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Niche models as a tool to inform restoration and conservation strategies: the case of *Jubaea chilensis* (palm, *Arecaceae*) and its seed disperser *Octodon degus* (rodent, *Octodontidae*)

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Introduction: Biotic interactions are a crucial component of the plant regeneration process, which has been traditionally studied at more local scales, providing the tools for planning and decision-making. Studies showing the signature of species interactions at coarser spatial scales contrasting with animal-plant interactions at fine scales have been scarce. This study aimed at integrating an approach, over both biogeographic and local scales, by testing two endemic species of Mediterranean central Chile: the relict and southernmost threatened Chilean palm *Jubaea chilensis* (Chilean palm; Molina; Baillón) and the caviomorph scatter-hoarding rodent *Octodon degus* (Degu; Molina), on which this palm currently relies for seed dispersal.

Methods: Integrating Geographic Information Systems and Ecological Niche Modeling, the intensity of seed-rodent interactions from a territorial perspective was evaluated in the range of the palm, at a biogeographic scale, identifying areas with greater or lesser potential for seed-rodent interactions; and in local populations, incorporating a variety of environmental factors that might affect palm regeneration.

Results: The present results show that the rodent (*Octodon degus*) may play a role in Chilean palm (*Jubaea chilensis*) seed dispersal and seed establishment, since; Chilean palm regeneration is higher in areas where both species co-occur. At a local scale, a prominent overlap between palm seedlings and degu burrows was also found, which, allied with other abiotic variables such as altitude and topographic humidity, are crucial for successful palm regeneration.

Discussion: Understanding the full extent of animal-plant interactions and how they are affected by habitat perturbation in a wide range will provide essential information for the design of effective conservation and management strategies, such as rewilding based on plant species.

KEYWORDS

Jubaea chilensis, biological interactions, species distribution models (SDMs), multi-scale approach, effective disperser, ecological conservation

Introduction

Global change has caused drastic declines in species populations worldwide (Dirzo et al., 2014), impoverishing ecosystems and ecological interactions (Valiente-Banuet et al., 2015; Genes et al., 2017). The dispersal of plant seeds by frugivores is a key biotic interaction (BI), and the disruption of this mutualistic interaction can impede ecosystem functioning. This matter is especially important for large-seeded species that rely on animals for the dispersal of their seeds (Galetti et al., 2006; Kurten, 2013).

Frugivory is a seed dispersal process of plant-animal interaction that links the reproductive cycle of mature plants with the establishment of their offspring (Blanco et al., 2018) and with their animal dispersers through seed consumption, increasing the chance of seeds to reach safe sites for seedling survival (Schupp, 1993; Nathan and Muller-Landau, 2000; Muscarella and Fleming, 2007; Schupp et al., 2010). Plant-animal interactions are a key process in ecosystem conservation because they promote ecosystem functionality (Svenning et al., 2016); they also enhance ecosystem functions (Dirzo et al., 2014; Peres et al., 2016), trophic interactions, complement other approaches like habitat rewilding (Genes and Dirzo, 2022) and enhance corridor restoration in fragmented landscapes (Schooler et al., 2020) or reduce defaunation (Young et al., 2016).

Recent studies suggest that BI signatures can be expressed geographically (Dormann et al., 2018; Poggiato et al., 2021); however, empirical studies to test these assertions are scarce and deserve further analysis. Some attempts to consider BIs in a spatially explicit way include: (i) the use of correlation matrices to assess positive, neutral, or negative spatial patterns of co-occurrence (Carvajal et al., 2018; Poggiato et al., 2021); (ii) the use of surrogates of BIs such as productivity gradients (Pottier et al., 2013), and (iii) the linkage of dynamic thermodynamics equations obtained from macro-ecology with spatial grids (Violle et al., 2014). However, there is a need to establish more accessible and parsimonious methods, such as the use of Species Distribution Models (SDMs), which correlate large-scale abiotic factors (climate) with the realized presence points of species in a certain region, supporting ecological interactions for decision-makers who must make urgent decisions for conservation, reintroduction, and rewilding policies. SDMs provide a map showing suitable and unsuitable habitats in the geographic space (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005; Elith, 2016; Carvajal et al., 2018; Alaniz et al., 2020). However, the inclusion of BIs in SDMs is regarded as a real challenge both in theory and in practice because the change of scales does not necessarily imply that the interaction between species will be maintained (Araújo and Luoto, 2007; Heikkinen et al., 2007; Schweiger et al., 2008; Broennimann et al., 2012). Here, SDMs was employed to explore BIs at a broader spatial scale, intersecting the resulting models obtained from interacting species (see Lany et al., 2017; Alaniz et al., 2020) and thus capturing the geographic co-occurrence zones of the species and their potential spatial interaction.

Jubaea chilensis [Chilean palm, (Molina) Baillón; Arecaceae] is a monotypic palm endemic to Central Chile. It has been regarded as a biogeographic relict whose ancestor originated in Tertiary subtropical forests (Parsons, 2007; González et al., 2009). The current palm population is estimated to be only 2.5% of the original abundance of palms prior to the arrival of the Spaniards (∼5 million individuals), which is why nowadays this palm is considered as an endangered species (Michea, 1988; Cabello, 2006; González et al., 2017; CONAF, 2020). Long-distance seed dispersal is usually the most important mechanism in plant communities (Wills et al., 1997; Harms et al., 2000). The fruit of this palm is a drupe 4 cm in length with one spherical seed (the "*coquito*") with a diameter of 2–2.5 cm. This large and fleshy-pulped fruit species of this Chilean palm is considered a paleo tropical fruit, which was originally dispersed by megafauna nowadays geographically extinct (mammals >103 kg; Guimarães et al., 2008). Extinct dispersers (camelids) have been replaced by abiotic factors (i.e., gravity, water, and runoff), by introduced horses and cattle that consume the fallen fruits pericarp (phase one), and are then secondarily dispersed by rodents, which act as substitute dispersers (phase two; Hunter, 1989; Vander Wall and Longland, 2004; Jansen et al., 2012).

Although seeds are consumed by livestock and horses, these animals do not ingest the Chilean palm seeds. They consume the fruit pericarp and regurgitate seeds on the surface of the soil. These seed are then prone to rapid desiccation or consumption by exotic rats, if they are not buried in the soil by the two Chilean food-hoarding endemic species of Central Chile, *Octodon degus* [Degu; (Molina)], and to a lesser extent, *Spalacopus cyanus* [Coururo; (Molina)] (Vander Wall and Longland, 2004; Quispe et al., 2009; González et al., 2017). Several tropical palm species have proved to be strongly dependent on scatter hoarding rodents, such as squirrels (Sciurus), spiny rats (Trinomys, Proechimys, Heteromys), acouchies (Myoprocta), and agoutis (Dasyprocta) (Vander Wall, 1990). The Degu rodents largely consume the Chilean palm seeds where the species coexist (Zunino et al., 1992; Yates et al., 1994); however, evidence for their potential role as secondary seed dispersers is still lacking.

Octodon degus is a seed predator that also acts as disperser because of their collection of non-consumed cached seeds may be "forgotten" and can subsequently germinate (i.e., safe sites; Harper, 1977), allowing the seeds to succeed to the seedling stage. The abundance of cached seeds is abundant in late summer when degu populations are in their peak of hoarding activities (Zunino et al., 1992).

