ORIGINAL PAPER

Macroecological perspectives on the competition between the native and invasive bumblebees in southern South America under climate change

Jose Montalva · **Bruce Hoagland** · **Marina P. Arbetman** ·
Carolina L. Morales · **Marcelo A. Aizen** · **Bruno Vilela** ·
Daniel Paiva Silva

Abstract A handful of known bumble bee species (*Bombus*) have been transported worldwide and introduced in non-native regions for crop pollination, leading to long-lasting biological invasions. The introductions and invasions of European *Bombus terrestris* and, previously, of *Bombus ruderatus* in southern South America have been associated with sharp population declines of the giant Patagonian bumblebee, *Bombus dahlbomii*. We gathered a comprehensive database of occurrence records for *B. dahlbomii*, *B. ruderatus*, and *B. terrestris* from museums and citizen science sources. Multivariate bioclimatic niche analyses and species distribution models were used to determine the extent of climatic niche overlap between invasive and native species and the potential effects of current and future climatic scenarios on the distribution of these bumblebees. We found extensive pairwise niche overlap between the three bumble bee species, *B. terrestris* versus *B. ruderatus* (67%), *B. terrestris* versus *B. dahlbomii* (61%), and *B. ruderatus* versus *B. dahlbomii* (46%). Compared to its historical records, the current distribution of *B. dahlbomii* is narrowing and is expected to shrink even more under the most climatically pessimistic future scenario, while that of *B. terrestris* shows an extensive, still expanding distribution. However, the models show that in the case of a climatic pessimistic future scenario, *B. terrestris* will also slow down its expansion on the continent. Finally, we discuss the consequences of the large niche overlap between the introduced bumble bee species and endangered *B. dahlbomii* and the effect of climate change on these three species of bumble bees in South America.

Keywords Conservation biogeography ·
Distribution models · Pollinators · Wallacean shortfall

J. Montalva (✉)
Department of Biological and Environmental Sciences,
East Central University, Ada, OK, USA
e-mail: jmontalv@ecok.edu

B. Hoagland
Department of Geography and Environmental
Sustainability, Oklahoma University, Norman, OK, USA
e-mail: bhoagland@ou.edu

M. P. Arbetman · C. L. Morales · M. A. Aizen
Grupo de Ecología de la Polinización (EcoPol),
INIBIOMA (CONICET Universidad Nacional del
Comahue), Quintral 1250, 8400 San Carlos de Bariloche,
Rio Negro, Argentina

B. Vilela
Laboratório de Ecologia Espacial, Instituto de Biologia,
Universidade Federal da Bahia, Rua Barão de Jeremoabo,
número 668, Campus Universitário de Ondina, Salvador,
Bahia, Brazil

D. P. Silva
Departamento de Ciências Biológicas, Instituto Federal
Goiano, Rodovia Geraldo Silva Nascimento, KM 2,5, Zona
Rural, Urutaí, GO CEP 75790-000, Brazil
e-mail: daniel.paivasilva@ifgoiano.edu.br

Introduction

Biological invasions are considered one of the paramount threats to biodiversity (Clavero and García-Berthou 2005). Invasive species can affect the composition and function of invaded communities, often exacerbated by anthropic effects (Kolar and Lodge 2001; Lodge 1993; Mack et al. 2000; Mooney and Hobbs 2000). Such processes could trigger the extinction of native species, homogenization of the local biota, and disruption of ecological interactions (Simberloff et al. 1997; Traveset and Richardson 2006). Also, the economic losses in agriculture and fisheries due to invasive species have cost billions of dollars due to lost productivity and the expenses of controlling them (Diagne et al. 2021; Jackson 2015; Pimentel et al. 2000; Vitousek et al. 1996).

Despite the recognized negative impacts of invasive species, incomplete knowledge of their present and future geographical distribution and biotic interactions in the invaded regions curtail possibilities for correct impact evaluation. These knowledge limitations are known as the "Wallacean" and "Eltonian" shortfalls. The Wallacean shortfall is the absence of information about species distribution, and the Eltonian shortfall is the lack of knowledge about interactions among species groups (Hortal et al. 2015). Wallacean and Eltonian shortfalls are particularly prominent among non-native species because of the novelty of new environments (Wallacean) and the evolutionary time context (Eltonian). Additionally, these shortfalls are a significant barrier to assessing the impact and effective control of the introduced species (Whittaker et al. 2005). However, species distribution models (SDMs) and citizen science data can be valuable tools for addressing these Wallacean and Eltonian shortfalls and aid in identifying suitable areas for occupation by exotic species (Hinojosa-Díaz et al. 2005, 2009; Silva et al. 2014; Faleiro et al. 2015). Citizen science tracks bumble bees in several world regions (Suzuki-Ohno et al. 2017; Falk et al. 2019; MacPhail et al. 2019). For example, SDMs combining citizen science data have helped track invasive *B. terrestris* in Japan and some other regions of East Asia (Acosta et al. 2016; Montalva et al. 2017; Suzuki-Ohno et al. 2017; Naeem et al. 2018; Morales et al. 2022).

The movement and trade of crop pollinators are increasing sources of biological invasions. *Bombus ruderatus* (Fabricius, 1775) and *B. terrestris* (Linnaeus, 1758) are two European bumble bee species introduced for crop pollination in Chile (Aizen et al. 2019; Montalva et al. 2011; Smith-Ramírez et al. 2018). Queens of *B. ruderatus*, previously naturalized in New Zealand, were introduced near Temuco in the south of Chile in 1982–1983 to pollinate *Trifolium pratense* (red clover), a livestock forage crop (Arretz and Macfarlane 1986). Later, this species was first reported in Argentina in 1993 (Roig Alsina and Aizen 1996). European *B. terrestris* (buff-tailed bumble bee) is the leading commercial bumblebee species and has been introduced in several countries worldwide (Dafni et al. 2010; Kadoya and Washitani 2010; Matsumura et al. 2004; Naeem et al. 2018). *Bombus terrestris* was first introduced to central Chile in 1997 (Montalva et al. 2011), and since then, more than a million colonies have been imported into the country (Aizen et al. 2019; Smith-Ramírez et al. 2018). The continuous and massive importation of *B. terrestris* into Chile maximizes propagule pressure. Consequently, it has spread throughout Chile, reaching the Atacama Desert in the north (Montalva et al. 2017) and the subarctic island of Navarino in the south (Rendoll-Carcamo et al. 2017). *Bombus terrestris* was reported in Argentina in 2006, and its current distribution extends throughout Patagonia (Acosta et al. 2016; Torretta et al. 2006a; Morales et al. 2013).

