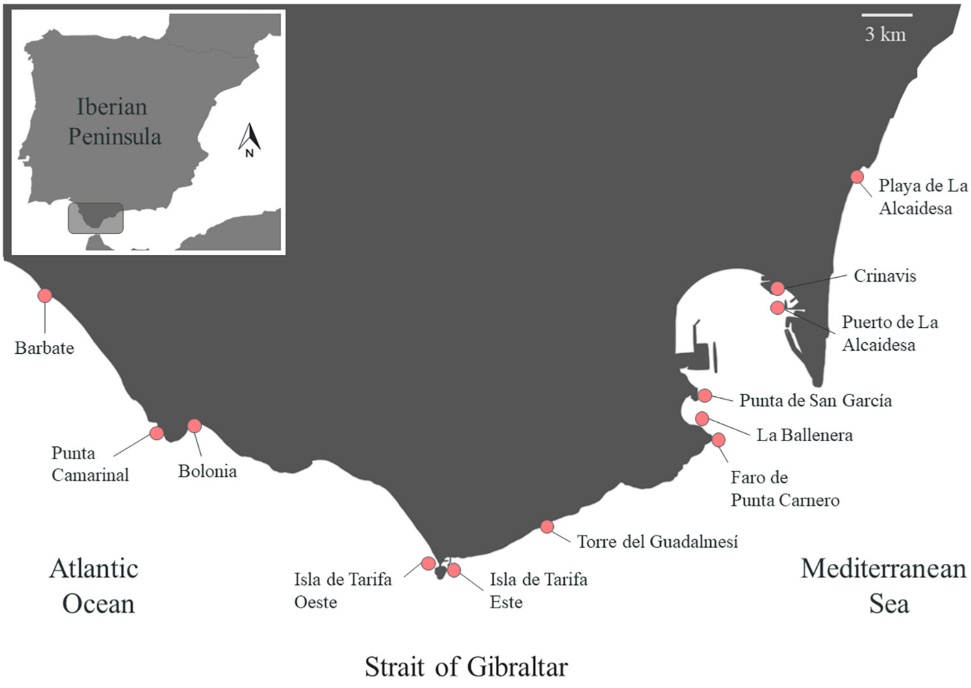

**FIGURE 1 |** Location of the sites surveyed across the northern coast of the Strait of Gibraltar and adjunct areas: Barbate (36°10′1.45″N, 5°53′28.60″O); Punta Camarinal (36°4′48.64″N, 5°47′58.51″O); Bolonia (36° 5′9.37″N, 5°47′4.56″O); Isla de Tarifa Oeste (36°0′16.72″N, 5°36′44.22″O); Isla de Tarifa Este (36°0′14.25″N, 5°36′20.41″O); Torre del Guadalmesí (36°2′8.30″N, 5°31′15.58″O); Faro de Punta Carnero (36°4′35.93″N, 5°25′29.14″O); La Ballenera (36°5′5.71″N, 5°25′57.41″O); Punta de San García (36°6′16.37″N, 5°25′48.19″O); Crinavis (36°9′52.15″N, 5°22′23.30″O); Puerto de La Alcaidesa (36°9′19.99″N, 5°21′57.90″O); and Playa de La Alcaidesa (36°13′58.02″N, 5°18′53.36″O).

species was classified as "present" (1) for that substratum; percent coverages between 31 and 60% were classified as "abundant" (2) and coverages over 61% as "dominant" (3). Resident macroalgal coverage was not included since competitive scenarios were not contemplated for this objective.

## Substrata Types and Colonization Strategies Associated With *R. okamurae* Establishment

In order to better understand how *R. okamurae* is spatially growing on the coastal habitats, the presence of the invasive macroalga was examined in, at least, one of all aforementioned sampling sites by direct—*in situ*—or indirect observation (photographs and/or videos). In surveys, we recorded the spatial growth scenarios where *R. okamurae* co-occurred with other macroalgal species when established at different recipient habitats. Habitats were differentiated attending to rocky substrata nature (natural and artificial), tide exposition (intertidal areas, tide pools, and subtidal areas), illumination (illuminated and shadow habitats), and bottom composition (sandy bottoms). The resident macroalgal community was identified to the lowest taxonomic level possible, and the percentage of co-occurring scenarios at different habitats was recorded. Because preliminary surveys revealed different coexistence patterns, the spatial colonization strategies by which *R. okamurae* seems to become established on generally illuminated rocky habitats were proposed.

To synthesize all the information obtained about the spatial growth of *R. okamurae*, Venn diagrams were created using Venny 2.1 online software (Oliveros, 2007). Venn diagrams allow to visualize and analyze relationships between different data groups by representing all possible combinations and elements contained in each one of them. Identifying the spatial growth strategies described as groups, displayed diagrams allow the identification of shared (overlapped circles) and unique species (independent regions of circles) performing each interaction described and/or their different combinations. No more than four group combinations were displayed in each analysis to comply with the requirements of the exotic geometries of the software (Oliveros, 2007).

# RESULTS

## Coverage of *R. okamurae* on Different Substrata and Lighting Conditions

*Rugulopteryx okamurae* dominated (i.e., 100% coverage) at highly illuminated areas (vertical and horizontal) and moderately illuminated horizontal surfaces (0–10 m depth) (**Table 1**). The species was abundant (31–60%) at vertical moderately illuminated areas, present (1–30%) at horizontal surfaces of the entrance of caves and crevices, and totally absent (0% coverage) at unlit areas and vertical poorly illuminated habitats. Concerning substrata nature, 100% of coverage was obtained for limestone and sandstone (natural rocky substrata), and limestone rip-rap boulders (artificial rocky substrata). The species was abundant (31–60% coverage) at ceramics, tires, and abandoned fishing nets and ropes, while present (1–30% coverage) on a wide variety of substrata, including breakwater boulders close to sandy bottoms, cement and concrete, glass bottles, metallic surfaces (including those from the upper zone of boats and ship hulls), and plastics.

## Habitats and Colonization Strategies Underlying *R. okamurae* Establishment

Forty-three macroalgal species were detected in relation to possible implications inferred by the spatial establishment of *R. okamurae*, including four NIS (*A. armata*, *A. taxiformis*, *C. cylindracea*, and *Dictyota cyanoloma*). Species which spatially co-occurred with *R. okamurae* at each habitat type are listed in **Table 2** (left section). In 22 and 23% of the cases, the invasive species co-occurred with the macroalgal community at natural and illuminated habitats, respectively (**Figure 2A**). Sublittoral habitats harbored 17% of the spatial growth scenarios, while tide pools, artificial structures, and intertidal zones recorded 10, 10, and 9%, respectively. Sandy (5%) and shadow bottoms (4%) were less represented, being the habitats where *R. okamurae* was rarely observed spatially growing and interacting with the resident community.