In this study, the interactions between *Octodon degus* and *Jubaea chilensis* over two spatial scales at (a) biogeographic scale (∼1 km), using Species distribution models (SDMs), and (b) at a local, or site-scale (∼12 m) was examined. To this aim the effects of *Octodon degus* on *Jubaea chilensis* seedling density in conjunction with other local environmental factors, like topographic exposure, elevation, or vegetation cover, were assessed in several known natural populations of the palm, in locations where both species co-occur.

Materials and methods

Biogeographic scale analysis

To estimate the potential spatial distribution for *Octodon degus* and *Jubaea chilensis,* species distribution models (SDMs) based on

TABLE 1 Palm populations described in González et al. (2009) and palm–degu burrow sampling.

ID	Locality	Decimal latitude	Decimal longitude	PIDM	Sampled	Number of samplings		
						Plots with degu burrows	Palm seedlings	Palm adults
1	Ocoa area	−32.971	−71.094	9	Yes	11	43	60
2	Cocalán area	−34.224	−71.135	9	Yes	9	41	35
3	Viña–valparaíso area	−33.127	−71.555	9	No	N/D	N/D	N/D
4	Cuesta los guindos–alhue	−34.048	−71.248	9	No	N/D	N/D	N/D
5	San miguel de las palmas	−34.657	−71.779	2	No	N/D	N/D	N/D
6	La candelaria	−34.897	−71.477	2	No	N/D	N/D	N/D
7	Tunel las palmas–pedegua (Petorca)	−32.165	−71.225	6	Yes	4	0	25
8	Tilama–pichidangui	−32.063	−71.176	6	No	N/D	N/D	N/D
9	Tapihue–pencahue	−35.302	−71.727	1	No	N/D	N/D	N/D
10	La serena	−29.957	−71.17	1	No	N/D	N/D	N/D
11	Limahuida–los vilos	−31.818	−71.066	3	No	N/D	N/D	N/D
12	Paredones–el asiento–talami–and others*	−34.759	−71.912	**	Yes	1	2	9

PIDM, potential interaction distribution models.

*Other minor populations (i.e., Hualañé).

**PIDM is not unique since various populations with different model interaction compound this locality.

the maximum entropy approach applied in MaxEnt version 3.4 (Phillips et al., 2006, 2017; Elith, 2016; Bosso et al., 2017) were used. These SDMs require information from two data sources: (i) species occurrence points and (ii) environmental variables. Our databases for both *Jubaea chilensis* and *Octodon degus* consisted of georeferenced records from the Global Biodiversity Information Facility (GBIF, 2018) and datasets from literature sources (Fulk, 1976; Fuentes et al., 1983; Meserve et al., 1993; Ebensperger and Bozinovic, 2000; Ebensperger and Wallem, 2002; Vasquez, 2002; Saavedra and Simonetti, 2003; Bozinovic et al., 2009; Díaz-Calderón, 2009; Pozo, 2009; Quispe et al., 2009; Medina, 2011; Correa et al., 2015; Davis et al., 2016; Miranda et al., 2016; Youlton et al., 2016). For environmental variables, the 19 bioclimatic variables obtained from Pliscoff et al. (2014) at the spatial resolution of one kilometer (Supplementary Table 1) were used.

We applied a distance filter (Brown et al., 2017) to identify and remove agglomerated and autocorrelated occurrence points, reducing their numbers from 217 to 141 for *Octodon degus* and 671 to 108 for *Jubaea chilensis* (Supplementary Table 2). Exploratory SDMs were performed for each species to find and assess spatial collinearity among environmental variables, employing all 19 bioclimatic variables, adding one replication model per ∼20 occurrence points (see Wisz et al., 2008; van Proosdij et al., 2016), for a total of nine and five replicates with k-fold cross-validation technique for *Octodon degus* and *Jubaea chilensis* models, respectively. In order to reduce the required number of variables for each model, Two statistics to assess model overfitting related to model complexity driven by excess of variables, Permutation Importance (PI) and Percent Contribution (PC) (Phillips et al., 2006) were used. In addition, the Shapiro–Wilk test to check

normality (Royston, 1983, 1992) and Spearman correlation (Myers and Sirois, 2014) to test for correlation among bioclimatic variables were employed. These statistical analyses were performed for each species' point-occurrence dataset.

The final SDMs for each species were built with the retained variables with low correlation ($r < \mid 0.7 \mid$) and the highest PI and PC (retained variables, including correlation matrices available on S3). The rest of the model parameters used to configure SDMs were maintained from preliminary models (see Supplementary Tables 4A, B). The area under the receiver operating characteristic (ROC) curve (AUC) was applied to assess the accuracy (sensitivity and specificity) of SDMs (Phillips et al., 2006).

We generated the Potential Interaction Distribution Model (PIDM), employing the two previously generated SDMs. First, the continuous suitability raster grids into new rasters with discrete suitability values ranging from low to high (1 = low; 2 = medium; 3 = high), leaving out suitability values below percentile ten, which were classified as null (0 = null), were reclassified. Then the new rasters were multiplied pixel-wise in the GIS environment (*sensu* Alaniz et al., 2020), resulting in a single model for both species as a surrogate of the intensity of BIs, which ranged from 1 (no interaction) to 9 (maximum interaction).

To seek the biogeographic signature of species interactions, our PIDM model categories were contrasted with palm seedling densities measured in the field; we expected the highest seedling density values to correspond to zones with the highest values of PIDM (raster values). The statistical analysis was performed using a non-parametric Wilcox significance test in four study sites, where we assessed palm seedling density: Ocoa (32°58′ S–71° 5′ W; ID = 1), Cocalán (34°13′ S–71° 8′ W; ID = 2), Petorca (32° 9′