The impact of these two invasive species on native South American ecosystems should concern researchers and land managers alike. Both European bumble bee species are now feral in Chile and parts of Argentina and are blamed for the decline of the Patagonian giant bumble bee, *B. dahlbomii* Guérin-Méneville 1835 (Aizen et al. 2019; Morales et al. 2016; Smith-Ramírez et al. 2018). Although there may be competition for floral resources between exotic and native species (Vergara et al. 2023), introducing diseases is the most relevant cause of decline (Aizen et al. 2019; Smith-Ramírez et al. 2018). Different studies have revealed the presence of European parasites in Chile, likely carried by European bumble bees, contributing to the decline of *B. dahlbomii* populations (Arbetman et al. 2013; Arismendi et al. 2016, 2021; Schmid-Hempel et al. 2014). In less than 20 years (or since the introduction of *B. terrestris*), the distribution of *B. dahlbomii* has shrunk considerably (Montalva et al. 2015; Morales et al. 2016). *Bombus dahlbomii* is now listed as endangered by both the International Union

for the Conservation of Nature (IUCN) Red List and the Chilean Ministerio de Medio Ambiente (MMA) (Montalva et al. 2015; Morales et al. 2016). According to a recent related study (Morales et al. 2022), climate change (CC) cannot be pointed out as a primary driver of population declines in *B. dahlbomii* observed in the last decades, with the role of invasive bumblebees still being the hypothesis with considerable support.

This research aimed to ascertain the potential for ecological interactions among these three species over space and time under the premise that these interspecific interactions can take place where the climatic niches of the species overlap. Specifically, we sought to answer the following questions: (1) Is there extensive climatic niche overlap among these *Bombus* species? (2) How will the current predicted distribution of the species change under expected future climatic scenarios? We applied multivariate bioclimatic niche analyses (Broennimann et al. 2012) and SDMs to answer these questions and evaluate the relationship between the distributions of the two European bumble bee species and native *B. dahlbomii*. Therefore, we calculated the pairwise overlap of species niches in geographic and climatic space to determine the potential threat of European species to native endangered species. We also used SDMs to predict the current and future distributions of these three bumble bee species in South America.

Methods

Species occurrence dataset

We gathered a comprehensive database of occurrence records for *B. dahlbomii, B. ruderatus*, and *B. terrestris* from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org; *B. dahlbomii* DOI: https://www.gbif.org/species/1340388, *B. ruderatus* DOI: https://www.gbif.org/species/1340383, *B. terrestris* DOI: https://www.gbif.org/species/1340503) online database and records from the Citizen Science initiative "Salvemos Nuestro Abejorro" (Save our Bumble bee; https://salvemosnuestroabejorro.wordpress.com/). From GBIF, we aggregated museum records (data from museum Pontificia Universidad Católica de Valparaíso; American Museum of Natural History New York; Museo Nacional de

Historia Natural Chile; Instituto de Entomología de la Universidad Metropolitana de Ciencias de la Educación; Institute Miguel Lillo, Argentina; Museo Argentino de Ciencias Naturales Bernardino Rivadavia; Instituto Patagónico de Ciencias Naturales San Martín Los Andes; Museo de La Plata, La Plata, Argentina; Natural History Museum (London) Collection Specimens; Illinois Natural History Survey Insect Collection; Naturalis Biodiversity Center; Snow Entomological Museum Collection; Bee Biology and Systematics Laboratory; ZFMK Hymenoptera collection were considered); from Salvemos Nuestro Abejorro, all images were curated by JM (Montalva et al. 2017). Citizen scientists with little or no training in bumble bee taxonomy were able to recognize *B. dahlbomii*, for example, due to its easily distinguished bright orange hairs (Falk et al. 2019; Montalva et al. 2011; Morales et al. 2022).

The existence or ability to assign accurate geographical coordinates to occurrence records is crucial for successful analysis. Therefore, an occurrence record in our preliminary dataset was retained to investigate whether the provided geographical coordinates or the locality string were sufficiently detailed to geocode a record using Google Earth. Additionally, dubious, unreliable, and duplicate occurrence records were discarded from the dataset. This process yielded 251 confident records for *B. ruderatus*, 885 for *B. terrestris*, and 321 for *B. dahlbomii* from the preliminary dataset of 5,307 records.

Climatic data for both current and future scenarios

We obtained climatic datasets from 19 Wordclim bioclimatic variables (www.worldclim.org) for temperature and precipitation from 1950 to 2000 (Hijmans et al. 2005), widely used in SDMs and used in other studies of bees in South America (Vivallo et al. 2019; Nascimento et al. 2022). Additionally, we used 19 bioclimatic variables available for 17 Atmosphere–Ocean Global Circulation Models (AOGCMs) from WorldClim to model the species in the future scenarios of climate change: ACCESS1-0, BCC-CSM1-1, CCSM4, CNRMCM5, GFDL-CM3, GISS-E2-R, HadGEM2-AO, HadGEM2-CC, HadGEM2-ES, INMCM4, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MPI-ESM-LR, MRICGCM3, and NorESM1-M. from the latest IPCC report on the world's climate (IPCC 2019).

These scenarios were also obtained on the WorldClim website to predict climate-suitable areas for species in 2070, considering the carbon representative pathway (RCP 8.5) available in the IPCC (2019) global climate report.

However, using many climatic variables can lead to overfitting models (Beaumont et al. 2005; Jiménez-Valverde et al. 2011). Therefore, in the species distribution models, we reduced the number of our variables to improve the prediction of the range of the species using principal component analysis. For this, we standardized the variables to have their mean equal to zero and variances equal to |1|. Later, we ran a principal component analysis (PCA hereafter) to obtain independent principal components (PCs onwards) representing the environment variables to predict the species range. The selected PCs explained 95% of the original climatic variation. We also standardized the variables for future scenarios by setting means equal to zero and variances equal to |1|. Before the PCA was run for the variables in the future scenarios, the linear coefficients obtained for the current variables were projected into each one of the future scenarios. Finally, the PCA was run for each of the future scenarios. This method was applied to obtain a dependency between the current climatic scenario and every future climatic scenario.