Six spatial growth strategies by which *R. okamurae* becomes established at generally illuminated rocky habitats were proposed regarding possible effects on the resident macroalgae (right section of **Table 2** and **Figures 2B**, **3**). In two of the strategies identified, we suggest the space colonization as a result of the direct interaction with the resident macroalgae. Thus, competition by lateral compression (LAT) and overgrowth as epiphyte (EPI) were proposed for 28% and 16% of the total cases, respectively, where *R. okamurae* was established on the substrata interacting (i.e., co-occurring) with the resident macroalgal community. Other settlement scenarios did not show signs of direct macroalgal interaction although the final occupancy by the invasive species was expected to occur. Thus, the invasive species was observed to grow and develop on the resident macroalgae without being attached on the adult thalli (GRO) (9%) and, in 28% of the cases, the resident species were surrounded by *R. okamurae*, which remained abundantly established around the resident macroalgal populations (OCC). In this last strategy, and according to overall observations, *R. okamurae* became established on the space left by the previously established populations with the resident macroalgae death, as a consequence of its biological cycle or another unidentified factors (e.g., abiotic stressors, predation).

Surveys revealed other cases where, despite that biological interactions between both macroalgae were apparently perceived, no direct evidences of negative impacts on the resident community were observed. However, it must be taken into account that physicochemical factors, physiological impacts, or other indirect effects from *R. okamurae* competitiveness have not been examined here, so results obtained for the latter mechanisms must constitute just the preliminary basis to further investigate patterns observed if they happened (impacts). Two main processes needed to be differentiated in this case: on the one hand, we described spatial growth events where disturbance/stress processes may be occurring

**TABLE 1 |** Coverage of *Rugulopteryx okamurae* under different lighting conditions and substrata nature (natural and artificial substrata).

| | | | |
|---|---|---|---|
| Light exposition and surface orientation | Unlit (dark) areas | Vertical | |
| | | Horizontal | |
| | Poorly illuminated areas (entrance of caves and crevices) | Vertical | |
| | | Horizontal | █ |
| | Moderately illuminated areas | Vertical | ██ |
| | | Horizontal | ███ |
| | Highly illuminated areas | Vertical | ███ |
| | | Horizontal | ███ |
| Natural substrata | Maerl and pebbles (<5 cm of diameter) | | █ |
| | Limestone | | ███ |
| | Sandstone | | ███ |
| | Slate | | █ |
| | Wood | | █ |
| Artificial substrata | Breakwater boulders near sandy bottom | | █ |
| | Cement and concrete | | █ |
| | Ceramics | | ██ |
| | Limestone rip-rap boulders | | ███ |
| | Abandoned fishing nets and ropes | | ██ |
| | Glass bottles | | █ |
| | Metallic surfaces | | █ |
| | Metallic surfaces from boats and ships | | █ |
| | Plastics | | █ |
| | Tires | | ██ |
| | *Coverage categories* | | 0 1 2 3 |

*Grey bars represent the percentage ranges of observed coverage of R. okamurae during the visual samplings (0–10 m depth). The absence of grey bars reveals that R. okamurae was absent in all locations surveyed. Coverage categories correspond to the following coverage ranges: 0: Absent (0% coverage); 1: Present (1–30% coverage); 2: Abundant (31–60% coverage); 3: Dominant (61–100% coverage).*

even though they are not perceived yet. Despite the lack of negative evidences of resident species death or damaged tissues in our surveys, this strategy was assumed to lead to disturbance events in the species involved since indirect implications derived from similar competitive scenarios have been obtained and could be likely to occur in the study area (e.g., indirect implications like shading, chemical alteration, bioturbation). In this regard, only one strategy was proposed for the 13% of the overall co-occurrence cases. It was described for those cases where *R. okamurae* mats, detached from the rocky bottom and dispersed in the water column, become free-floating on the resident species thallus without being totally attached on them (FLO). On the other hand, we also perceived colonization strategies leaded by the resident macroalgae. Unless *R. okamurae* was established on the substrata, the resident macroalgae seemed to take advantage from the spatial growth (e.g., epiphytes of the invasive macroalga) in the 6% of the cases surveyed. Hence, *R. okamurae* was observed as a basibiont (i.e., host to a macroalgal epibiont) (BAS) (**Figures 4A–C**) of *A. armata* (**Figure 4A**), *Colpomenia sinuosa*, *Halopteris scoparia*, *Plocamium cartilagineum* (**Figure 4B**), *Titanoderma pustulatum*, and *Sphaerococcus coropifolius.*

Mechanisms underlying spatial exclusion were those expected to seriously compromise resident species survival, so they were selected to be explored with Venn diagrams. Thus, relations between LAT, EPI, GRO, and OCC were together examined (**Figure 5A**). Besides, GRO, EPI, FLO, and BAS were independently studied in order to check possible relations in terms of disturbance/stress and overgrowth strategies (**Figure 5B**). Most of species displaced by LAT were also observed to suffer spatial pressure by OCC (seven common species were involved in LAT and OCC strategies: *D. cyanoloma*, *Dictyota dichotoma*, *Dictyota dichotoma* var. *intricata*, *Dictyota fasciola*, *Dictyopteris polypodioides*, *Stoechospermum polypodioides*, and *Ulva rigida*). In fact, despite that LAT was perceived to only affect two of the resident species in an exclusive way, it was the mechanism most combined with remaining interactions. In contrast, OCC was more exclusive in terms of species affected by only one spatial growth strategy of *R. okamurae* (i.e., five species were displaced only by OCC processes).

GRO was also poor combined with other interactions of spatial exclusion. Overall, macroalgae suffering overgrowth interactions by this strategy included the macroalgal species *Codium vermilara*, *C. sinuosa*, *Lithophyllum incrustans*, *Mesophyllum alternans*, *Mesophyllum lichenoides*, *Halopithys incurva*, *Peyssonnelia* ssp., and *Taonia atomaria*. Venn diagrams revealed that six species were observed to be affected by *R. okamurae* establishment only by epiphytic strategies:

**TABLE 2 |** Presence (shaded quadrats) of perceived interactions between *R. okamurae* and resident macroalgal species at introduced habitats.

