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MODELING THE DISTRIBUTION OF NATIVE AND INVASIVE SPECIES OF BUMBLE BEES (HYMENOPTERA: APIDAE) IN CHILE, USING CITIZEN SCIENCE DATA

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BY THE COMMITTEE CONSISTING OF

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"A bill preferd against a publique wrong,
the surely humble bee, who hath too long
Liv'd like an out-law and will neither pay
money or waxe, do service nor obey;
but like a fellon, coucht under a weed,
upon the top-branch blossomed, and by stealth
Makes dangerous inroads on your common-wealth;
robs the day-labourer of his golden prize
And sends him weeping home with emptie thighes.
And out-law-like doth challenge as his own
Your highnes due; nay, pyratick dataines
The waxen fleet sailing upon your plaines"

John Day, 1607

Abstract

There are around 260 species of bumble bees (*Bombus*) globally, many of them providing important pollination services. In fact, some species are bred and sold commercially to assure the successful pollination of crops. *Bombus terrestris* and *B. impatiens* are two species that are bred commercially. Since the 1980's some of these species have been imported to different countries worldwide, and these movements have created ecological problems, including (1) competition for resources with native pollinators, (2) importation of new diseases to the new environments, (3) hybridization with congeners, (4) disruption of the pollination of native plants, and (5) facilitation of invasion by introduced plants.

In this thesis, the utility and efficacy of citizen science data is analyzed and compared to the traditional use of distributional (museum data) records in Chile (chapter 2). Those data were then used to model the distribution of native and introduced bumble bees in Chile (chapter 3). Data provided by citizen scientists has become an important resource for conservation biologists. Between 2014-2020, Salvemos Nuestro Abejorro obtained over 4000 bumble bee records from citizen scientists in Chile. These data were significantly greater in number than museum data records for the introduced species. Thus, citizen science reports can have a broader impact on tracking the distribution of introduced species. In Chapter 3 we conducted multivariate bioclimatic niche analyses to evaluate the niche overlap of *Bombus terrestris, Bombus ruderatus*, and *Bombus dahlbomii*. The models indicated significant niche overlap between the invasive bumble bee species and the native species. *B. terrestris* had a high extent of suitable range in South America, meaning further invasion in the region is highly possible. Also, the models indicate that the distribution of *B. dahlbomii* will decrease due to future climate scenarios. Therefore, this

comprehensive review and analysis of the consequences of these pollinator invasions on South America is both timely and necessary.

Chapter 1: Literature review:

Species introductions into new environments have occurred throughout evolutionary time. But humans have accelerated this process in recent centuries, enhancing the rate and distances of species dispersion across the globe (Cadotte, 2006). In many instances, the arrival and establishment of new species in a region have little or no ecological consequences (Cadotte, 2006). In other cases, however, the arrival of a new species can have profound ecological and economic consequences. These events are referred to as biological invasions and the new species as invasive. Invasive species can affect the composition and function of the invaded communities (Kolar & Lodge, 2001; Lodge, 1993; Mack et al., 2000; Moller, 1996; Mooney & Hobbs, 2000), which is often exacerbated by anthropic effects, and could trigger the extinction of native species, homogenization of the local biota, and disruption of ecological processes (Simberloff et al., 1997; Traveset & Richardson, 2006). Economic losses in agriculture and fisheries due to invasive species have cost billions, from both lost productivity and the expense of combating them (Diagne et al., 2021; Jackson, 2015; Lodge, 1993; Pimentel et al., 2000; Vitousek et al., 1997).

Conceptual models have identified the stages that lead to the successful invasion of an ecosystem, which often resembles models that describe the natural process of dispersal (Ni et al., 2021; Simberloff, 2009). Shea and Chesson (2002) proposed a three-stage model: 1) introduction of a species in a new geographical area or new habitat, 2) successful establishment and 3) eventual rapid expansion to new areas.

In the first stage, the success of an invasive species would be influenced by the initial abundance of propagules, as well as the degree of "biotic resistance" exerted by a community to an invader (Green, 1997; Lodge, 1993; Richardson et al., 2000; Simberloff, 2009), both of can be affected by human activity (Byers, 2002; Kolar & Lodge, 2001; Mack, 2003; Vitousek et al., 1997) (Figure 1). Biotic resistance is inherent to stable ecosystems. And the more biological connections (i.e., interspecific interactions), the greater the impediment to exotic species (Richardson et al., 2000; Traveset & Richardson, 2006). However anthropogenic activities can reduce biotic resistance (Thuiller et al., 2006). In the worst-case scenario, a high anthropic disturbance could cause a drop in the biotic resistance, and if the initial abundance of propagules is high, the situation is ideal for a successful invasion (Figure 1).

In stage 2 of the Shea and Chesson (2002) model, should an exotic species establish reproducing and expanding populations, and recall that this does not assure that an exotic species will become invasive, there are three potential outcomes for the recipient community; negative (competition, herbivory, parasitism, etc.), neutral, or positive (facilitation, commensalism, mutualism, etc.) (Richardson et al., 2000; Simberloff & Von Holle, 1999). Research has historically focused on the outcome of antagonistic relationships between invaders and the recipient ecosystems (Simberloff & Von Holle, 1999).