S–71°13′ W; ID = 7), and Hualañe (approx 34°56′ S–71°48′ W; ID = 12; **Figure 1**). These localities were grouped into two sampling groups by their PIDM-scores as follows: Ocoa + Cocalan = Very High; Petorca + Hualañe = Medium-High. These four localities encompass almost 90% of the entire species' distribution range (González et al., 2009, 2017) (sampling procedure details in **Table 1**).
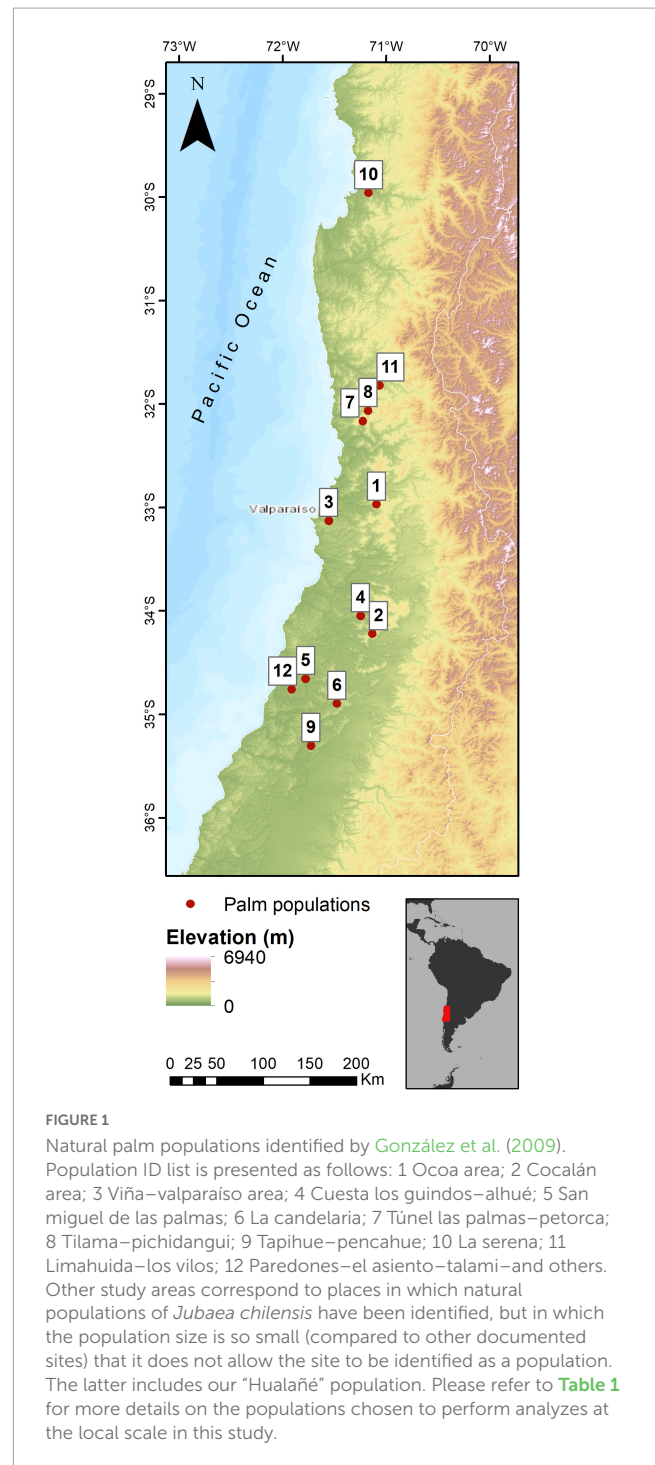
Local scale analysis

Local analysis was conducted in the same localities used to assess seedling density (Ocoa, Cocalán, Petorca, and Hualae; **Figure 1**). A proportional stratified random sampling design was adopted to establish fifteen sampling plots of 50 × 20 m per population, arranged 150 m from each other to assure spatial independence (Hurlbert, 1984). This distance exceeds more than ten times the normal range of aggregation observed in adult palm individuals (Miranda et al., 2016). Due to variation in palm density distribution over ecological gradients, sampling plots at (i) basin heads, (ii) water ravines, and (iii) bottom valleys were set up, with five plots per sampling location, totaling 1.5 ha in total for each locality.

All *Jubaea chilensis* seedlings, adult trees, and *Octodon degus* burrows in each sampling plot were recorded using a GPS. Burrows were considered suitable microhabitats for this rodent species. A degu burrow consists of an underground gallery that supports a family group of degus, which are aboveground connected with others by several runways (Vasquez et al., 2002; Ebensperger et al., 2004; Quispe et al., 2009). Pictures of burrows with the presence of eaten "coquitos" (picture in **Figure 2**), which had been hollowed out when eaten, were taken to discern between active and inactive burrows, these pictures were sent to specialists to ensure that burrows correspond to Degu and not to other fossorial species, such as the Coururo (*Spalacopus cyanus*), which coexists with Degu.

Principal Components Analysis (PCA) was performed to build both species local niches and their overlap based on local environmental requirements. The PCA analysis was made with the "ecospat" v3.3 R package (with the functions dudi.pca, suprow, ecospat.grid.clim.dyn and, ecospat.niche.overlap). The resulting overlaps were plotted employing the NiceOverPlot function (Fernández-López, 2017; Moreno-Contreras et al., 2020; Wan et al., 2020; Yap et al., 2022). The Schoener's *D* test was used to measure niche overlap (function name = ecospat.plot.overlap.test), a metric that varies between 0 for no overlap between niches to 1 for complete overlap. This metric is a proxy of niche similarity (Broennimann et al., 2012; Cola et al., 2017). Separately, we tested the effect of the presence of Degu burrows on palm abundance, plus the effect of other local environmental variables over seedling abundance, conducting a General Linear regressive Model (GLM) with Poisson distribution and log link function, in a single model.
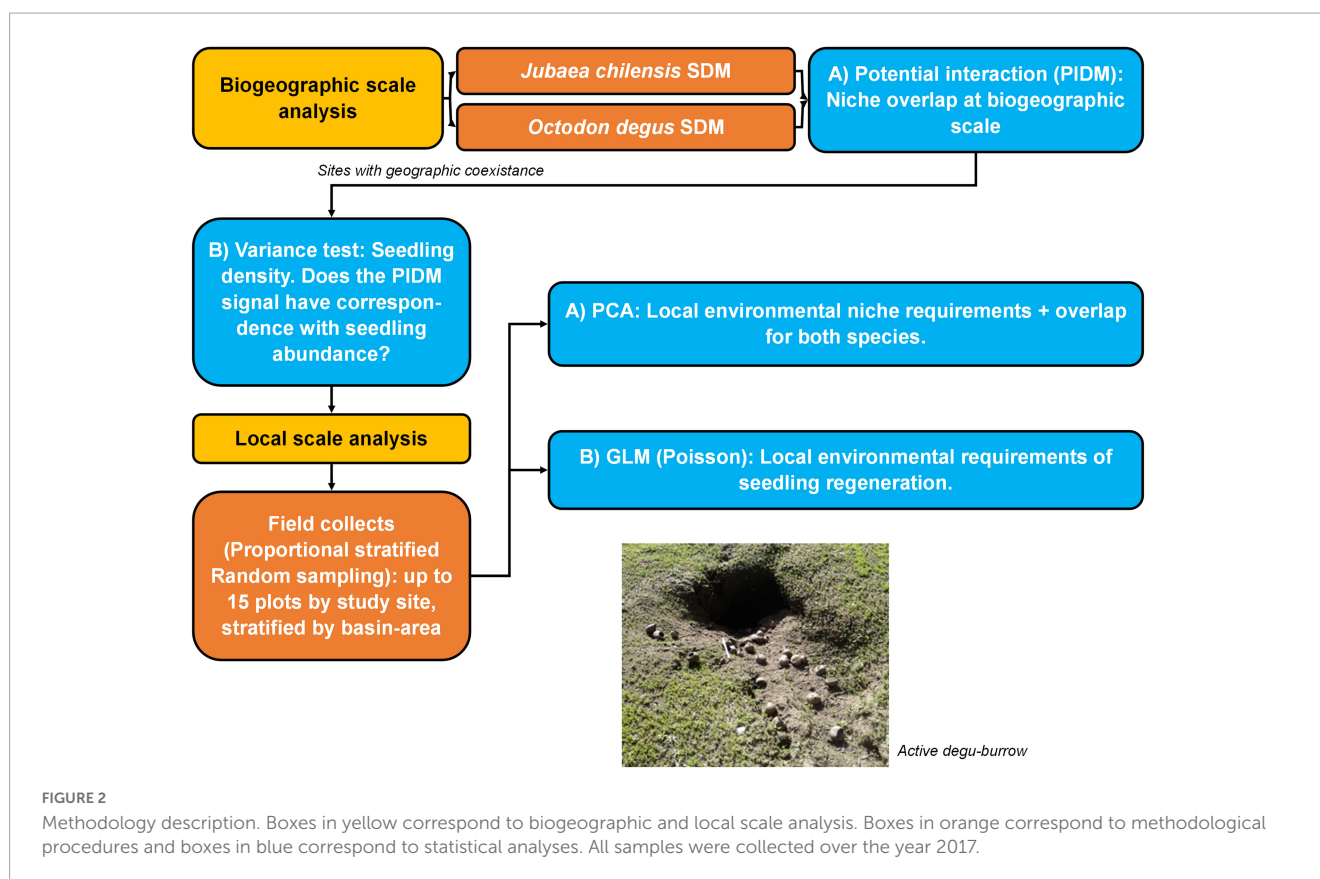
Both models (PCA and GLM) were based on local environmental variables (~12 m spatial resolution), with the distinction that GLMs were measured from the plot central coordinate (in perspective of field plots) and PCAs from each individual within every plot (which is equal to each burrow/palm seedling) coordinate.