| | **Habitats** | | | | | | | | **Space colonization strategies** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **ART** | **NAT** | **INT** | **TID** | **SUB** | **ILL** | **SHA** | **SAN** | **LAT** | **EPI** | **GRO** | **OCC** | **FLO** | **BAS** |
| *Amphiroa rigida* J. V. Lamouroux | ■ | ■ | | | ■ | | | | | | | | | |
| *Asparagopsis armata* Harvey | ■ | ■ | | ■ | ■ | ■ | | | ■ | ■ | | | ■ | ■ |
| *A. taxiformis* (Delile) Trevisan de Saint-Léon | ■ | ■ | | | ■ | ■ | | | ■ | ■ | | ■ | ■ | |
| *Caulerpa cylindracea* Sonder | | ■ | | | ■ | ■ | | ■ | ■ | ■ | | ■ | | |
| *Caulacanthus* sp./*Gelidium* sp. Turf | | ■ | ■ | | | ■ | | | | | | | | |
| *Chaetomorpha sp.* | ■ | ■ | ■ | | | ■ | | | | | | | | |
| *Cladophora laetevirens* (Dillwyn) Kützing | | ■ | ■ | | | ■ | | | | | | | | |
| *Codium adhaerens* C. Agardh | ■ | ■ | ■ | ■ | | ■ | ■ | | | | | | | |
| *C. bursa* (Olivi) C. Agardh | ■ | ■ | | | ■ | ■ | | | | ■ | | ■ | | |
| *C. vermilara* (Olivi) Delle Chiaje | ■ | ■ | | ■ | ■ | ■ | | | ■ | | ■ | ■ | | |
| *Cladostephus spongiosus* (Hudson) C. Agardh | | ■ | | | ■ | ■ | | ■ | | | | ■ | ■ | |
| *Colpomenia sinuosa* (Mertens ex Roth) Derbès and Solier | ■ | ■ | | ■ | ■ | ■ | | ■ | ■ | ■ | ■ | ■ | | ■ |
| *Cystoseira tamariscifolia* (Hudson) Papenfuss | | ■ | | ■ | ■ | ■ | | | | | | ■ | ■ | |
| *Dictyopteris polypodioides* (A. P. De Candolle) J. V. Lamouroux | | ■ | | ■ | ■ | ■ | | | ■ | | | ■ | | |
| *Dictyota cyanoloma* Tronholm, De Clerck, A.Gómez-Garreta and Rull Lluch | ■ | ■ | | ■ | ■ | ■ | | | ■ | | | ■ | | |
| *D. dichotoma* (Hudson) J. V. Lamouroux | ■ | ■ | | ■ | ■ | ■ | | ■ | ■ | | | ■ | | |
| *D. dichotoma var. intricata* (C. Agardh) Greville | | ■ | | | ■ | ■ | | | ■ | | | ■ | | |
| *D. fasciola* (Roth) J. V. Lamouroux | | ■ | ■ | ■ | ■ | ■ | | ■ | ■ | | | ■ | | |
| *Ellisolandia elongata* (J. Ellis and Solander) K. R. Hind and G. W. Saunders | | ■ | ■ | ■ | ■ | ■ | | | ■ | ■ | | | ■ | |
| *Fucus spiralis* Linnaeus | | ■ | ■ | | | ■ | | | | | | | | |
| *Gelidium corneum* (Hudson) J. V. Lamouroux | | ■ | ■ | | ■ | ■ | ■ | | | | | | | |
| *G. spinosum* (S. G. Gmelin) P. C. Silva | | ■ | ■ | | | ■ | | | | | | | | |
| *Halopithys incurva* (Hudson) Batters | | ■ | | | ■ | ■ | | | ■ | ■ | ■ | ■ | ■ | |
| *Halopteris filicina* (Grateloup) Kützing | ■ | ■ | | | ■ | ■ | | | ■ | ■ | | ■ | ■ | |
| *H. scoparia* (Linnaeus) Sauvageau | ■ | ■ | | ■ | ■ | ■ | | ■ | ■ | ■ | | ■ | ■ | ■ |
| *Jania rubens* (Linnaeus) J. V. Lamouroux | ■ | ■ | ■ | ■ | ■ | ■ | | | ■ | | | ■ | | |
| *Laurencia obtusa* (Hudson) J. V. Lamouroux | | ■ | ■ | | | ■ | | | | | | | | |
| *Lithophyllum byssoides* (Lamarck) Foslie | | ■ | ■ | | | ■ | | | | | | | | |
| *L. incrustans* Philippi | ■ | ■ | ■ | | ■ | ■ | | | ■ | | ■ | ■ | | |
| *Mesophyllum alternans* (Foslie) Cabioch and M. L. Mendoza | ■ | ■ | | ■ | ■ | ■ | ■ | | ■ | | ■ | ■ | | |
| *M. lichenoides* (J. Ellis) Me. Lemoine | ■ | ■ | | ■ | ■ | ■ | ■ | | ■ | ■ | ■ | ■ | | |
| *Osmundea pinnatifida* (Hudson) Stackhouse | | ■ | ■ | ■ | | ■ | | | | | | | | |
| *Peyssonnelia ssp.* | | ■ | | | ■ | ■ | ■ | | ■ | | ■ | | | |
| *Plocamium cartilagineum* (Linnaeus) P. S. Dixon | | ■ | | ■ | ■ | ■ | ■ | | ■ | ■ | | ■ | ■ | ■ |
| *Sargassum f. c.* C. Agardh | | ■ | | | ■ | ■ | | ■ | | | | ■ | | |
| *Sphaerococcus coronopifolius* Stackhouse | | ■ | | | ■ | ■ | | ■ | ■ | | | | ■ | ■ |
| *Stoechospermum polypodioides* (J. V. Lamouroux) J. Agardh | | ■ | | ■ | ■ | ■ | | | ■ | | | ■ | | |
| *Taonia atomaria* (Woodward) J. Agardh | | ■ | | ■ | | ■ | | | | | ■ | | | |
| *Titanoderma pustulatum* (J. V. Lamouroux) Nägeli | ■ | ■ | | | ■ | | | | | | | | | ■ |
| *Treptacantha usneoides* (Linnaeus) Orellana and Sansón | | ■ | | ■ | ■ | ■ | | ■ | | | | ■ | ■ | |
| *Ulva rigida* C. Agardh | ■ | ■ | ■ | | | ■ | | | ■ | | | ■ | | |
| *Valonia utricularis* (Roth) C. Agardh | ■ | ■ | ■ | | ■ | ■ | ■ | | | ■ | | | | |
| *Zonaria tournefortii* (J. V. Lamouroux) Montagne | | ■ | | | ■ | ■ | | | ■ | ■ | | | | |

*"Habitats" columns refer to the different habitats where R. okamurae (RO) has been observed interacting with the resident macroalgal species (ART, artificial substrata; NAT, natural substrata; INT, area extended from the low intertidal to the high intertidal zone; TID, tidepools; SUB, sublittoral zone; ILL, illuminated habitats; SHA, shaded habitats; SAN, sandy habitats near to rocky shores). "Space colonization strategies" columns refer to the observed interactions between R. okamurae and the resident species on generally illuminated rocky habitats [LAT, RO laterally compress the resident species; EPI, RO epiphytes the resident species; GRO, RO grows and develops on the resident species without being attached on it; OCC, RO is established on the free substrata left by the resident species when the latter dies; FLO, RO remains free-floating on the resident species thallus without being attached on it; BAS, RO is epiphyted by the resident species (i.e., RO was observed as basibiont)].*

*Amphiroa rigida*, *C. cylindracea*, *Codium bursa* (**Figure 6**), *Ellisolandia elongata* (**Figures 4D,E**), *Valonia utricularis*, and *Zonaria tournefortii*. Species epiphited by *R. okamurae* did not experience GRO events during the sampling process. Contrarily, spatial occupancy by free-floating mats on resident species thalli (FLO) involved the species *Cladostephus spongiosus*, *E. elongata*, *A. taxiformis*, *Halopteris filicina*, *P. cartilagineum*, and *Treptacantha usneoides*. The latter three species were also observed to be epiphited by *R. okamurae*. Contrarily, epibiosis on *R. okamurae* (BAS) was less frequent and relegated to few species: *A. armata*, *C. sinuosa*, *H. scoparia*, *S. coronopifolius*, and *T. pustulatum*.