Neutral relationships are complicated and challenging to identify. They depend on the existence of an “empty niche” (Levine & D’Antonio, 1999; Richardson et al., 2000), meaning that an exotic species becomes established in an unoccupied ecological space. The existence of empty niche is hotly debated and seems highly unlikely in most ecosystems (Levine & D’Antonio, 1999; Richardson et al., 2000).

Positive relationships describe a situation in which the presence of an introduced species favors a native species, possibly even one that is imperiled. For example, an invasive species could present a new prey resource for a native predator. If the predator is facing low food resources, it could be favored by the arrival of a new prey species. A similar scenario involves plants that lack pollinators, or pollinators with insufficient host and/or nectar resources (Simberloff & Von Holle, 1999).

The existence of evolutionary anachronisms, or plants species that have lost their animals seed dispersers to extinction, represents another example of a positive relationship (Guimarães et al., 2008). After the massive extinction of the megafauna in the Americas, many plant species were left without dispersers. But horses returned to the Americas with the arrival of Europeans in the 16th century, which inadvertently assumed the role of disperser for plant species such as *Crescentia alata* (Guimarães et al., 2008). Still, these exotic/native positive interactions are considered isolated cases (Simberloff & Von Holle, 1999).

To understand how frequently negative, positive, and neutral relations have been reported in the literature, Simberloff and Von Holle (1999) conducted a meta-analysis of 254 articles published on invasion biology from 1993 and 1997. In 156 cases, there was a positive effect on the invader and a negative impact on native species (+, -) in a recipient ecosystem. In 30 cases, there was a positive interaction between two invasive species; there was facilitation in only 10 cases (+, +), in 12 cases interference or competition (-, -), and no cases of amensalism or neutral relations (Simberloff & Von Holle, 1999). The authors referred to a positive interaction between two or more invasive species as an “invasional meltdown”, defined as a mutualism between exotic species that facilitates the invasion process (Simberloff, 2006; Simberloff & Von Holle, 1999).

Invasional meltdowns could have considerable impacts on the structure of mutualistic networks of native species (Aizen et al., 2008; Bjerknes et al., 2007; Traveset & Richardson, 2014). For example, the invasive capacity of an exotic pollinator and an exotic plant could prove to be mutually beneficial; the success of one facilitates the success of the other. This relationship could modify and potentially interfere with the structure of the existing pollination network of native plants and native pollinators in the recipient ecosystem, resulting in weakened mutualisms (Figure 2)(Aizen et al., 2008; Traveset & Richardson, 2014; Tylianakis, 2008). A possible outcome of this process is an increased reliance of native generalist species on resources provided by a "supergeneralist" invasive species (Figure 2) (Aizen et al., 2008; Morales et al., 2017; Traveset & Richardson, 2014; Tylianakis, 2008). A classic example is adoption by *Apis mellifera scutellata* (Africanized honeybee) of native floral resources in the Americas that in turn facilitates its colonization and dispersion (Roubik & Villanueva-Gutierrez, 2009). Within most biological communities, however, these interactions are much more dynamic. The actuation of more than one relationship occurring at a given time has been documented in pollination – plant networks where both antagonistic and mutualistic interactions may occur (Figure 3, Table 1) (Simberloff & Von Holle, 1999; Traveset & Richardson, 2006).

In the context of pollination – plant networks specifically, exotic pollinators could compete with native pollinators for floral resources and/or nesting sites (Hingston, 2006; Inoue et al., 2008; Kato et al., 1999; Madjidian et al., 2008; Paini, 2004; Stout et al., 2002) or transmit pathogens to native pollinators (Cameron & Sadd, 2020; Colla et al., 2006; Goka et al., 2006; Meeus et al., 2011; Otti et al., 2008; Plischuk et al., 2020) (Figure 3, Table 1). There are three possible facilitation (+,+) scenarios that involve the geographic origin of the species; exotic plant-exotic pollinator or native plant-native pollinator, or exotic plants-native pollinators (Figure 1)(Table 1); competition or adverse effects (+,-) occurs, in most cases, will result when the species has a different origin (exotic plant-native plant or exotic pollinator-native pollinators [Figure 3]). And of course, exotic plants could have positive and/or negative impacts on the native ecosystems (Figure 3, Table 1).

Plants often compete for pollinators, and in some cases, exotic plants become more attractive than native plants. Thomson (1978) coined the term "magneto species" to describe this phenomenon (Laverty, 1992; Molina-Montenegro et al., 2008; Muñoz & Cavieres, 2008). A classic example is the invasive *Taraxacum officinale*, an apomictic plant that does not require pollinators (Muñoz & Cavieres, 2008). But pollinators are attracted to it nonetheless and are effectively kidnapped, thus depriving native plants of pollination services and negatively impacting plant populations (Bjerknes et al., 2007).