Data analysis

Ecological niche overlap

We applied the analysis framework of Broennimann et al. (2012) to determine the extent to which similarities existed in the environmental space occupied by the three bumble bee species. First, we created a background distribution map based on a minimum convex polygon (MCP) from the occurrence records of each species. In addition to the MCP, we added a 2-degree buffer around the occurrences as an estimate related to the species dispersal abilities and to avoid making all climatic cells, even those deemed unreachable for the species, to be used in the niche analysis. Next, the data were compiled into a matrix and analyzed using principal component analysis (PCA) to generate an environmental space [PCA-env in Broennimann et al. (2012)]. We chose to apply a PCA considering all the environmental spaces together, as this strategy reached the best

performance when comparing niches (Broennimann et al. 2012). Next, we calculated the occurrence density within each cell (4 km) of the environmental space grid for each species. The occurrence density was then modeled using a smooth kernel density function that analyzed the geographical conditions of each species (Broennimann et al. 2012). The species pairwise niche overlap was then calculated using Schoener's D metric between the modeled occurrence densities in the PCA ordination space (Broennimann et al. 2012; Schoener 1970; Warren et al. 2008).

We tested the significance of the D metric by calculating the niche equivalency and similarity between the three pairs of species (Broennimann et al. 2012) using the ecospat package (Di Cola et al. 2017) in R, with code modifications in Silva et al. (2016). The niche equivalency test determines whether the niches of two species in two geographical ranges are equivalent (i.e., whether the niche overlap is constant when randomly reallocating the occurrences of both species among the two ranges). First, all occurrences were pooled to retain the same number of occurrences as in the original datasets and were randomly divided into two datasets. Then, niche overlap statistic D is calculated. This process was repeated 100 times (to increase the likelihood that the null hypothesis could be confidently rejected), and a histogram of the simulated values was constructed. If the observed value of D falls within the density of 95% of the simulated values, the null hypothesis of niche equivalency cannot be rejected. The niche similarity test differed from the equivalency test in determining whether the overlap between niches observed in the two ranges was distinct from those niches and whether niches were randomly chosen from the other ranges. In other words, the niche similarity test determined whether an environmental niche occupied in one range was more similar to another than predicted by chance. We shifted the observed density of occurrences in one range at random (the location of the simulated density of the center of the occurrences was chosen randomly from a pool of environments) to conduct this test. We then determined how closely the simulated niche matched the observed niche in the other range. We based the niche similarity test on 100 repetitions. If the observed overlap is greater than 95% of the simulated values, then the species occupies environments in both ranges that are more similar to each other than

expected by chance (Broennimann et al. 2012; Silva et al. 2016).

SDMs

For the SDMs, we used a spatially structured partition of the occurrences of the modeled species. Consequently, we gridded the study extent in a checkerboard fashion with an aggregation factor of two, in which the occurrences of the modeled species were allocated. Initially, we used one subset to train the models, while the second enabled us to evaluate the produced distribution range. Next, we used the occurrences from the first modeling run to train a second modeling run. Finally, we used the training occurrences to evaluate those produced in the second modeling round.

We used six different models in an ensemble approach: the Generalized Linear Model (GLM), Random Forest (RDF), Maximum Entropy (MAX), Gaussian Model (GAU), Support Vector Machines (SVM), and Maximum Likelihood (MLK). GLM and RDF are statistical methods, MAX and SVM are machine-learning methods, and GAU and MXL are Bayesian methods. The models were evaluated using the Jaccard similarity index metric (Leroy et al. 2018; Barahona-Segovia et al. 2023; Booth et al. 2013; Fern et al. 2019). This procedure measures the similarity between predictions and observations on a scale of 0 to 1. Values near 1 indicate that the model predictions perfectly match the general observations of the species, and values near 0 indicate that the models do not correspond to actual observations (Leroy et al. 2018). In addition, we used a threshold that maximizes Jaccard values concerning sensitivity and specificity. Since similarity indices do not consider pseudoabsences during model evaluation, they are less biased than other evaluation metrics. Finally, we used a weighted consensus method to produce the final species distribution considering all methods.

Results

Climatic niche overlap

The first two PCs of the PCA captured 71.39% of the variation in the climate dataset. The first PC (43.5%) corresponded to temperature variables, and the second (27.89%) corresponded to precipitation. Additionally, the European bumble bee species exhibited niche overlap with the native species *B. dahlbomii*, with 46% (D: 0.46) overlapping with *B. ruderatus* and 61% with *B. terrestris* (D: 0.61) (Table 1; Fig. 1).

SDMs

The models for *B. dahlbomii, B. ruderatus*, and *B. terrestris* reached mean Jaccard values of 0.85 ± 0.04, 0.89 ± 0.03, and 0.92 ± 0.01, respectively (mean $\pm$ standard error). For *B. dahlbomii*, GAU (0.94 ± 0.01), RDF (0.94 ± 0.01), and SVM (0.94 ± 0.0) had comparably high Jaccard values. For *B. ruderatus*, MAX had the highest Jaccard value (0.91 ± 0.07) and RDF for *B. terrestris* (0.90 ± 0.01; Table 2). MLK performed poorly for all three species (Table 2).

In the current climate scenario, the native species *B. dahlbomii* occurred throughout the southern portion of South America, comprised of the

Table 1 Main results of the multivariate analyses, considering Schoener's D metric and the *p* values obtained using the similarity test (I), niche unfilling (*U*), niche expansion (*E*), and niche stability (*S*) of the climatic niche of the species

	B. ruderatus	*B. terrestris*	*B. dahlbomii*
Schoener's D metric			
B. ruderatus	–	–	–
B. terrestris	0.67	–	–
B. dahlbomii	0.46	0.61	–
Niche similarity			
B. ruderatus	–	**0.01**	0.05
B. terrestris	**0.01**	–	**0.02**
B. dahlbomii	0.05	**0.02**	–
Niche unfilling			
B. ruderatus	–	0.006	0.005
B. terrestris	0.162	–	0.005
B. dahlbomii	0.166	0.026	–
Niche expansion			
B. ruderatus	–	0.162	0.166
B. terrestris	0.006	–	0.026
B. dahlbomii	0.005	0.005	–
Niche stability			
B. ruderatus	–	0.838	0.834
B. terrestris	0.994	–	0.974
B. dahlbomii	0.995	0.995	–