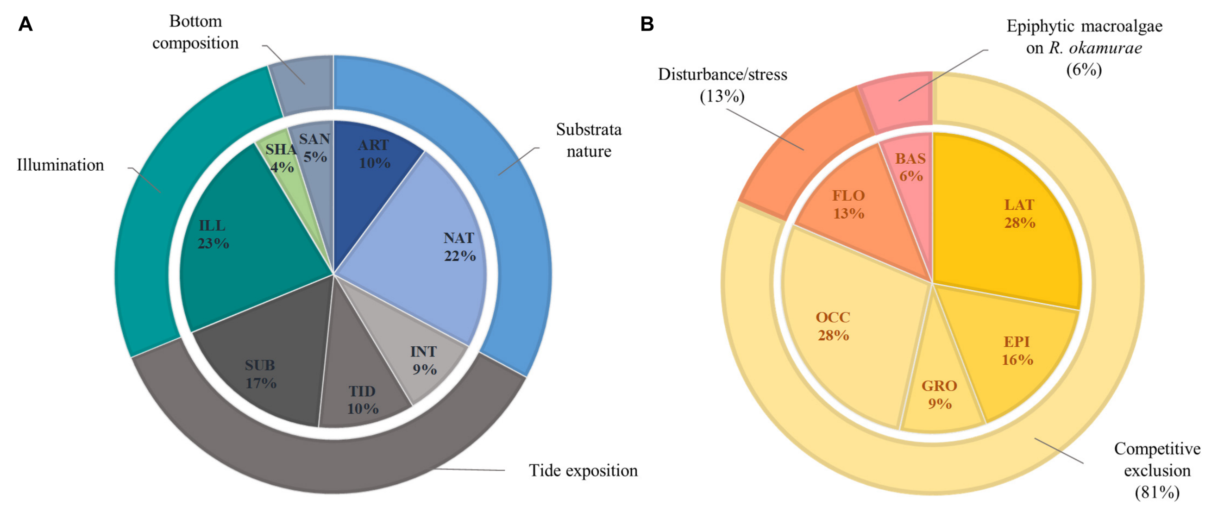

**FIGURE 2 | (A)** Percentage of total observed interactions between *R. okamurae* (RO) and the 43 resident macroalgal species present at each habitat surveyed in the study area (ART, artificial substrata; NAT, natural substrata; INT, area extended from the low intertidal to the high intertidal zone; TID, tidepools; SUB, sublittoral zone; ILL, illuminated habitats; SHA, shaded habitats; SAN, sandy habitats near to rocky shores). **(B)** Percentage of space colonization strategies between RO and the resident macroalgal community [LAT, RO laterally compress the resident species; EPI, RO epiphytes the resident species; GRO, RO grows and develops on the resident species without being attached on it; OCC, RO is established on the free substrata left by the resident species when the latter dies; FLO, RO remains free-floating on the resident species thallus without being attached on it; BAS, RO is epiphyted by the resident species (i.e., RO was observed as basibiont)].

# DISCUSSION

It is crucial to perform observational studies to obtain full ecological characterizations in environmental assessments (Moschella et al., 2005). In this regard, this study evidences the high establishment success and preliminary spatial colonization strategies underlying the invasive potential of *R. okamurae* for the first time at the northern coasts of the Strait of Gibraltar. Although findings reflect a difficult scenario for mitigation strategies on the invaded areas, information about the invasibility of the resident communities could result useful in the development of early detection and rapid responses in areas not yet invaded (Lodge et al., 2006; Williams and Smith, 2007). In this respect, these preliminary results aim to advance our understanding in marine community ecology, targeting conservation efforts on the present bioinvasion case.

## Substrata Conditions and Establishment Success

Results obtained for natural habitats agree with those from previous contributions (see García-Gómez et al., 2020) that well-illuminated hard rocky bottoms may present a major propagule pressure at the local range expansion of *R. okamurae* in the Strait of Gibraltar. Likewise, shelter conditions from subtidal rocky habitats may also facilitate the presence of introduced species even if detrimental to light availability (Piazzi and Ceccherelli, 2002), as observations performed in this study and the high coverages of *R. okamurae* at coralligenous (Sempere-Valverde et al., 2020) and precoralligenous habitats reflect (García-Gómez et al., 2020).

Acclimation capacity plays a key role in the success over the native communities, particularly at scenarios of environmental change (Tronholm et al., 2012; Papacostas et al., 2017). In this regard, any knowledge about the type of substrata colonized could help to better develop management actions to prevent potential dispersal vectors and to minimize the range expansion of the invasive species (Checoli-Mantelatto et al., 2020). According to our surveys, *R. okamurae* was present and even abundant in a number of artificial surfaces, from harbor infrastructures (e.g., breakwaters, limestone rip-rap boulders and metallic surfaces of boats) to marine litter (abandoned fishing nets, ropes, plastics, tires, and glass bottles). The diversity of artificial substrata colonized led to give attention to the potential ability of the species to take advantage to ecosystem degradation, which increases the scale of the impact on recipient communities (Occhipinti-Ambrogi and Savini, 2003). The development and survival through time and distance on different substrata nature must complement results obtained in this work for futures researches. Furthermore, raised awareness must be adopted to those sectors which may be involved in the accidental dispersion of the invasive species (e.g., correct cleaning of fishing and diving equipments). In this regard, beyond the socioeconomic impacts reported in fisheries (see García-Gómez et al., 2018; Altamirano et al., 2019), the spatial growth of *R. okamurae* on materials related to artificial coastal defense structures, commercial shipping, recreational boats, and even fishing equipment could imply the establishment and dispersion of the species at short (<1 km) and/or long (>1 km) distances (Ruitton et al., 2005; Lord et al., 2015). In the same way, most of materials derived from marine litter also showed to constitute adequate substrata for the invasive species, and thus the permanence or increase in marine litter in the area could become another key donor habitat for secondary spread events (Kiessling et al., 2015).

