



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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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 Facility¹, Atlas of Living Australia², South Australian Museum³ provided upon request by Doctor Peter Hudson, Australian National Insect Collection⁴ provided upon request by Doctor Juanita Rodriguez, Invasive Plants in Portugal – Invasoras.pt⁵ (Marchante et al., 2017), Southern Africa Plant Invaders Atlas (Henderson, 1999), literature references (Dennill, 1985, 1987; Prinsloo and Naser, 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 v2.0⁶ (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*,

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>

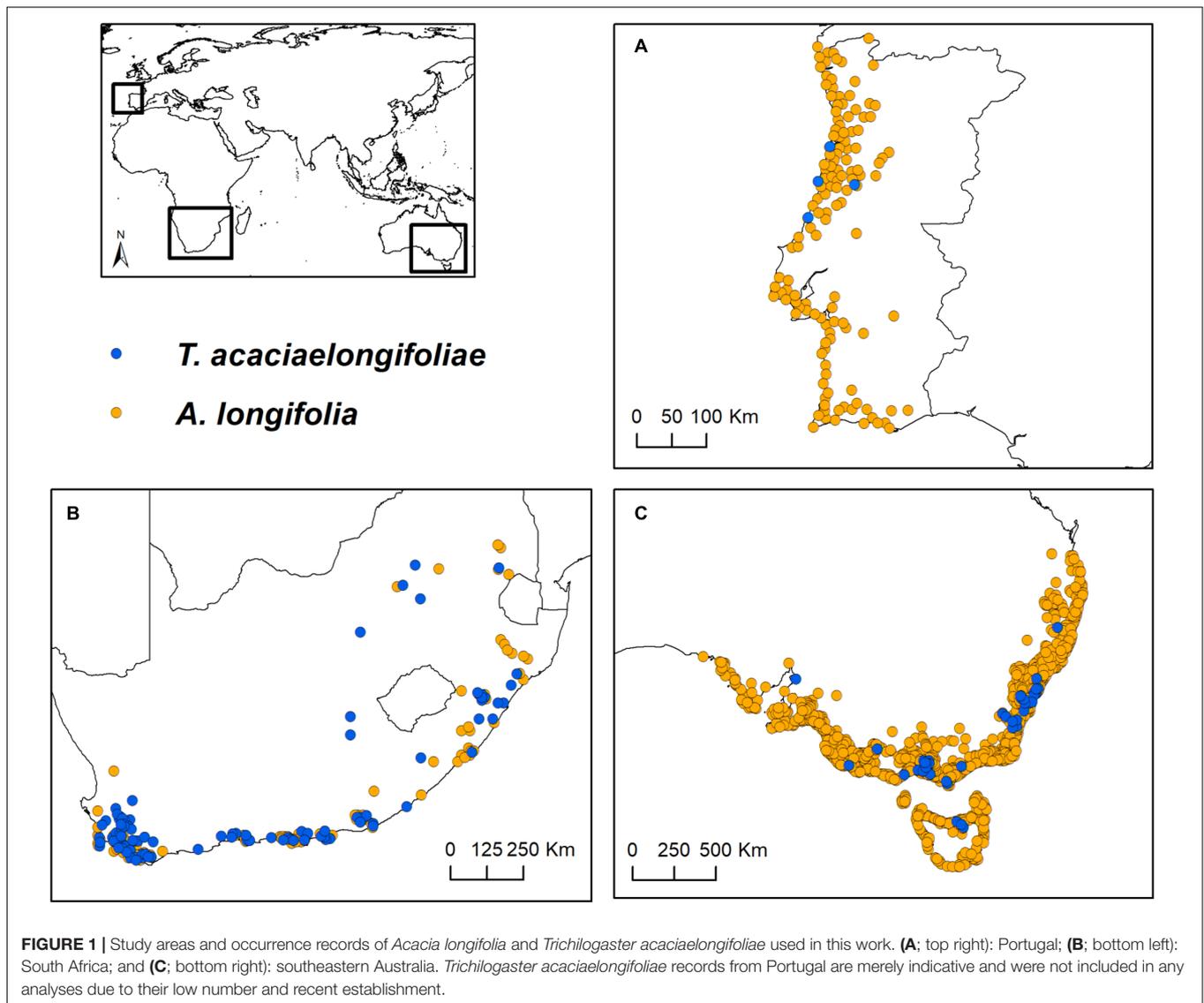


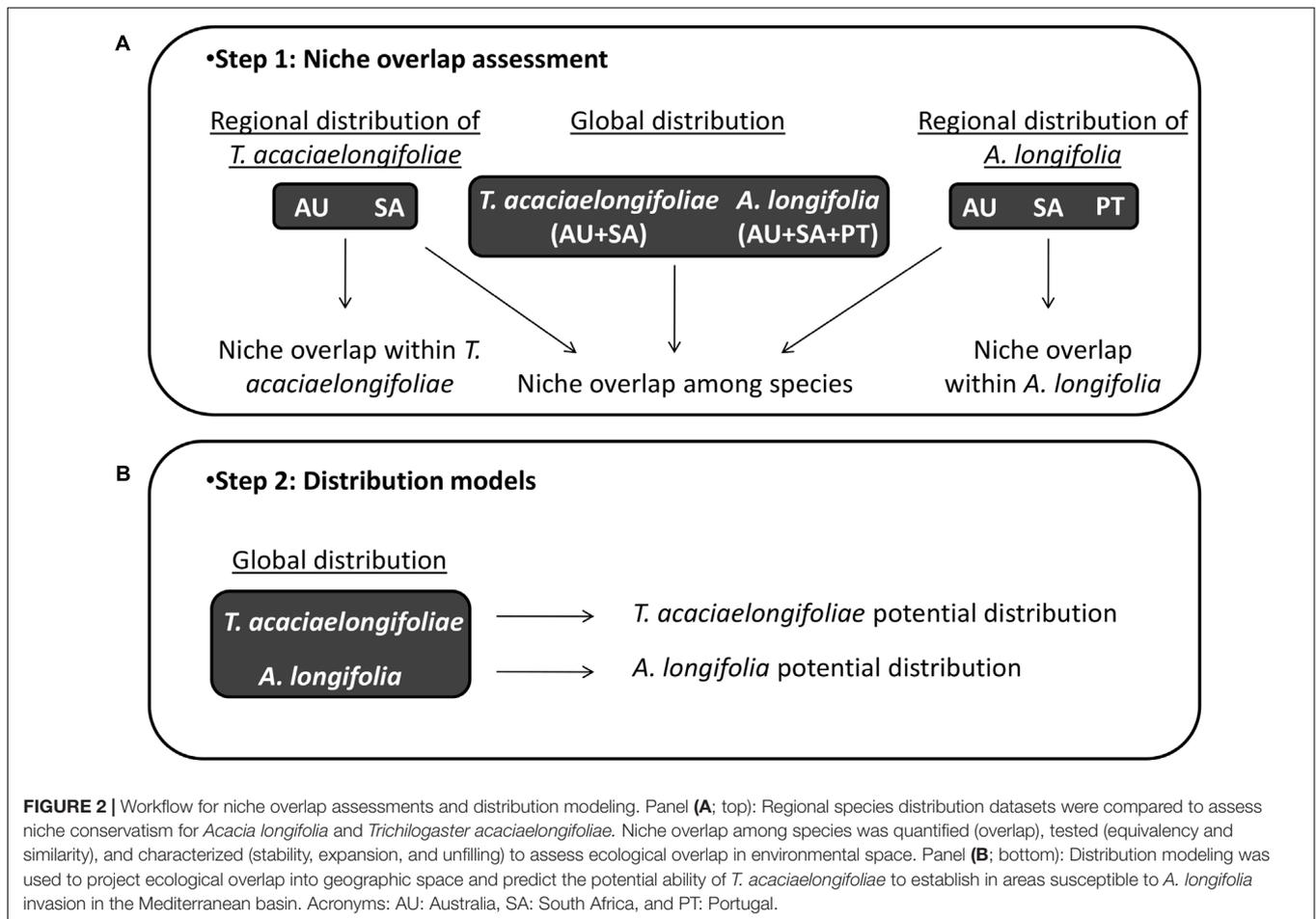
Figure 2). All operations were performed in ArcMap 10.1 (Environmental Systems Research Institute, 2012).

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



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.

| | | <i>Acacia longifolia</i> | | | <i>Trichilogaster acaciaelongifoliae</i> | | |
|-------|---|--------------------------|--------|--------|--|--------|-------|
| | | 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 (\pm SD). AUC of models for *T. acaciaelongifoliae* ranged between 0.71 and 0.92, with a weighted average of 0.85 ± 0.04 (\pm 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