Bold values were statistically significant.
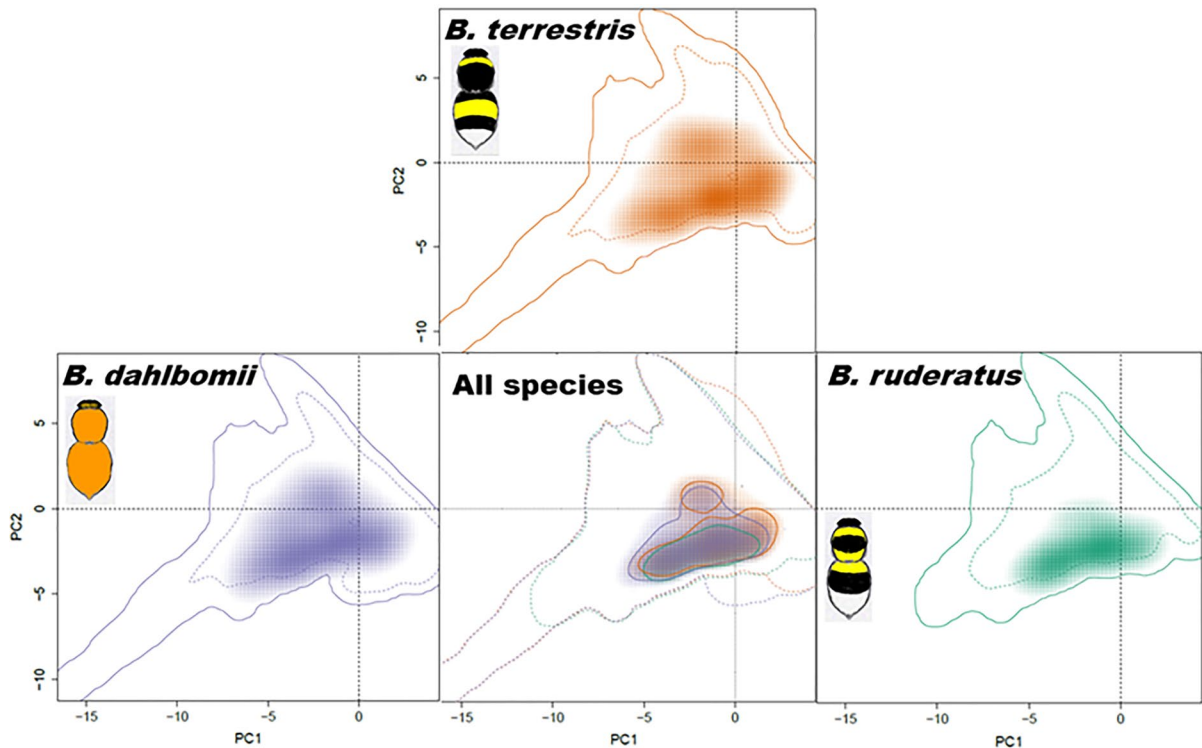
Fig. 1 Climatic conditions suitable for *B. dahlbomii* (left panel), *B. terrestris* (upper panel), *B. ruderatus* (right panel), and the overlap of all three bumble bee species (middle panel). Results obtained from the environmental niche analysis. The solid and dashed lines illustrate 100% and 50% of the available (background) climate for each bumble bee species in their South American ranges. PC: principal components

Table 2 Summary of the SDMs obtained for the GAU, GLM, MLK, MAX, RDF, and SVM algorithms based on Jaccard values ($\pm$ 1 SE)

| Modeling method	*B. ruderatus*	*B. terrestris*	*B. dahlbomii*
GAU	0.81 ± 0.07	0.88 ± 0.01	0.94 ± 0.01
GLM	0.73 ± 0.02	0.78 ± 0.12	0.77 ± 0.04
MLK	0.50 ± 0.00	0.50 ± 0.00	0.50 ± 0.00
MAX	0.91 ± 0.07	0.88 ± 0.01	0.91 ± 0.03
RDF	0.85 ± 0.07	0.90 + 0.01	0.94 ± 0.01
SVM	0.85 ± 0.07	0.86 ± 0.01	0.93 ± 0.01

Mediterranean regions of Chile, the Andes Mountains range (from the latitude 30° to south), the Patagonia of Argentina/Chile, the Malvinas/Falkland Islands, and the Atlantic region of Argentina/Uruguay near Mar del Plata (Figs. 2 and 3). *Bombus ruderatus* distribution is associated with the Mediterranean zone of Chile, reaching the temperate rainforest (Valdivian rainforest) and some parts of the Argentinean Patagonia (Figs. 2 and 3). For *B. terrestris*, the models reached a pattern similar to that of *B. dahlbomii*. The models also predicted suitable regions for *B. terrestris* in the northern parts of Chile, including areas of the Atacama Desert and regions of the southern Andes Mountains of Peru and Bolivia (Figs. 2 and 3). According to the models, the predicted current distribution for *B. ruderatus* was more restricted.

Considering the predicted future distribution of the three species (Fig. 3), the native bumble bee species, *B. dahlbomii*, showed a slight retraction in the northern part of its geographic range (Chilean Mediterranean region). However, the models predicted a suitable area in southern Peru (Fig. 3). The most prominent retraction in the predicted distributions under the pessimistic scenario was near the Río de la Plata region of Argentina/Uruguay. Under the pessimistic scenario, the European bumble bee *B. terrestris* predicted distribution retracted, mainly in Argentinean Patagonia. However,