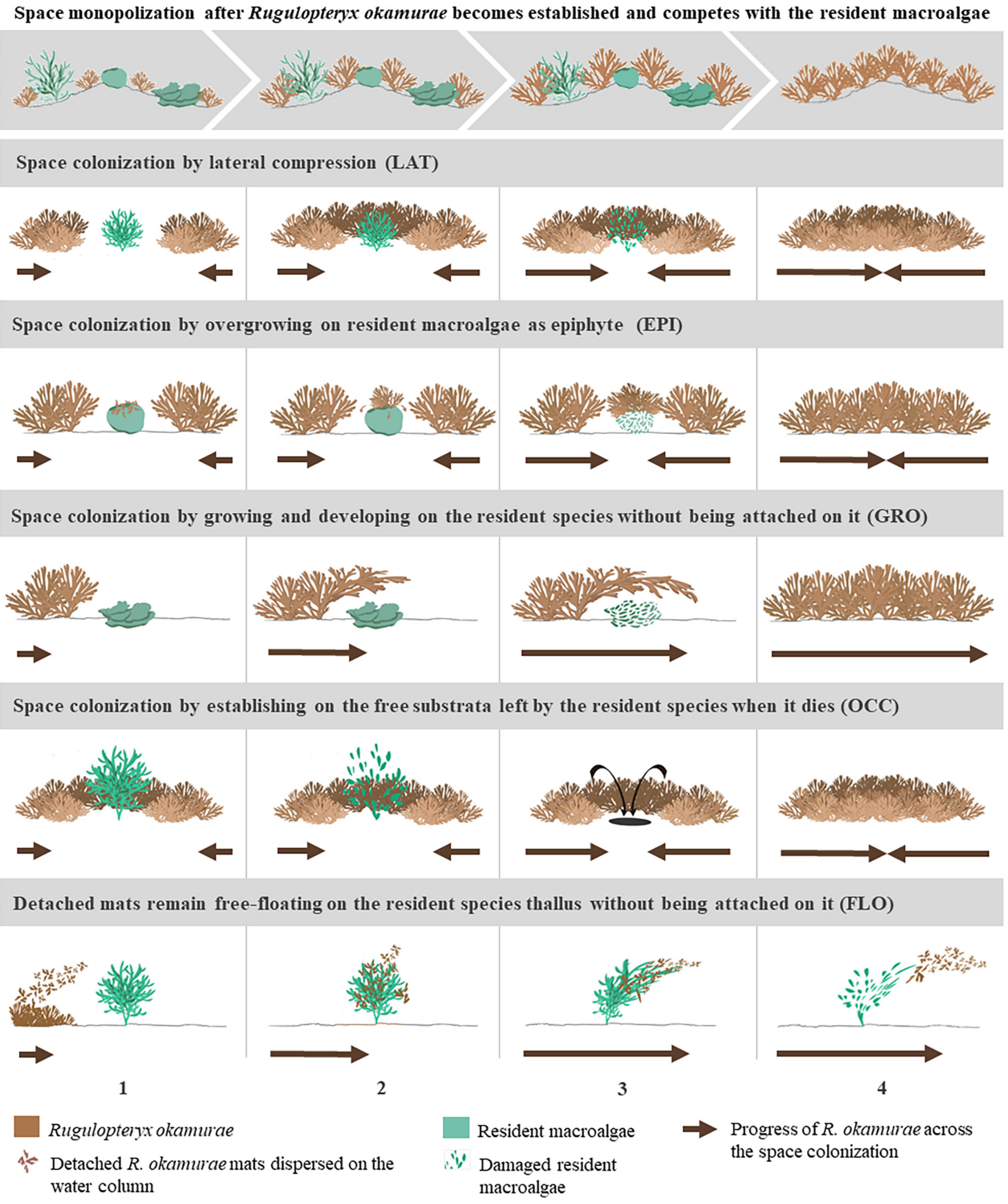

**FIGURE 3 |** Ilustrative diagram showing space colonization strategies described between *R. okamurae* and resident marine macroalgae and subsequent implications in generally illuminated rocky bottoms of the Strait of Gibraltar. Numbers represent the sequential stages of the process.

## Habitat Conditions Associated With General *R. okamurae*–Resident Macroalgae Interactions

Once established on the rocky substrata, *R. okamurae* seems to be much more effective in competing for the space than most of the resident species (García-Gómez et al., 2018, 2020). Thus, competing with the photophilous community, it usually becomes dominant over other benthic taxa (García-Gómez et al., 2020; **Figure 7**). Parallel schemes were perceived in this study, since illuminated and natural habitats harbored most of the interactive scenarios between *R. okamurae* and the resident macroalgae.