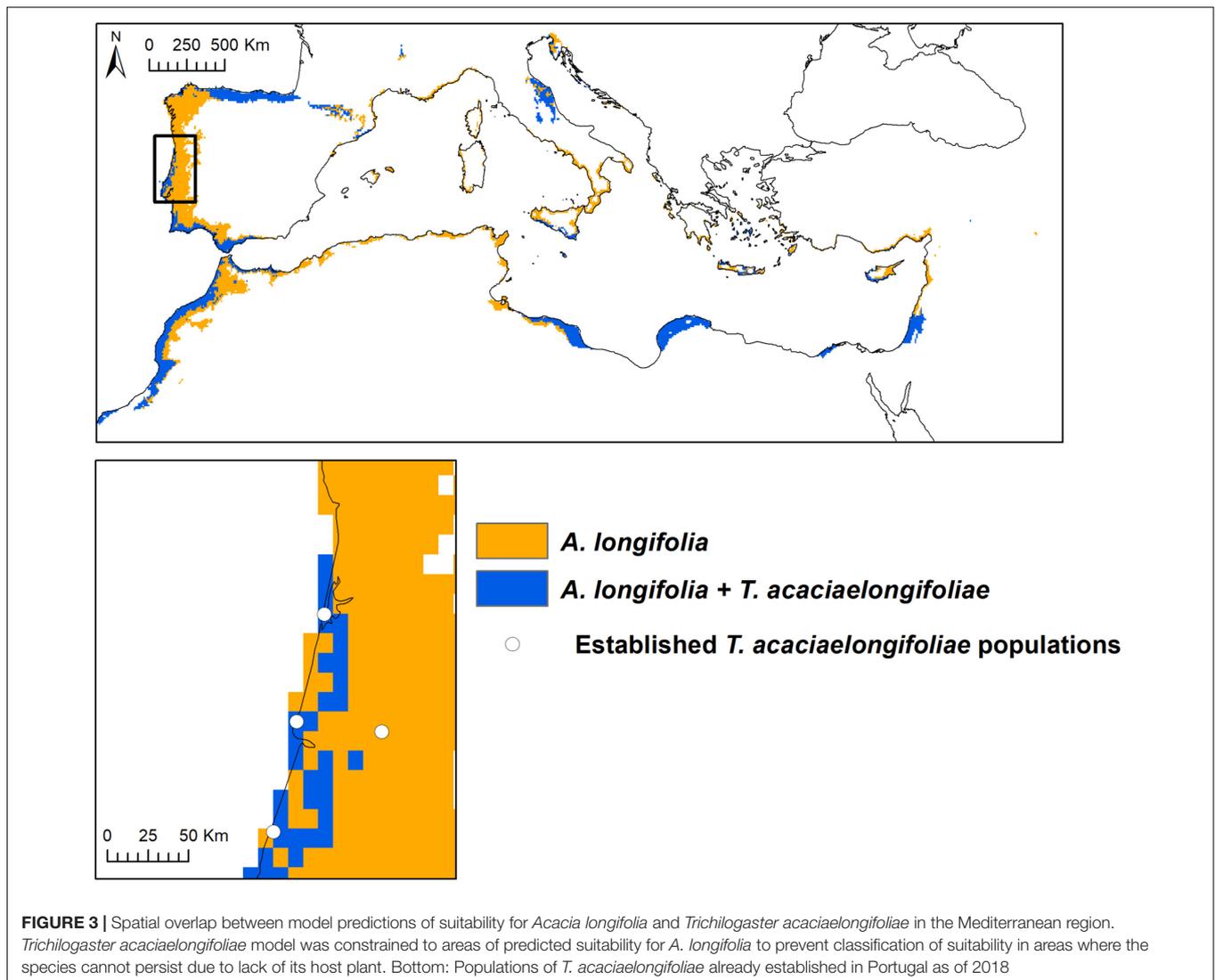
TABLE 2 | Niche overlap and dynamics between all pairs of native (AU: Australia) and introduced (SA: South Africa; PT: Portugal) *Acacia longifolia* (Al) and *Trichilogaster acaciaelongifoliae* (Ta).

| | Pairs | PC1 | PC2 | Niche overlap (D) | Equivalency (sig = non-eq.) | Similarity A- > B | Similarity B- > A | Expansion | Stability | Unfilling |
|--|-----------|-------|-------|-------------------|-----------------------------|-------------------|-------------------|-----------|-----------|-----------|
| <i>Acacia longifolia</i> | 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 |
| <i>Trichilogaster acaciaelongifoliae</i> | AU-SA | 37.24 | 26.64 | 0.157 | 0.987 | 0.141 | 0.134 | 0.561 | 0.439 | 0.254 |
| Among species | AISA-TaSA | 35.02 | 27.08 | 0.846 | 0.604 | 0.004* | 0.005* | 0.039 | 0.961 | 0.053 |
| | AIAU-TaAU | 48.96 | 22.37 | 0.526 | 0.94 | 0.094 | 0.084 | 0.001 | 0.999 | 0.227 |
| | AIAI-TaAI | 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 (AIAI-TaAI). 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 |
|--|------|---------------|----------------|----------------|----------------|---------------|---------------|----------------|
| <i>Acacia longifolia</i> | 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) |
| <i>Trichilogaster acaciaelongifoliae</i> | 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) | |



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.

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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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