Fig. 2 Results of SDMs depicting current and future scenarios for the three bumblebee species based on GAU, GLM, MLK, MAX, RDF, and SVM algorithms
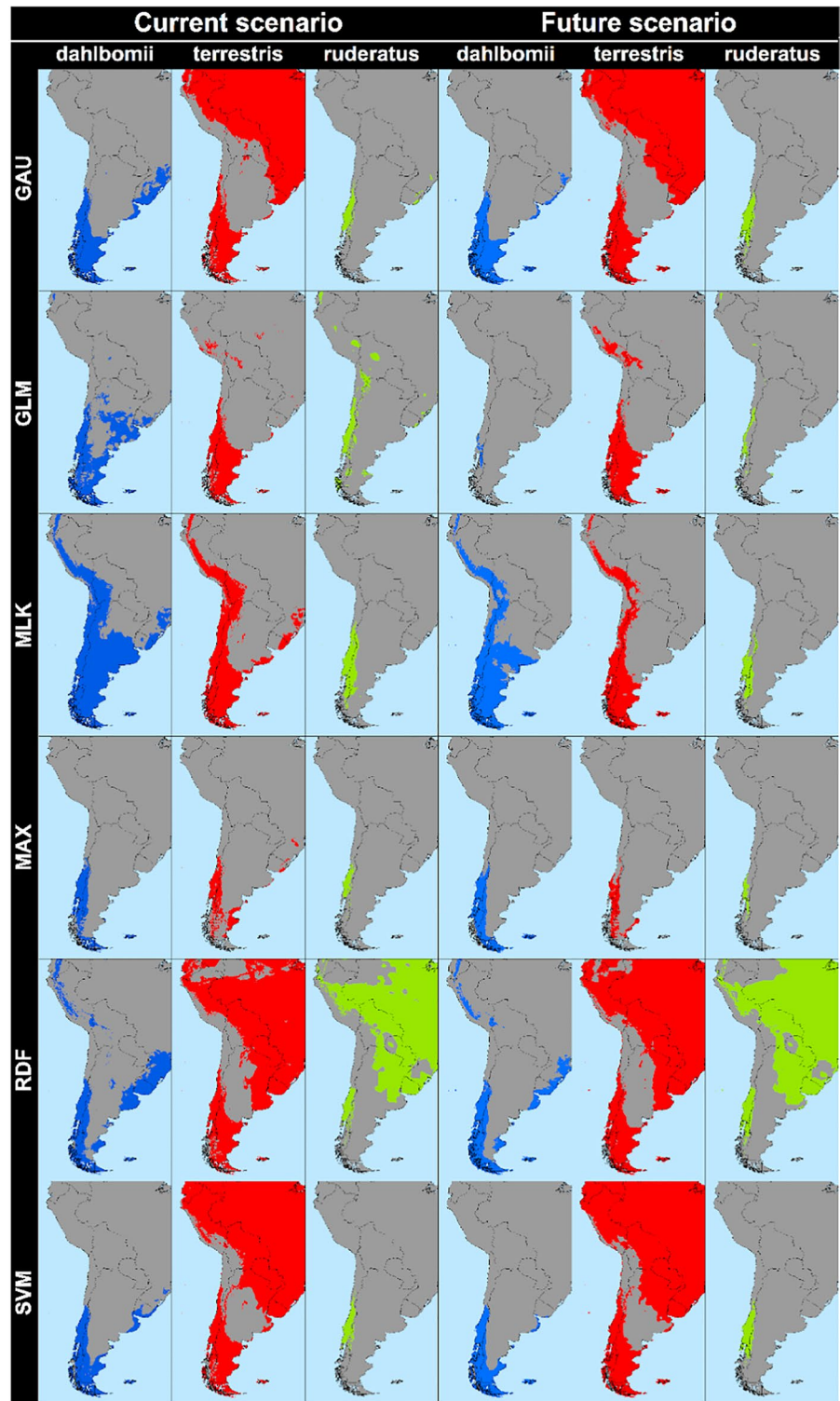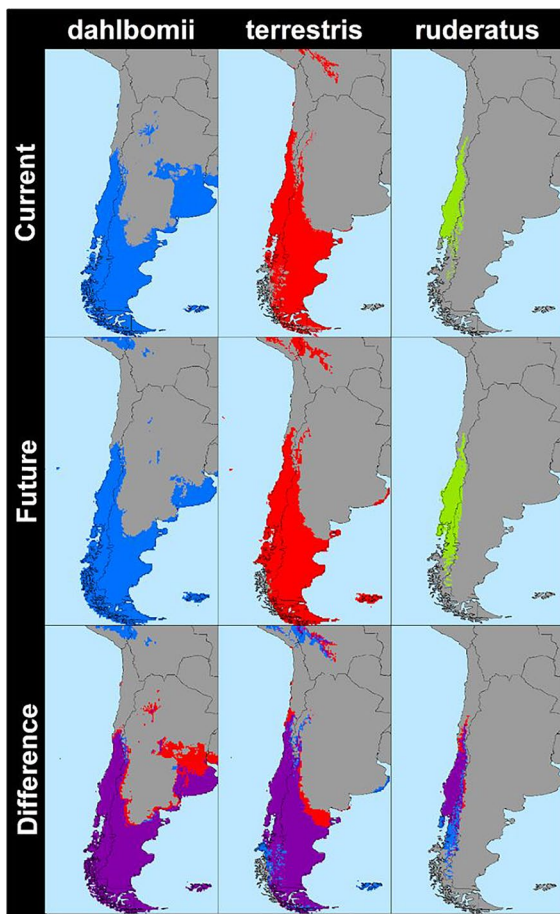
Fig. 3 Summary of SDM results showing the current, future, and differences between scenarios. For the current scenario panels, each color (e.g., blue, red, and green) represents the predicted distribution for each *Bombus* species (blue for *B. dahlbomii*, red for *B. terrestris*, and green for *B. ruderatus*). For future panels, each color represents the predicted distributions for each *Bombus* species (blue for *B. dahlbomii*, red for *B. terrestris*, and green for *B. ruderatus*). For the difference panels, red represents the area predicted to be lost, blue represents the area predicted to be gained, and purple represents the climatically stable areas that do not change from current to future model predictions for the three species

similar to *B. dahlbomii*, a suitable area was predicted in southern Peru (Fig. 3). In the case of *B. ruderatus*, the species moved toward southern Chile and Argentina (Fig. 3).

Discussion

Hortal et al. (2015) identified seven data shortfalls that challenge the progress of ecological and biogeographic research fields. This research addresses two shortfalls considering the cases of the native *B. ruderatus* and invasive *B. terrestris* and *B. ruderatus* in South America. More specifically, our study addresses the Wallacean shortfall, i.e., the lack of data for the geographic distribution of a species or taxon (Whitaker et al. 2005). Depending upon the extent of missing data, the impacts of either species conservation or the detection of invasive species can affect the outcome of analyses and decision making (Lomolino and Heaney 2004; Whittaker et al. 2005). Our study also addresses the Eltonian shortfall, i.e., "the lack of knowledge about interactions among species or among groups of species" (Hortal et al. 2015).

Citizen science and SDMs were effective tools for tracking and predicting the distribution patterns of the endangered *B. dahlbomii* and the introduced species *B. ruderatus* and *B. terrestris*. However, despite the widespread use of SDMs, this method may present concerns when considering the nature of interactions between species on macroecological scales and across large areas, as biotic and abiotic variables interact in complex ways (Silva et al. 2018). While recognizing these limitations, we demonstrated that modeling could help address the knowledge gaps that arise following the invasion of a new species.