FIGURE 1
Natural palm populations identified by González et al. (2009). Population ID list is presented as follows: 1 Ocoa area; 2 Cocalán area; 3 Viña–valparaíso area; 4 Cuesta los guindos–alhué; 5 San miguel de las palmas; 6 La candelaria; 7 Túnel las palmas–petorca; 8 Tilama–pichidangui; 9 Tapihue–pencahue; 10 La serena; 11 Limahuida–los vilos; 12 Paredones–el asiento–talami–and others. Other study areas correspond to places in which natural populations of *Jubaea chilensis* have been identified, but in which the population size is so small (compared to other documented sites) that it does not allow the site to be identified as a population. The latter includes our "Hualañé" population. Please refer to **Table 1** for more details on the populations chosen to perform analyzes at the local scale in this study.

Results

Biogeographic distribution models (SDMs) and potential interaction models (PIDM)

The performance of the SDMs measured by the AUC values for *Jubaea chilensis* were 0.961 (SD ± 0.014), and were 0.996 (SD ± 0.001) for *Octodon degus*. Climatic preferences for both species have fitted for Mediterranean climates, where

FIGURE 2
Methodology description. Boxes in yellow correspond to biogeographic and local scale analysis. Boxes in orange correspond to methodological procedures and boxes in blue correspond to statistical analyses. All samples were collected over the year 2017.

precipitation accumulates in the cold season, followed by a drier, warmer season. The precipitation of the warmest quarter (bio18) was the most important climatic variable for *Octodon degus* [Permutation Importance (PI) = 57.8%; Percent Contribution (PC) = 81%], followed by precipitation of the coldest quarter (bio19; PI = 13.2%; PC = 14), accounting for more than 94% of the total variation of the Degu model. *Octodon degus* seem to be less tolerant to mild, wet winters, where suitability values in curves dropped from near 90 to 0% (>0 mm). Under the coldest quarter, the model suggests a monotonic curve between 0 and 600 mm, with maximum suitability of 90% near 200–400 mm (see **Supplementary Figure 6A**).

In the *Jubaea chilensis* model, precipitation of the driest month (bio14, PI = 40.5%; PC = 30.1%) and the coldest quarter (bio19; PI = 26.9%; PC = 19.4%) explained more than 65% of the model (see **Supplementary Figure 6B**). For the driest month, palm habitat suitability values in curves are up to 4 mm, indicating adult individuals' toleration to dry climates, while in the coldest quarter, palm-suitable habitats ranged from 200 to 1,200 mm, as the suitability curves suggest.

In the PIDM (interaction model), higher values of interactions were obtained toward the center of the distribution of *Jubaea chilensis* (between 32 and 34°S), specifically between the Coast and Andes ranges of Central Chile (or between Ocoa and Cantillana localities; 71–72'W). Lower values were obtained toward the northern and southern distribution ranges, i.e., above 31'S and below 34'S (**Figures 3A–C**).

Several variables for PCA, GLM, or both, were used as follows: (A) both models: (i) elevation (DEM), (ii) Topographic exposure (Aspect), (iii) Land Surface Temperature (LST), (iv) Enhanced Vegetation Index (EVI). (B) Only PCAs: (vi) Topographic Roughness Index (TRI), (vii) Topographic Wetness Index (TWI), (viii) Normalized Salinity Index (NDSI), (ix) Euclidean distance to watercourses (Disthidro), and (x) Euclidean distance to palm adults (Distad). (C) Only GLMs: (v) presence or absence of Degu burrows inside each plot (IsMadr; as the most parsimonious approach); (vi) Number of *Jubaea chilensis* adults within each plot (n_adult). Variables were obtained from satellite images from Sentinel-2A annual composites ("COPERNICUS/S2_SR_HARMONIZED"; median composite; year = 2018; which have a ∼12 m spatial resolution at Central Chile) obtained from Google Earth Engine, a cloud-based supercomputer for geoscientific spatial analyses (from which the clouds before conducting the image composites were masked out; Gorelick et al., 2017; see S5 for each variable details). All R analyses were made with version 4.2 (For a graphic description of the methodology, please refer to **Figure 2**).