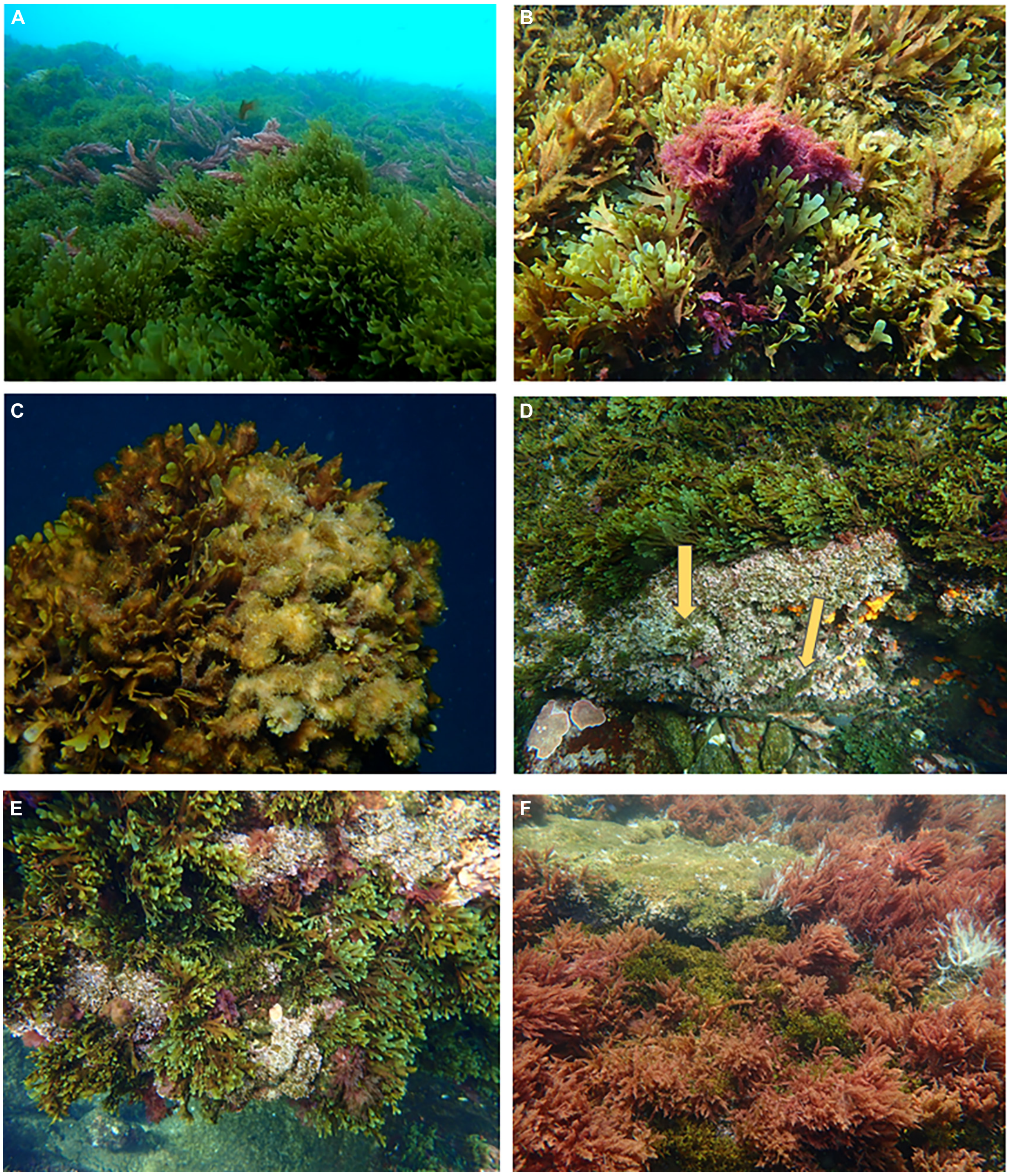

**FIGURE 4 | (A)** Overgrowth of *Asparagopsis armata* on *Rugulopteryx okamurae* in the Strait of Gibraltar (1–5 m depth) after 2017. **(B)** Overgrowth of *Plocamium cartilagineum* and **(C)** generalist algae on *R. okamurae*. **(D)** *Ellisolandia elongata* surrounded by *R. okamurae* fronds with small specimens already inserted on *E. elongata* specimens (arrows). **(E)** Expansion of *R. okamurae* in detriment of *E. elongata* in rocky illuminated habitats. **(F)** *Asparagopsis armata* laterally compressed by *R. okamurae* before 2017.

However, particular caution is required interpreting spatial competitive interactions and direct consequences on recipient communities, as other factors not considered can influence distribution patterns (McCook et al., 2001). More exposed habitats may compromise the adequate development of macroalgae due to abiotic stressors (i.e., canopy erosion by hydrodynamics and/or sediment abrasion) (Ruitton et al., 2005), which also makes difficult the direct observation of interactions with the recipient biota. Even more, spatial competition due to invasive macroalgae establishment may be enhanced in habitats where resources are limited (light, nutrients, or space) (Ólaffson, 2017). For example, good adaptation to low-light conditions may endow competitive advantages over other resident macroalgae in introduced habitats (e.g., the study case of the invasive *Agarophyton vermiculophyllum*) (Zi-Min and Lopez-Bautista, 2014). In accordance, co-occurring events detected at shadow environments stress effects already reported on endangered sciaphilic taxa by *R. okamurae* (Ocaña et al.,

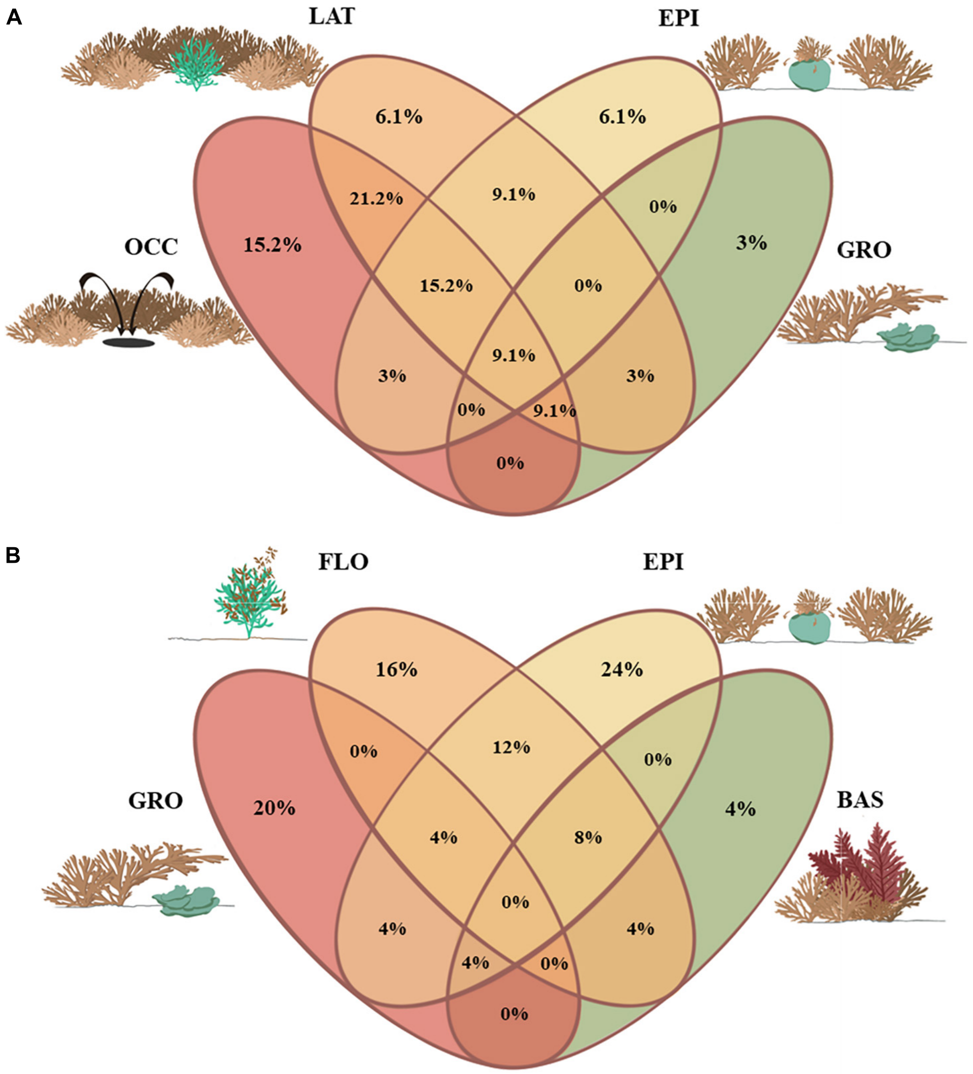

**FIGURE 5 |** Venn diagrams showing the percentage of resident macroalgal species contained in each possible combination of the colonization strategies described for *R. okamurae* (RO) and the resident macroalgal community: **(A)** spatial exclusion interactions and **(B)** overgrowth interactions. [LAT, RO laterally compress the resident species; EPI, RO epiphytes the resident species; GRO, RO grows and develops on the resident species without being attached on it; OCC, RO is established on the free substrata left by the resident species when the latter dies; FLO, RO remains free-floating on the resident species thallus without being attached on it; BAS, RO is epiphyted by the resident species (i.e., RO was observed as basibiont)].

2016; García-Gómez et al., 2018; Sempere-Valverde et al., 2020).

## Colonization Strategies Underlying *R. okamurae* Establishment

Despite that the recent loss of resident macroalgal habitats has been associated with the spread of *R. okamurae* in the Strait coasts to a large extent (Ocaña et al., 2016; García-Gómez et al., 2018, 2020; Altamirano et al., 2019), mechanisms underlying the invasion success of *R. okamurae* remain misunderstood. In this study, the spatial collision between the invasive species and the resident macroalgae allowed to better understand the spatial colonization strategies at generally illuminated rocky habitats, driving different patterns in the settlement of the introduced species.