Here, we showed the potential distribution of three bumble bee species, two invasive species (*B. ruderatus* and *B. terrestris*) and one native species (*B. dahlbomii*). Specifically, we evaluated the spatial and multivariate overlap of introduced and native bumble bee species using SDMs and multivariate analyses. We show a high niche climatic overlap between *B. ruderatus* and *B. terrestris* (D: 0.67, Fig. 1; Table 1). Additionally, there is an overlap in the niche between these species and *B. dahlbomii* (Fig. 1; Table 1). These values indicate possible competition for resources or a high risk of disease spillover between these species with *B. dahlbomii*, with *B. terrestris* being the most likely threat (Arbetman et al. 2013; Arismendi et al. 2016; Madjidian et al. 2008; Morales et al. 2013; Schmid-Hempel et al. 2014). Furthermore, in some areas where species distributions are sympatric, *B. dahlbomii* populations sharply declined (Morales et al. 2013, 2016). For this reason, a high niche

overlap signals an increased threat to the persistence of *B. dahlbomii* (Morales et al. 2016).

In the current scenario, the distribution maps implied that both introduced species could potentially migrate to and occupy an extensive area in South America (Figs. 2 and 3). Although *B. ruderatus* was more restricted to Patagonia, the non-native distribution of *B. terrestri*s extended north into Peru and Bolivia. Should this scenario unfold, *B. terrestris* could put more strain on *B. funebris* populations and could potentially affect the populations of other native pollinators with adverse outcomes (Morales et al. 2013; Vanbergen et al. 2018; Nascimento et al. 2022). The models indicated areas suitable in the Mediterranean region of Chile for *B. terrestris* (Fig. 3), which Acosta et al. (2016) reported as having low suitability. In addition, our models present a wider distribution for *B. terrestris* compared to the results of Fontúrbel et al. (2021).

The future scenario shows a decrease in the area occupied by the bumble bee species (Fig. 3), especially *B. ruderatus* and *B. dahlbomii*. The models indicated that *B. ruderatus* would probably move toward southern Patagonia, while *B. dahlbomii* would likely disappear near the northern Mediterranean region of South America, confirming the trends shown in a previous study (Morales et al. 2022). This is analogous to the trend of European and North American bumble bee species that have experienced northward or high-elevation shifts in distribution (Kerr et al. 2015). Furthermore, in South America, *B. bellicosus* has shown declines in distribution due to climatic conditions (Martins and Melo 2010; Martins et al. 2015). These movements could affect the abundance of these bumble bee species and cause pollination mismatches (Miller-Struttmann et al. 2015; Valdivia et al. 2016).

Invasive exotic bees can negatively impact native ecosystems (Goulson 2003; Iwasaki and Hogendoorn 2022). Notably, they can compete with native pollinators for floral and local nesting resources and transmit parasites and pathogens (Arbetman et al. 2013; Schmid-Hempel et al. 2014; Arismendi et al. 2016, 2021; Morales et al. 2016; Smith-Ramírez et al. 2018; Aizen et al. 2019). Although the pervasive examples of invasive species are numerous, some exotic bees may cause positive effects on their invaded ranges, for instance, in insular environments (Silva et al. 2017). When there is overlap in the species niches, these impacts may be exacerbated according to the classical competitive exclusion principle (Hardin 1960). For example, in a recent study, *B. terrestris* was defined as an ecological niche constructor, where its foraging behavior over the native plant *Fuchsia magellanica* Lam. (Onagraceae) harms *B. dahlbomii* (Rosenberger et al. 2022). We found substantial evidence of climatic niche overlap between exotic species (*B. ruderatus* and *B. terrestris*) and native species (*B. dahlbomii*) in current and future climatic scenarios.

Moreover, the niche of the native species *B. dahlbomii* fitted almost entirely inside the niche of the European bumblebee *B. terrestris*. Therefore, under future CC projections, native species continue to share most of their niche with exotic species. We urge conservation efforts toward prohibiting the importation of this and other exotic species that have become invasive in this region to safeguard the well-being of native bumblebees and prevent potential harm to similar species in neighboring countries. (Aizen et al. 2019).

In summary, we expect that the ongoing populational decrease of *B. dahlbomii* will continue in the near future. This is likely to occur either because both *B. terrestris* and *B. ruderatus* are relentless competitors for resources at local scales or because of their significant niche and potential distribution overlaps. Considering existing population data and modeled predictions, the existence of *B. dahlbomii* in South America relies on active decisions related to the effective control of commercial hives of *B. terrestris* and *B. ruderatus* and the management of natural environments to increase populational recruitment of *B. dahlbomii*. Nonetheless, even with such active actions taking place, the future of the southernmost bumble bee worldwide remains uncertain.

Declarations

References

Acosta AL, Giannini TC, Imperatriz-Fonseca VL, Saraiva AM (2016) Worldwide alien invasion: a methodological approach to forecast the potential spread of a highly

invasive pollinator. PLoS One 11:e0148295. https://doi.org/10.1371/journal.pone.0148295

Aizen MA, Smith-Ramírez C, Morales CL et al (2019) Coordinated species importation policies are needed to reduce serious invasions globally: the case of alien bumblebees in South America. J Appl Ecol 56:100–106. https://doi.org/10.1111/1365-2664.13121

Arbetman MP, Meeus I, Morales CL et al (2013) Alien parasite hitchhikes to Patagonia on invasive bumblebee. Biol Invasions 15:489–494. https://doi.org/10.1007/s10530-012-0311-0

Arismendi N, Bruna A, Zapata N, Vargas M (2016) Molecular detection of the tracheal mite *Locustacarus Buchneri* in native and non-native bumble bees in Chile. Insectes Soc 63:629–633. https://doi.org/10.1007/s00040-016-0502-2

Arismendi N, Riveros G, Zapata N et al (2021) Occurrence of bee viruses and pathogens associated with emerging infectious Diseases in native and non-native bumble bees in southern Chile. Biol Invasions 23:1175–1189. https://doi.org/10.1007/s10530-020-02428-w

Arretz PV, Macfarlane RP (1986) The introduction of *Bombus ruderatus* to Chile for red clover pollination. Bee World 67:15–22. https://doi.org/10.1080/0005772X.1986.11098855

Barahona-Segovia RM, Smith-Ramirez C, Duran-Sanzana V, Huaranca JC, Pleiscoff P (2023) Bad company expands in highland areas: overlapping distribution, floral resources and habitat suggest competition between invasive and native bumblebees. Glob Ecol Conserv 46:e02595. https://doi.org/10.1016/j.gecco.2023.e02595