Jubaea chilensis survey

We recorded 215 individuals of *Jubaea chilensis* in the four sites analyzed: 86 seedlings and 129 adults. Higher abundances were recorded in Ocoa (43 seedlings; 60 adults) and Cocalán (41 seedlings; 35 adults), which are the geographic zones with higher interaction intensity (PIDM). In contrast, seedling densities in Petorca and Hualañé were lower (0 seedlings; 25 adults; 2 seedlings; 9 adults, respectively) and in the predicted zones with lower PIDM (Wilcoxon, $P = 0.0158$; **Figure 4** and **Table 1**).
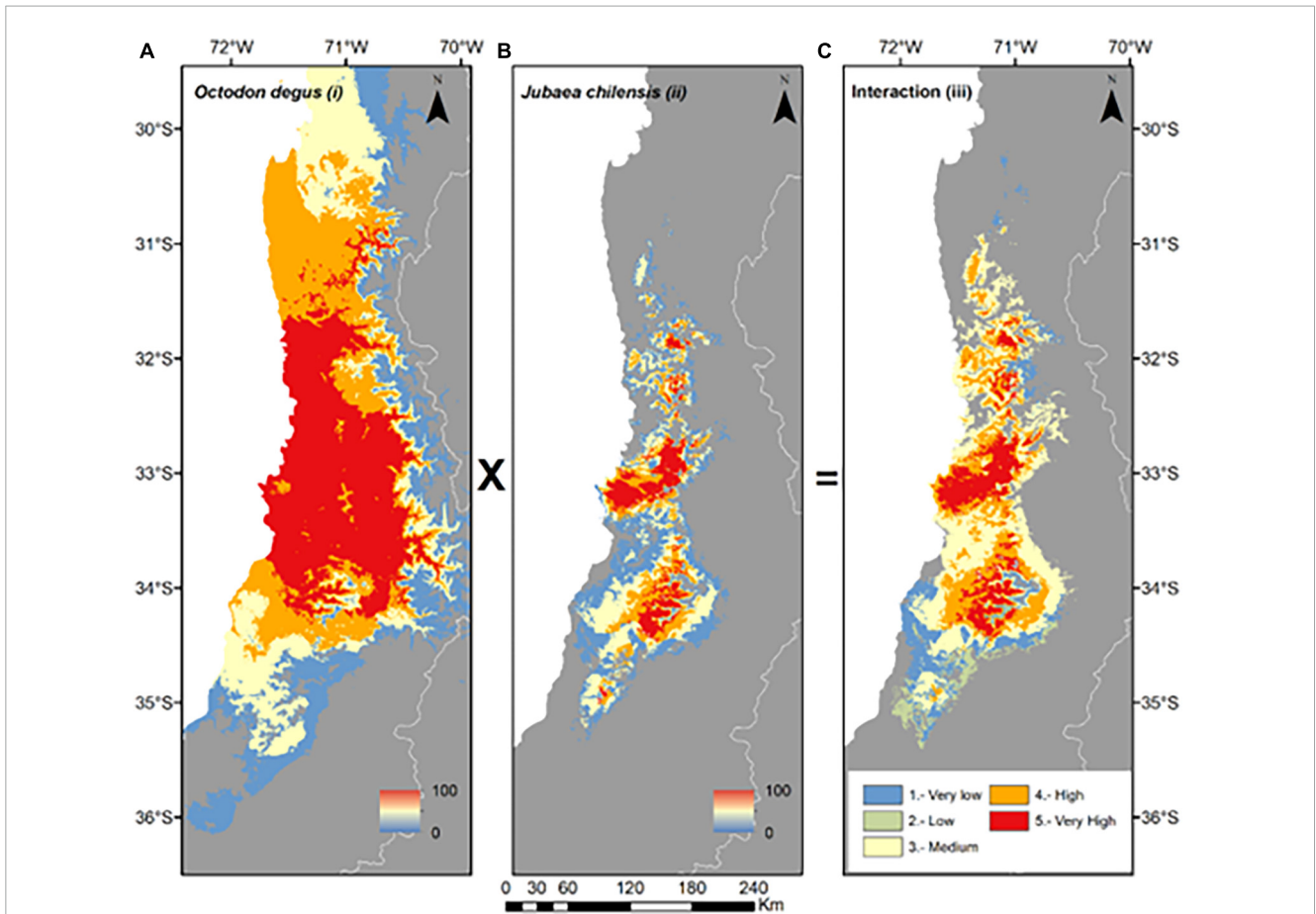
FIGURE 3
Spatial distribution models and potential spatial interactions (PSI) between *Octodon degus* and *Jubaea chilensis*. **(A)** SDM for *Octodon degus*; **(B)** SDM for *Jubaea chilensis*; **(C)** PIDM model between both species, which resulted from the product of **(A)** and **(B)**, weighted in five values (1, Very low; 2, Low; 3, Medium; 4, High; and 5, Very high).
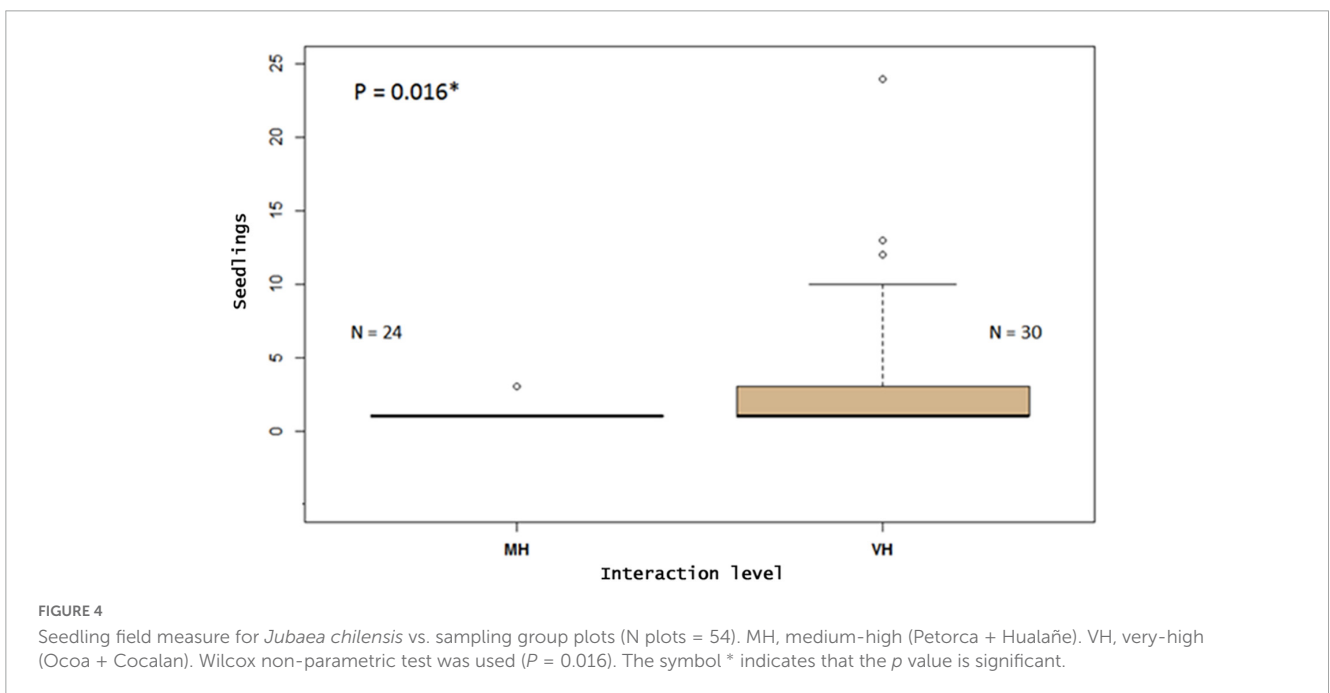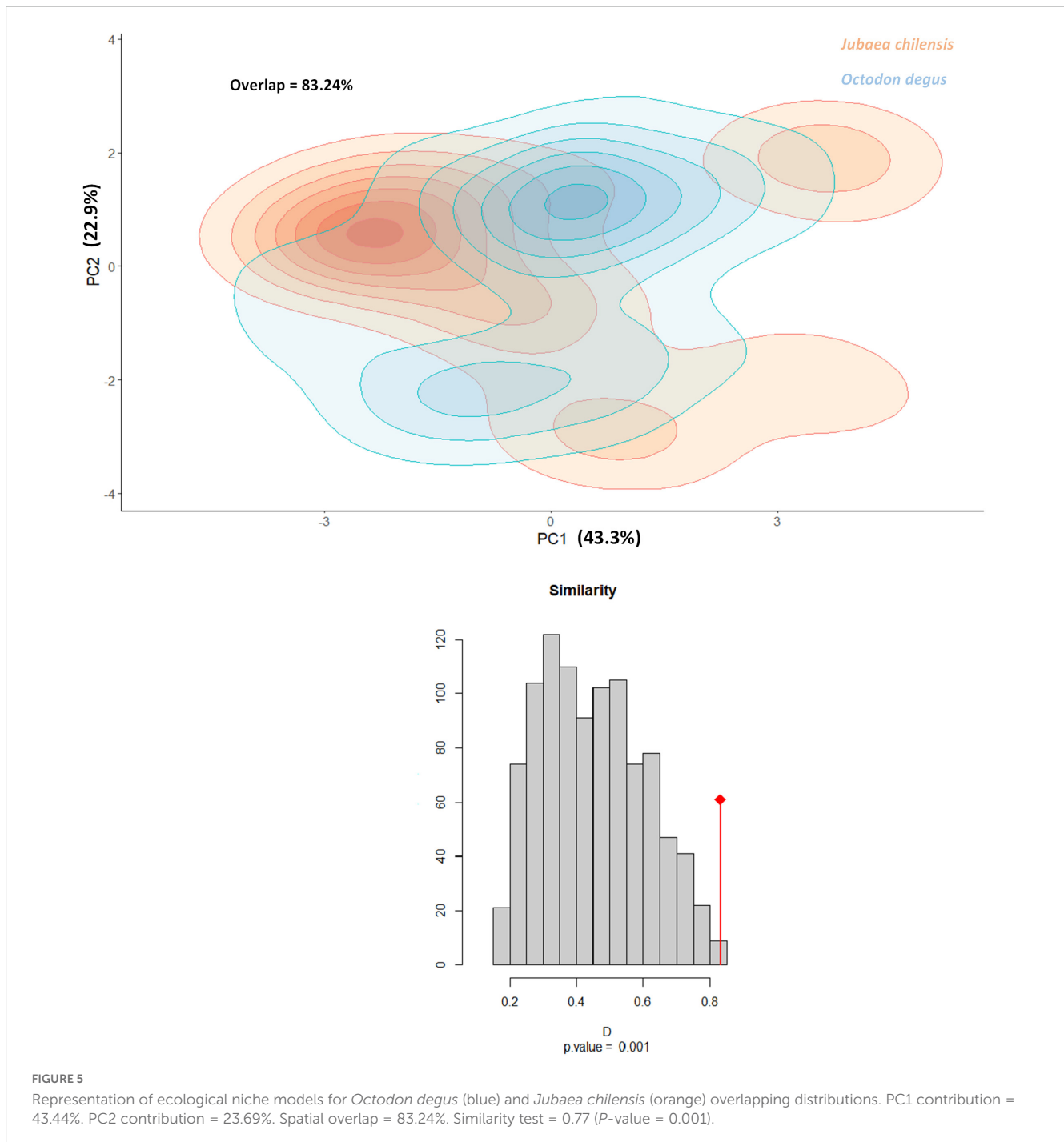