Eighty-one percent of the scenarios observed were conceived as negative for the resident community, and thus the total displacement of the resident macroalgae was conceived as the most common consequence of the spatial establishment of *R. okamurae*. The strategies most addressed for scenarios perceived were the spatial exclusion by LAT and the total occupancy of the space when the resident species dies because of unidentified factors (e.g., natural death). Species exclusion and replacement can become critical in terms of habitat modification in rocky environments, especially when talking about engineered species (Buschbaum et al., 2006; Alomar et al., 2016). Indirect consequences of species replacement are

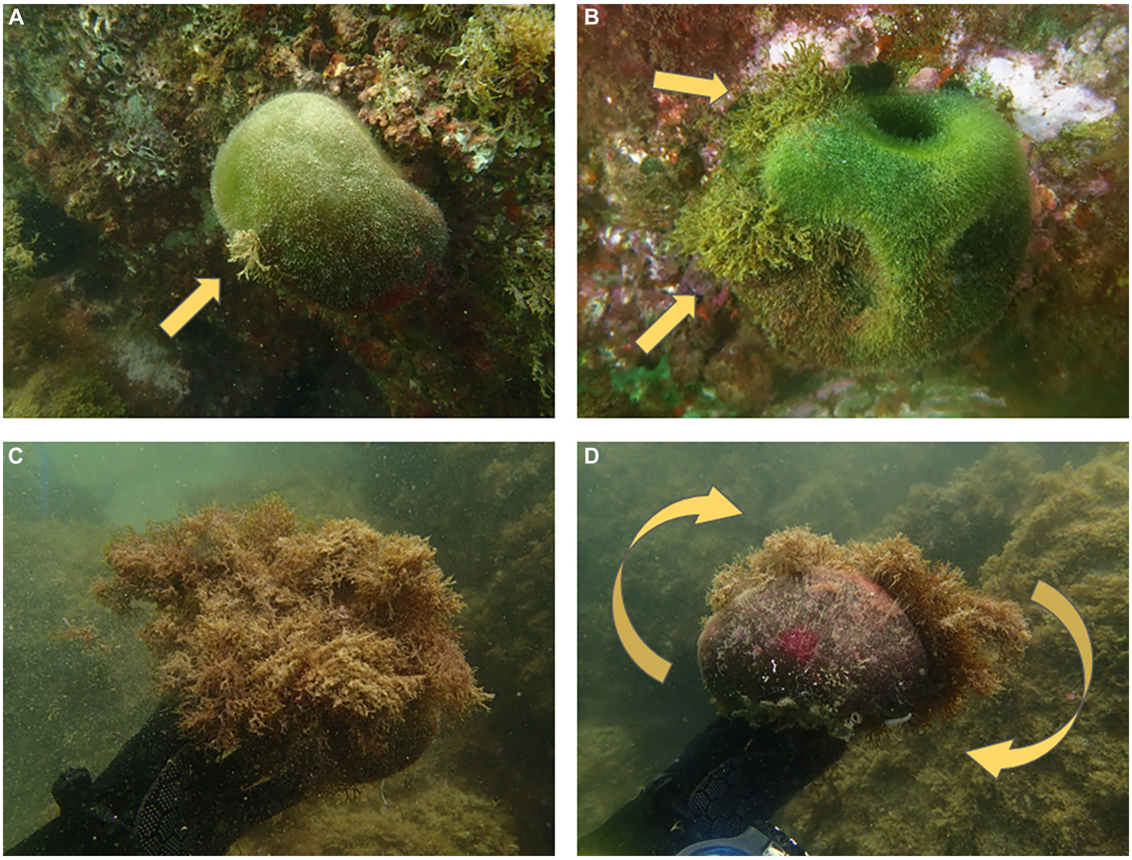

**FIGURE 6 |** Example of progressive epibiosis of *Codium bursa* by *Rugulopteryx okamurae*. **(A)** Incipient occurrence after *R. okamurae* establishment. **(B)** Progress of *R. okamurae* spatial growth. **(C)** *C. bursa* extremely epiphyted by *R. okamurae*. **(D)** Opposite side of the same individual of *C. bursa* showing depigmented tissue in lateral and basal areas.

not contemplated here. However, habitat changes derived from *R. okamurae* displacement could promote cascade effects on benthic ecosystems (e.g., associated fauna and higher trophic levels), even when habitat complexity is not compromised because species competing are morphologically similar (e.g., Navarro-Barranco et al., 2019). Together with impacts already reported on macroalgal communities (e.g., García-Gómez et al., 2018; 2020), potential implications in associated biota enhance the need to encompass the percentage cases of total exclusion found in this study to ecological repercussions under a more holistic view of the impacts at nonnative habitats.

With thermal tolerance, allelopathic defense in macroalgal communities (mainly on tropical areas) constitutes an important factor in the success of marine bioinvasions (Pereira and Da Gama, 2008; Tronholm et al., 2012). Settlement inhibition by chemical defenses does not necessarily imply significant negative impacts at community level when considering faunal taxa, because settling larvae can usually settle on other substrata (Ólaffson, 2017). Otherwise, it could become crucial for the establishment success of sessile or sedentary species dispersing by passive mechanisms (e.g., macroalgal propagules). In this regard, *R. okamurae* contains bioactive compounds which may limit settlement inhibition from the sesquiterpene family and spatane and seco-spatane skeleton diterpenes (Kurata et al., 1988; Ninomiya et al., 1999; De Paula et al., 2011). Indeed, epibiosis on the invasive species was an event scarcely represented when compared with other strategies of space colonization. However, epibiosis on *R. okamurae* must also be attributed when considering impacts on the recipient communities, especially taking into account that dense populations of the invasive macroalga have colonized wide surfaces through its bathymetric range of distribution in the northern and southern coasts of the Strait of Gibraltar (e.g., over 90% coverage at 10–20 m depth) (García-Gómez et al., 2020; Sempere-Valverde et al., 2020).

Resident species able to take advantage of the spatial growth of other species can also exist depending on the environmental conditions (Ólaffson, 2017). The established invasive species *A. armata* has been to overgrow *R. okamurae* populations in shallow subtidal bottoms after 2018 (1–5 m depth) (**Figures 4A,F**). It could be expected that certain competitors can limit the invasion success through time (Levine et al., 2004). Otherwise, *R. okamurae* could be contributing to provide habitat for other invasive species, facilitating the establishment when available space is inaccessible (Olyarnik et al., 2009). Biotic resistance in marine environments is often not strong enough (Papacostas et al., 2017), and scenarios of facilitation

**FIGURE 7 |** Resident benthic species exclusion and subsequent monopolization of the space by *R. okamurae* in the rocky bottoms of the Strait of Gibraltar. **(A)** First scheme of *R. okamurae* establishment on rocky substrata of the Strait of Gibraltar (–10 m depth) in the presence of resident species, as *Sphaeroccocus coronopifolius* (arrows). **(B)** *S. coronopifolius* expressing signs of degeneration (arrow) after/while interacting with the introduced species. **(C)** Resident species lost and subsequent monopolization of rocky bottoms by *R. okamurae*.