Beaumont LJ, Hughes L, Poulsen M (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecol Modell 186:251–270. https://doi.org/10.1016/j.ecolmodel.2005.01.030

Booth TH, Nix HA, Busby JR, Hutchinson MF (2013) BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current maxent studies. Divers Distrib 20:1–9. https://doi.org/10.1111/ddi.12144

Broennimann O, Fitzpatrick MC, Pearman PB et al (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21:481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x

Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:110. https://doi.org/10.1016/j.tree.2005.01.003

Di Cola V, Broennimann O, Petitpierre B et al (2017) Ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40:774–787. https://doi.org/10.1111/ecog.02671

Dafni A, Kevan P, Gross CL, Goka K (2010) *Bombus terrestris*, pollinator, invasive and pest: an assessment of problems associated with its widespread introductions for commercial purposes. Appl Entomol Zool 45:101–113. https://doi.org/10.1303/aez.2010.101

Diagne C, Leroy B, Vaissière A-C et al (2021) High and rising economic costs of biological invasions worldwide. Nature 592:571–576. https://doi.org/10.1038/s41586-021-03405-6

Faleiro FV, Silva DP, de Carvalho RA et al (2015) Ring out the bells, we are being invaded! Niche conservatism in exotic populations of the yellow bells, *Tecoma stans* (Bignoniaceae). Nat Conserv 13:24–29. https://doi.org/10.1016/j.ncon.2015.04.004

Falk S, Foster G, Comont R et al (2019) Evaluating the ability of citizen scientists to identify bumblebee (*Bombus*) species. PLoS One 14:e0218614. https://doi.org/10.1371/journal.pone.0218614

Fern RR, Morrison ML, Wang H-H, Grant WE, Campbell TA (2019) Incorporating biotic relationships improves species distribution models: modeling the temporal influence of competition in conspecific nesting birds. Ecol Model 408:108743. https://doi.org/10.1016/j.ecolmodel.2019.108743

Fontúrbel FE, Murúa MM, Vieli L (2021) Invasion dynamics of the European bumblebee *Bombus terrestris* in the southern part of South America. Sci Rep 11:15306. https://doi.org/10.1038/s41598-021-94898-8

Goulson D (2003) Effects of introduced bees on native ecosystems. Annu Rev Ecol Evol Syst 34:1–26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Hinojosa-Díaz IA, Feria-Arroyo TP, Engel MS et al (2009) Potential distribution of orchid bees outside their native range: the cases of *Eulaema polychroma* (Mocsáry) and *Euglossa viridissima* Friese in the USA (Hymenoptera: Apidae). Divers Distrib 15:421–428. https://doi.org/10.1111/j.1472-4642.2008.00549.x

Hinojosa-Díaz IA, Yáñez-Ordóñez O, Chen G (2005) The north American invasion of the giant resin bee (Hymenoptera: Megachilidae). J Hymenopt Res 14:69–77

Hortal J, de Bello F, Diniz-Filho JAF et al (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. Annu Rev Ecol Evol Syst. 46:523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

IPCC (2019) Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems [P.R. Shukla, J. Skea, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, D. C. Roberts, P. Zhai, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, J. Portugal Pereira, P. Vyas, E. Huntley, K. Kissick, M. Belkacemi, J. Malley, (eds.)]

Iwasaki JM, Hogendoorn K (2022) Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. Curr Res Insect Sci 2:100043. https://doi.org/10.1016/j.cris.2022.100043

Jackson T (2015) Addressing the economic costs of invasive alien species: some methodological and empirical issues. Int J Sustain Soc 7:221–240. https://doi.org/10.1504/IJSSOC.2015.071303

Jiménez-Valverde A, Peterson AT, Soberón J et al (2011) Use of niche models in invasive species risk assessments.

Biol Invasions 13:2785–2797. https://doi.org/10.1007/s10530-011-9963-4

Kadoya T, Washitani I (2010) Predicting the rate of range expansion of an invasive alien bumblebee (*Bombus terrestris*) using a stochastic spatio-temporal model. Biol Conserv 143:1228–1235. https://doi.org/10.1016/j.biocon.2010.02.030

Kerr JT, Pindar A, Galpern P et al (2015) Climate change impacts on bumblebees converge across continents. Science 349:177–180. https://doi.org/10.1126/science.aaa7031

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204. https://doi.org/10.1016/s0169-5347(01)02101-2

Leroy B, Delsol R, Hugueny B et al (2018) Without quality presence-absence data, discrimination metrics such as TSS can be misleading measures of model performance. J Biogeogr 45:1994–2002. https://doi.org/10.1111/jbi.13402

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137. https://doi.org/10.1016/0169-5347(93)90025-K

Lomolino MV, Heaney LR (2004) Frontiers of biogeography: new directions in the geography of nature. Oxford University Press Incorporated, Oxford

Mack RN, Simberloff D et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

MacPhail VJ, Richardson LL, Colla SR (2019) Incorporating citizen science, museum specimens, and field work into the assessment of extinction risk of the American Bumble bee (*Bombus pensylvanicus* De Geer 1773) in Canada. J Insect Conserv 23:597–611. https://doi.org/10.1007/s10841-019-00152-y

Madjidian JA, Morales CL, Smith HG (2008) Displacement of a native by an alien bumblebee: lower pollinator efficiency overcome by overwhelmingly higher visitation frequency. Oecologia 156:835–845. https://doi.org/10.1007/s00442-008-1039-5

Martins AC, Melo GAR (2010) Has the bumblebee *Bombus bellicosus* gone extinct in the northern portion of its distribution range in Brazil? J Insect Conserv 14:207–210. https://doi.org/10.1007/s10841-009-9237-y

Martins AC, Silva DP, De Marco P, Melo GAR (2015) Species conservation under future climate change: the case of *Bombus bellicosus*, a potentially threatened south American bumblebee species. J Insect Conserv 19:33–43. https://doi.org/10.1007/s10841-014-9740-7

Matsumura C, Yokoyama J, Washitani I (2004) Invasion Status and potential ecological impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae). Global Environ Res 8:51–66

Miller-Struttmann NE, Geib JC, Franklin JD et al (2015) Functional mismatch in a bumble bee pollination mutualism under climate change. Science 349:1541–1544. https://doi.org/10.1126/science.aab0868