FIGURE 4
Seedling field measure for *Jubaea chilensis* vs. sampling group plots (N plots = 54). MH, medium-high (Petorca + Hualañe). VH, very-high (Ocoa + Cocalan). Wilcox non-parametric test was used ($P = 0.016$). The symbol * indicates that the p value is significant.

FIGURE 5
Representation of ecological niche models for *Octodon degus* (blue) and *Jubaea chilensis* (orange) overlapping distributions. PC1 contribution = 43.44%. PC2 contribution = 23.69%. Spatial overlap = 83.24%. Similarity test = 0.77 (*P*-value = 0.001).

Local spatial analysis

The two axes of the PCA explained 66.20% of the variance, strongly characterized by specific environmental requirements for *Jubaea chilensis* seedling establishment as well as *Octodon degus* burrows. The *Jubaea chilensis* and *Octodon degus* requirements overlapped by 83.24%, much more than expected by chance (*P*-value = 0.001; **Figure 5**). Non-overlapping areas corresponded to exclusive environmental areas for palm seedlings and Degu burrows, which were even smaller for seedlings (**Figure 5**). PC1 is characterized by specific NDSI, NDVI, EVI, NDWI, LST, and TWI, while for PC2 the most contributing variables to each component

were Slope, TRI, DEM, and TWI (for further details, see **Figure 6**). Following the latter argument, PC1 is more weighted by salinity, vegetation, wetness, and temperature variables than PC2, which is more influenced by topographic variables. Nevertheless, TWI, an index related to watercourses, influenced both components.

In our GLM for *Jubaea chilensis*, several variables were found to be significant (*P*-value < = 0.05), listed here in decreasing order of contribution to the model's intercept: the EVI index (vegetation), the NDWI index (wetness), the number of adult *Jubaea chilensis* trees, DEM (altitude), and LST (surface temperature). Both DEM and LST had negative estimates, whereas the other listed variables had positive estimates (further details on **Table 2** and **Figure 7**).
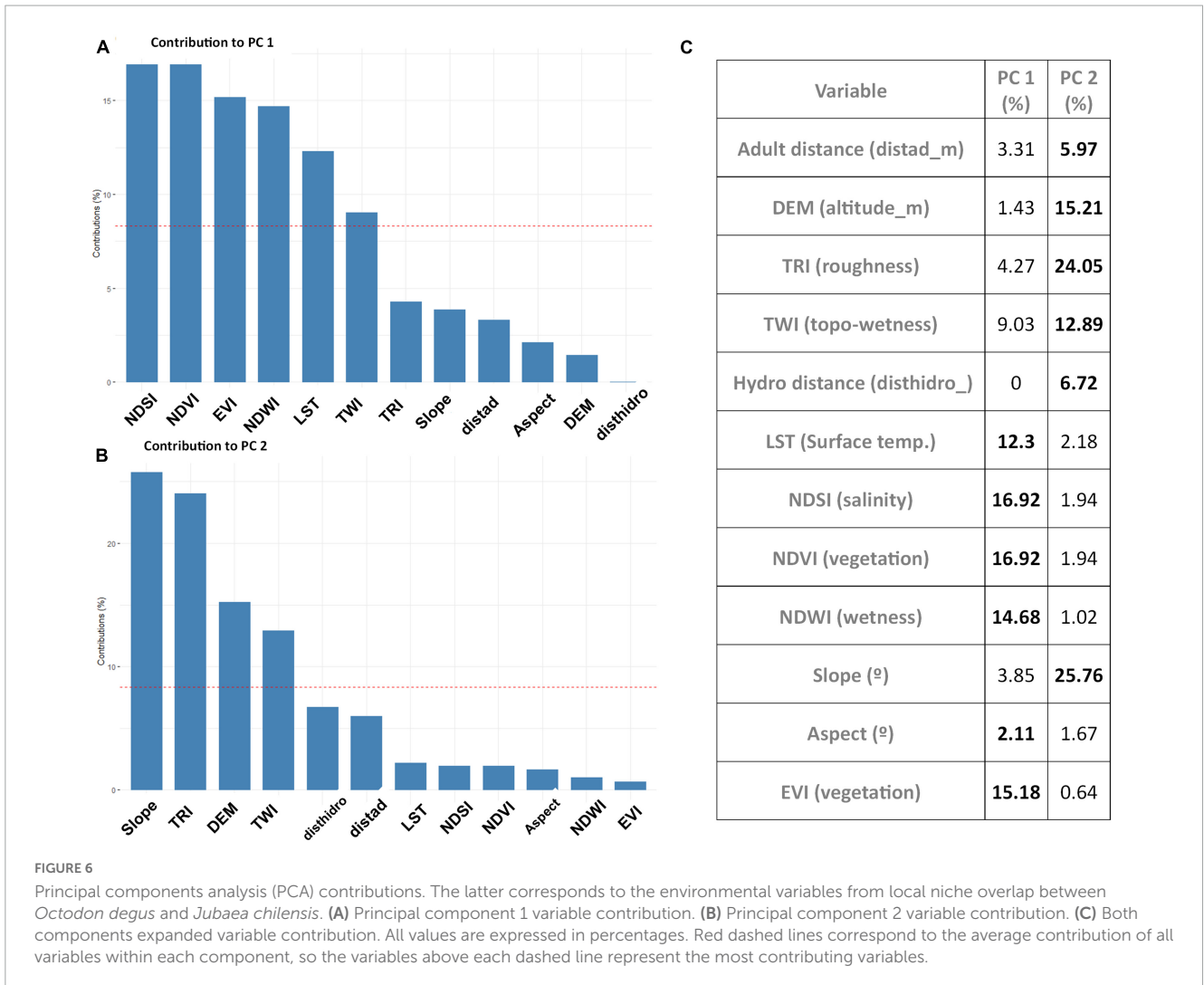
FIGURE 6
Principal components analysis (PCA) contributions. The latter corresponds to the environmental variables from local niche overlap between *Octodon degus* and *Jubaea chilensis*. **(A)** Principal component 1 variable contribution. **(B)** Principal component 2 variable contribution. **(C)** Both components expanded variable contribution. All values are expressed in percentages. Red dashed lines correspond to the average contribution of all variables within each component, so the variables above each dashed line represent the most contributing variables.