between invaders could make this susceptibility to progressively increase by altering the competitive landscape (Simberloff and Von-Holle, 1999). In the Strait of Gibraltar, different notorious invasions by macroalgae have happened in the latter years (e.g., *A. armata*, *A. taxiformis*, *Lophocladia lallemandii*, *C. taxifolia*, *C. cicylindracea*) (Boudouresque and Verlaque, 2002; Andreakis et al., 2004; Rilov and Galil, 2009; Rivera-Ingraham et al., 2010). These successive scenarios, together with other drivers of global change (e.g., changing temperature conditions), destabilize not only the current species distribution but also the structure and function of resident communities in the Mediterranean Sea (Occhipinti-Ambrogi, 2007). On the other hand, it has not been tested yet if the reproductive and vegetative behavior of *R. okamurae* varies throughout time, leading other species to take advantage of those moments of minimum biomass production. As in its native habitats, *R. okamurae* can be observed all year round in the Strait coasts, but whether the species is able to complete its life stage is still unknown (Verlaque et al., 2009; Altamirano-Jeschke et al., 2016, 2017). Studies carried out during the months of maximum algal expansion (2016–2017) have shown that *R. okamurae* achieves coverages greater than 30% even in the winter months at 15-m depth (García-Gómez et al., 2020), periods when it would be expected that the low temperatures make the species reduces its maximum biomass. Also, experiences on *C. taxifolia* by (Glasby et al., 2005a,b) show that even when the total disappearance of the algal populations occur over relatively short periods of time, recoveries in the native biota may not occur. Further studies on mentioned interactions will elucidate the capability of resident species (invasive or native) to buffer against *R. okamurae* displacement. Meanwhile, according to Piazzi et al. (2001), it is possible that only when resident species are able to be invaded but not displaced can the macroalgal community be said to resist the invasion of the introduced macroalga.

A different pattern is perceived when *R. okamurae* grows on other species thalli, as direct overgrowth often results in the total displacement of the basibiont. One example is the interaction between *R. okamurae* and *C. bursa*, represented in **Figure 6**. Unlike this growth strategy, the rest of observed overgrowth conditions did not imply the direct attachment of *R. okamurae* rhizomes or thallus. In this respect, it was noteworthy that the macroalgal species affected by the horizontal elongation of *R. okamurae* thallus were highly characterized by flattened and encrusting taxa, where crustose macroalgae are included. According with other marine bioinvasion cases, it should be verified whether habitat type (Piazzi et al., 2001; Ceccherelli et al., 2002) and allelopathic substances from coralline macroalgae (Vermeij et al., 2011) influence interactions by which *R. okamurae* rhizomes remain attached to other species.

Yet the consequences of the introduction of *R. okamurae* are not necessarily limited to interactions performed when attached to the rocky substrata. Mats of *R. okamurae* can be released after being established on the bottom becoming free-floating on the water column. It has not been clarified yet if the wrack depositions of the invasive macroalga are due to the thorough water agitation in specific geographic areas (e.g., high tidal coefficient or groundswell), the result after completing the natural life cycle, or the combination of all mentioned processes. Meanwhile, results indicate that disturbances by floating mats trapped on the thallus of resident erect macroalgae could be minimal because, at least in current areas, these mats shed shortly afterward. However, albeit negative impacts were not perceived, consequences on the macroalgal community can be wide and diverse. For example, physical damages can occur since contact can reduce light levels by shading (Kennelly, 1989), abrasion, chemical effects, and the facilitation of direct overgrowth (McCook et al., 2001). Also, overall floating mats may serve as physical barriers for settling larvae (Zi-Min and Lopez-Bautista, 2014) or pelagic organisms, whose behavior can result as modified due to the decreased visibility nearshore (Kirby et al., 2000). Figueroa et al. (2020) have pointed out that *R. okamurae* mats detached from the rocky bottoms and transported by currents to a certain depth are capable of maintaining high photosynthetic activity and physiologically viable spores. Because the easy dispersion of *R. okamurae* constitutes a threat facing other European marine areas (Altamirano et al., 2019), the role of released mats needs to be accounted also considering potential secondary spread events.

## CONCLUSION

All the available data clarify that the high propagation capacity of *R. okamurae*, in combination with its competitive and spatial establishment capacity, enhances the settlement of the species once having entered an area that presents favorable biotic and abiotic factors (Altamirano et al., 2019; García-Gómez et al., 2020). Results obtained in this study reinforces the high ability of *R. okamurae* to grow on different substrata types, formed by not only abiotic but also biotic compounds, since macroalgal species also constitute suitable substrata and thus they could facilitate the invasion in a similar way than hard bottoms (Olyarnik et al., 2009). The high representation of strategies which implied the spatial exclusion of the resident macroalgae, together with other interactions of potential disturbance, claims the development of major biodiversity assessments in the Strait of Gibraltar. This, combined with the high propagation capability of the species (Altamirano-Jeschke et al., 2017 and Altamirano et al., 2019), makes the dispersion to habitats susceptible to be invaded, an alarming phenomenon that needs to be managed. So far, the life history of *R. okamurae* remains uncertain in the Mediterranean and Atlantic waters, more change the future of this bioinvasion represents. The spatial establishment capability observed in this work enhances the performance of observational and experimental investigations including environmental factors which influence patterns obtained. This could help to fully understand those elements which favor the establishment success of the species on lit and semi-lit rocky substrata and thus to lend further urgency for management actions focused on *R. okamurae* impacts.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JG-G: investigation, obtaining data *in situ*, data analysis, supervision, validation, funding acquisition, and project administration. MF: investigation, data analysis, and data curation. JG-G and MF cowrote the manuscript. All the authors contributed substantially to revisions. LO-P: investigation, obtaining of data *in situ*, and data curation. JS-V: investigation. CM: investigation and supervision.

## FUNDING

This study was funded by CEPSA Foundation and Red Eléctrica de España (REE). Additional financial support was provided by the Organization of Fish Producers of Almadrabas (OPP-51), ENDESA, ACERINOX, and Diputación Provincial de Cádiz. This project has also benefited from scientific equipment and infrastructures financed by the Autoridad Portuaria (AP) of Seville and the Aquarium of Seville.

## ACKNOWLEDGMENTS

We are deeply grateful to the city of La Línea, particularly to the logistical support provided by Puerto La Alcaidesa, the Yacht Club (RCNLL), and the Maritime Club, as well as by the town halls of La Línea and Tarifa. Special thanks are given to Darren Fa and Stephen for facilitating information from Gibraltar shores. Thanks are also given to Campo de Gibraltar (La Linea) and to the CIES (Algeciras) diving clubs. Finally, we express our gratitude to Antonio Vegara, Juanjo Quintero, Salvador Magariño, Juan Antonio Parada, José Fosela, Isabel Cárdenas, Candela Sánchez, and José Cantera for their continued collaboration.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.631754/full#supplementary-material

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