Montalva J, Dudley L, Arroyo MK et al (2011) Geographic distribution and associated flora of native and introduced bumble bees (*Bombus* spp.) in Chile. J Apic Res 50:11–21. https://doi.org/10.3896/IBRA.1.50.1.02

Montalva J, Sepulveda V, Vivallo F, Silva DP (2017) New records of an invasive bumble bee in northern Chile: expansion of its range or new introduction events? J Insect Conserv 21:657–666. https://doi.org/10.1007/s10841-017-0008-x

Montalva J, Vieli L, Castro B, Allendes JL, Amigo V (2015) Status report on the Chilean bumblebee, *Bombus dahlbomii*. Santiago

Mooney HA, Hobbs RJ (2000) Invasive species in a changing world. Island Press, Washington

Morales CL, Arbetman MP, Cameron SA, Aizen MA (2013) Rapid ecological replacement of a native bumble bee by invasive species. Front Ecol Environ 11:529–534. https://doi.org/10.1890/120321

Morales CL, Montalva J, Arbetman MP et al (2022) Does climate change influence the current and future projected distribution of an endangered species? The case of the southernmost bumblebee in the world. J Insect Conserv 26:257–269. https://doi.org/10.1007/s10841-022-00384-5

Morales C, Montalva J, Arbetman M, Aizen MA, Smith-Ramírez C, Vieli L, Hatfield R (2016) *Bombus dahlbomii*. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T21215142A100240441.en. Accessed on 27 Apr 2023

Naeem M, Yuan X, Huang J, An J (2018) Habitat suitability for the invasion of *Bombus terrestris* in East Asian countries: a case study of spatial overlap with local Chinese bumblebees. Sci Rep 8:11035. https://doi.org/10.1038/s41598-018-29414-6

Nascimento AC, Montalva J, Ascher JS et al (2022) Current and future distributions of a native Andean bumble bee. J Insect Conserv 26:559–569. https://doi.org/10.1007/s10841-022-00395-2

Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65. https://doi.org/10.1641/0006-3568(2000)050[0053:eaecon]2.3.co;2

Rendoll-Carcamo JA, Contador TA, Saavedra L, Montalva J (2017) First record of the invasive bumblebee *Bombus terrestris* (Hymenoptera: Apidae) on Navarino Island, southern Chile (55°S). J Melittol. https://doi.org/10.17161/jom.v0i71.6520

Roig Alsina A, Aizen M (1996) *Bombus ruderatus* Fabricius, un nuevo Bombus para la Argentina (Hymenoptera: Apidae). Physis 5:49–50

Rosenberger NM, Aizen MA, Dickson RG, Harder LD (2022) Behavioural responses by a bumble bee to competition with a niche-constructing congener. J Anim Ecol 91:580–592. https://doi.org/10.1111/1365-2656.13646

Schmid-Hempel R, Eckhardt M, Goulson D et al (2014) The invasion of southern South America by imported bumblebees and associated parasites. J Anim Ecol 83:823–837. https://doi.org/10.1111/1365-2656.12185

Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418. https://doi.org/10.2307/1935376

Silva DP, Dew RM, Vilela B et al (2018) No deaths in the desert: predicted responses of an arid-adapted bee and its two nesting trees suggest resilience in the face of warming climates. Insect Conserv Divers 11:449–463. https://doi.org/10.1111/icad.12318

Silva DP, Groom SVC, Silva CRB et al (2017) Potential pollination maintenance by an exotic allodapine bee under climate change scenarios in the Indo-Pacific region. J Appl Entomol 141:122–132. https://doi.org/10.1111/jen.12337

Silva DP, Vilela B, Buzatto BA et al (2016) Contextualized niche shifts upon independent invasions by the dung beetle *Onthophagus taurus*. Biol Invasions 18:3137–3148. https://doi.org/10.1007/s10530-016-1204-4

Silva DP, Vilela B, De Marco P Jr, Nemésio A (2014) Using ecological niche models and niche analyses to understand speciation patterns: the case of sister neotropical orchid bees. PLoS One 9:e113246. https://doi.org/10.1371/journal.pone.0113246

Simberloff D, Schmitz DC, Brown TC (1997) Strangers in paradise: impact and management of nonindigenous species in Florida. Island Press, Washington

Smith-Ramírez C, Vieli L, Barahona-Segovia RM et al (2018) The reasons why Chile should stop importing commercial bumblebee *Bombus terrestris* (Linnaeus) and to start controlling it. Gayana 82:118–127. https://doi.org/10.4067/s0717-65382018000200118

Suzuki-Ohno Y, Yokoyama J, Nakashizuka T, Kawata M (2017) Utilization of photographs taken by citizens for estimating bumblebee distributions. Sci Rep 7:11215. https://doi.org/10.1038/s41598-017-10581-x

Torretta JP, Medan D, Abrahamovich AH (2006) First record of the invasive bumblebee *Bombus terrestris* (L.) (Hymenoptera, Apidae) in Argentina. Trans Am Entomol Soc 132:285–289

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol Evol 21:208–216. https://doi.org/10.1016/j.tree.2006.01.006

Valdivia CE, Carroza JP, Orellana JI (2016) Geographic distribution and trait-mediated causes of nectar robbing by the European bumblebee *Bombus terrestris* on the Patagonian shrub *Fuchsia magellanica*. Flora Morphol Distrib Funct Ecol Plant 225:30–36. https://doi.org/10.1016/j.flora.2016.09.010

Vanbergen AJ, Espíndola A, Aizen MA (2018) Risks to pollinators and pollination from invasive alien species. Nat Ecol Evol 2:16–25. https://doi.org/10.1038/s41559-017-0412-3

Vergara PM, Fierro A, Carvajal MA et al (2023) Environmental and biotic filters interact to shape the coexistence of native and introduced bees in northern Patagonian forests. Agric Ecosyst Environ 349:108465. https://doi.org/10.1016/j.agee.2023.108465

Vitousek PM, D'antonio CM, Loope LL et al (1996) Introduced species: a significant component of human-caused global change. N Z J Ecol 21:1–16

Vivallo F, Vilela B, Silva DP (2019) Inferring host-cleptoparasite complexes of South American Centridine bees (Hymenoptera: Apidae) using macroecological perspectives. Org Divers Evol 19:179–190. https://doi.org/10.1007/s13127-019-00394-3

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Whittaker RJ, Araújo MB, Jepson P et al (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11:3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x