Interestingly we observed that the presence-absence of degu burrows had a greater impact on the model (estimate = 0.410) than the number of adult *Jubaea chilensis* trees (estimate = 0.335); however, the variable effect was not significant (*P*-value = 0.1246). Our analysis also revealed that the wetness index positively correlated with seedling density, suggesting that sites with dryer conditions are associated with lower seedling densities when contrasted with wetter conditions sites (refer to **Table 2** and **Supplementary Figure 5** for more details).

Discussion

In this study, we examined whether the mutualistic interactions between *Jubaea chilensis* and *Octodon degus* are expressed at two spatial scales: (a) at a biogeographic scale, using SDMs for palms and Degu and exploring co-occurrence zones as indirect evidence of mutualism (Araújo and Rozenfeld, 2014); (b) at a local scale, firstly exploring niche overlap between both species using local environmental variables, and secondly examining whether palm seedling density responds to the presence/absence of degu burrows as well as to local environmental variables.

Mutualistic effects of degus on palms

The present results support the existence of mutualistic interactions between *Jubaea chilensis* and *Octodon degus*, which may be perceptible at both evaluated spatial scales. There was indeed a high seedling density in localities with the highest potential interactions (predicted from SDMs) relative to those localities with lower potential interactions, reinforcing the idea of a biogeographic signal of biotic interactions (BI). These findings oppose previous reports in the literature that suggests that animal-plant BI can be detected only at local scales (Wisz et al., 2013; Cabra-Rivas et al., 2016). This large-spatial scale effect is a consequence of a long-term coevolutionary history of more than six million years between the Chilean palm and the Degu (Valladares, 2009; Rivera et al., 2016).

Regarding the local scale analysis, significant overlap between the palm and degu niches was detected, suggesting a positive association between both species; however, the presence of Degu burrows did not increase significantly seedling density. This issue deserves to be analyzed with caution. The positive effect of seed dispersers can occur at earlier life cycle stages, such as the seed stage (Bustamante and Canals, 1995), which we did not analyze in our study. Moreover, (i) by digging seeds, Degus provides refuge

TABLE 2   General linear model results of the effects of variables explaining seedling densities of *Jubaea chilensis* in our four study areas and at local scale (~12 m).

Term	Full name	Units of measure	Estimate	Std. error	*t* value	*P*-value
(Intercept)		–	16.459	3.189	5.162	<0.001
IsMadr	Degu burrow presence/absence	*Numeric*	0.410	0.267	1.536	0.125
n_adult	Chilean palm adult density	*Numeric*	0.335	0.061	5.505	<0.001
DEM	Altitude	*Meters*	−0.004	0.001	−4.240	<0.001
Slope	Topographic slope	*Degrees*	−0.038	0.023	−1.652	0.098
EVI	Enhanced vegetation index	*Index*	26.588	3.946	6.737	<0.001
NDWI	Normalized difference water index	*Index*	21.156	3.275	6.460	<0.001
LST	Land surface temperature	*Degrees celsius*	−0.438	0.093	−4.711	<0.001

We employed the estimate value to differ from the most and least important variables, as well with the reported *p*-value. *t*-value equals to the estimate/std. error.

for seeds against other seed predators such as native and exotic rodents; (ii) the soil affected by rodent activity increases fertility as a consequence of digging, urine, and feces, thus increasing germination and seedling growth; (iii) as seedlings become older, the positive effects of Degu (i.e., fertility) may be diluted by the preeminence of other local factors, such as those evaluated in our GLM.

Influence of local scale factors over *Jubaea chilensis* seedling abundance

We found that NDWI, EVI/NDVI, and Slope were important local variables for the Chilean palm seedling density. Most of these factors can be a proxy of water availability and vegetation cover, which have been regarded as determinant elements for plant survival along ecological gradients (Pettorelli et al., 2017). Water availability and vegetation cover are essential in Mediterranean ecosystems as limiting factors for native plant abundance and distribution (Matías et al., 2011), explicitly affecting seedling survival (McDowell et al., 2008). We have evidence that palm seedlings grow preferentially beneath the canopy of Mediterranean vegetation (Fleury et al., 2015; Flores et al., 2016; Miranda et al., 2016) because native shrubs provide refuge against herbivores (cattle, rabbits) and are as well fertile nutrient patches, which in turn favor seedling growth (Maestre et al., 2009).

Spatial scale of studies

We argue that the study of BI at different spatial scales is a complementary approach. SDMs provide clues about the locations where mutualistic interactions should be more intense; those locations (local scale) should be used to address the underlying mechanisms that explain the fitness responses of interacting species. Using SDMs, we detected in the present study the zones where mutualistic interactions should be more intense, and also
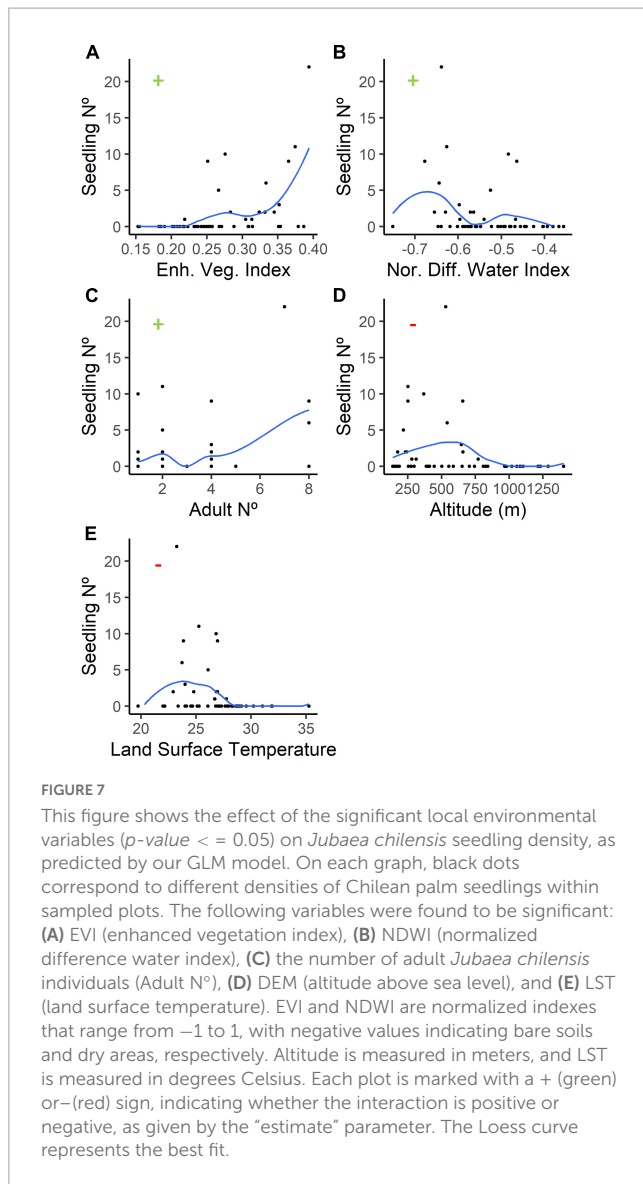
examined this interaction at a local scale, assessing the effect of Degus and other factors on palm regeneration. In sum, SDMs constitute the first step to examine the hypothetical sites within the geographic mosaic (Thompson, 2005), where mutualistic interactions are more probable (Araújo and Luoto, 2007).

The conservation of *Jubaea chilensis*: current threats, restoration, and rewilding

Seed harvesting by people constitutes a significant threat to the future of palm populations (Youlton et al., 2016), due to massive seed removal since colonials time (González et al., 2017). Given that seed abundance is regarded as a modulator of the intensity of seed predation (predator satiation hypothesis; *sensu* Janzen, 1971; Xiao et al., 2013), we hypothesize that human overharvest can be detrimental to Chilean palm regeneration because the available seeds could be not enough to satiate the Degu, which will tend to burrow more seeds. Further research should be conducted to test this prediction because if this mechanism occurs in our case, assessing the seed density threshold (available after harvesting) will be mandatory to define whether Degu is a net seed predator or a net seed disperser.

The current conservation status of the Chilean palm is endangered (CONAF, 2020). Consequently, it is mandatory to conduct conservation actions to enhance the persistence of this singular component of biodiversity in Central Chile. However, it is challenging to conduct efficient conservation actions, as the Chilean palms are part of a subtle and complex network of BI that includes degus, humans, exotic species, and the environment.

Habitat rewilding (see Mittelman et al., 2022) appears to be a viable alternative since it focuses on restoring lost interactions through different actions. In the case of the Chilean palm, habitat rewilding could be addressed by reintroducing the Andean camelids (*Lama guanicoe* and *Lama glama*) to restore lost trophic interactions that were predominant before

How can SDMs guide restoration and rewilding?

Given our current SDMs results, we hypothesize two scenarios. A first scenario characterized by places where *Octodon degus* is unsuitable and in which *Jubaea chilensis* is suitable (but not present). In this case, we can dispose of palm seedlings under the native vegetation canopy as they are micro-habitats for Mediterranean seed survival. Therefore, the reintroduction with camelids could be conducted to restore the ancient mutualistic interactions. A second scenario, in which there are places suitable for both *Octodon degus* and *Jubaea chilensis*, but in which the rodent is not present (but the palm is). In this case, *Octodon degus* could be trained to capture, cache, and consume the palm seeds (Tokimoto and Okanoya, 2004; Okanoya et al., 2008; Nakajima et al., 2016) and reintroduce them in the wild. This last strategy, however, must be guided in the first phase because Degus do not recognize palms as a resource, as they are not part of their habitat. However, *Octodon degus* is a species with learning skills (Vasquez et al., 2002), which can learn to consume palm seedlings if given enough time.

The use of Joint SDMs (JSDMs) to disentangle species co-occurrence patterns in the geographic space is becoming a novel approach to examining BI in the geographic space (Poggiato et al., 2021). Our attempt to examine mutualisms between two species using SDMs for only two species is the first stage to better comprehending BI. Future work may involve the development of more complex models that consider multi-species interactions, such as the possible interactions among palms, rats, rabbits, camelids, cattle, or even vegetation and humidity, to find zones that will allow to identify competition, herbivory, seed predation, or mutualism. The latter is now possible extracting the residual correlation matrix from JSDMs (Poggiato et al., 2021); the best regions as potential candidates to begin rewilding efforts should be those which include the majority of biotic interactions among native species.

Concluding remarks

In this study, we report that the interactions between *Jubaea chilensis* and *Octodon degus* are expressed at both biogeographic and local scales. The high seedling density in localities with high potential interactions reinforces the idea of a biogeographic signal of biotic interactions. Moreover, we also detected a significant overlap between the palm and degu niches at the local scale, suggesting a positive association between both species. However, the presence of Degu burrows did not increase significantly seedling density (if this variable is contrasted with other local variables), an issue which deserves further analysis. Seed harvesting by humans constitutes a significant threat to the future of palm populations, and habitat rewilding appears to be a viable alternative to enhance their conservation. Finally, we argue that the study of biotic interactions at different spatial scales is a complementary approach, with SDMs providing clues about locations where mutualistic interactions are more intense, and local studies addressing the underlying mechanisms.

the colonial times, because Andean camelids are considered the original seed dispersers for many plant species of southern South America (Hubbe et al., 2013; Root-Bernstein and Svenning, 2016). Furthermore, we argue that rewilding with camelids could significantly increase the chance of the Chilean palm expanding its geographic range as these mammals can disperse seeds at larger distances, sometimes encompassing several kilometers (Root-Bernstein and Svenning, 2016).

Mediterranean shrublands were one of the native habitats for camelids and palms; they should also be rewilded to provide them with conditions to maintain viable and healthy populations over time (Benayas et al., 2009; Jones et al., 2018). However, rewilding must include overhunting regulations, since their lack explains why there are no natural populations of camelids in central Chile nowadays (see Westreicher et al., 2007). Alongside habitat rewilding, there is a need to control exotic rodents (*Rattus rattus* and *Rattus norvegicus*), as they are active seed consumers (Towns et al., 1997; Dukes and Mooney, 2004; Gosse et al., 2011; Cordero et al., 2021).

Data availability statement

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

Author contributions

IN-H and RB conceived the idea and the study design. IN-H collected and analyzed the data and was responsible for manuscript writing. IN-H, MF, and RB helped with the methodology and revised the manuscript. All authors contributed to the final draft and gave their final approval for publication.

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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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1143208/full#supplementary-material

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