Bombus ruderatus and *B. terrestris* are two European bumble bees that were introduced for crop pollination in Chile (Aizen et al., 2019; Montalva et al., 2011; Smith-Ramírez et al., 2018). *Bombus ruderatus* was introduced to pollinate *Trifolium pratense* (red clover), a livestock forage crop. During the 1982/1983 growing season, approximately 400 queens were imported from New Zealand and released at two locations near Temuco (38°S 72°W), in the south of Chile (Arretz & Macfarlane, 1986). In 1993, *B. ruderatus* was first reported in Argentina, and likely originated from individuals who arrived precedent from Chile (Roig Alsina & Aizen, 1996) (Figure 4).

The European *Bombus terrestris* (buff-tailed bumble bee) is one of the leading commercially distributed species and has been introduced in several countries worldwide (Figure 5) (Dafni et al., 2010; Kadoya & Washitani, 2010; Matsumura et al., 2004; Naeem et al., 2018). It was first introduced to central Chile in 1997 (Montalva et al., 2011), and since that date, more than a million individuals have been imported into the country (Aizen et al., 2019; Smith-Ramírez et al., 2018) (Fig. 7). Its availability throughout Chile maximizes propagule introduction (Figure 7), and could affect other countries (Aizen et al., 2019; Smith-Ramírez et al., 2018). In fact, *B. terrestris* was reported from Argentina in 2006 (Torretta et al., 2006; Morales 2007).

For the reasons mentioned at the beginning of this review, the impact of these two invasive species on native South American ecosystems should be of concern to researchers and land managers alike. Both European bumble bee species are now feral in Chile and parts of Argentina and are blamed for the decrease in the native *B. dahlbomii* populations (Morales et al., 2016; Smith-Ramírez et al., 2018) (Fig. 6). They have also been observed pollinating invasive plants that negatively affect the native plants of Chile and Argentina (Morales & Aizen, 2002; Morales pers. com.; Valdivia et al., 2016).

Although there may be competition for flower resources between exotic species and native species, disease introduction is a current problem (Aizen et al., 2019; Smith-Ramírez et al., 2018). In 2013, two studies revealed the presence of European parasites in Chile, probably carried by the European bumble bees, and is contributing to the decline of *B. dahlbomii* populations (Arbetman et al, 2013; Arismendi et al, 2016; Schmid-Hempel et al., 2014). These parasites inhibit colony founding by inducing sterility in queens, increasing the mortality of workers, and causing other severe physical and behavioral effects (Meeus et al., 2011). In less than 20 years (or since the introduction of *B. terrestris*), the distribution of *B. dahlbomii* has shrunk considerably and it is now listed as endangered by both the International Union for the Conservation of Nature (IUCN) Red List and on the Chilean Ministerio de Medio Ambiente (MMA) (Montalva et al., 2015; Morales et al., 2016).

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Table 1. The possible relation of interactions (+, -) between exotic pollinators and plants and the invaded areas.

Organism type	Interaction	References
Exotic pollinator	(-) Compete with native pollinators for floral resources and nesting sites.	Hingston, 2006; Inoue et al., 2008; Kato et al., 1999; Madjidian et al., 2008; Morales, 2007; Paini, 2004; Russo, 2016, Stout et al., 2002
Exotic pollinator	(-) Transmit pathogens to native pollinators	Cameron & Sadd, 2020; Colla et al., 2006; Goka et al., 2006; Meeus et al., 2011; Otti et al., 2008; Plischuk et al., 2020, 2009; Plischuk & Lange, 2009; Schmid-Hempel et al., 2014
Exotic pollinator	(-) Hybridize with genetically related species	Kanbe et al., 2008; Kondo et al., 2009; Matsumura et al., 2004
Exotic pollinator	(+) Pollinating exotic plants increasing their invasion rate	Barthell et al., 2001; Cariveau & Norton, 2009; Goulson, 2005; Goulson & Derwent, 2004; Hanley & Goulson, 2003; Hingston, 2006; Mciver et al., 2009; Mitchell et al., 2006; Morales & Aizen, 2002
Exotic pollinator	(+) Provide pollination services when native pollinators are scarce	Bjerknes et al., 2007; Madjidian et al., 2008; Medel et al., 2018; Nadel, et al., 1992; Roubik, 1994; Sanguinetti & Bustos, 2014
Exotic pollinator	(-) disrupt pollination on native plants	Aizen et al., 2014; Kenta et al., 2007; Valdivia et al., 2016
Exotic plant	(-) Compete for various resources with native plants	Bjerknes et al., 2007

Organism type	Interaction	References
Exotic plant	(-) Have allelopathic effects, being able to significantly modify an ecosystem, and this may even indirectly facilitate other invaders	Bjerknes et al., 2007; Callaway & Aschehoug, 2000; Maron & Connors, 1996; Shea & Chesson, 2002
Exotic plant	(-) Alter pollination and reproduction services in native plants	Bjerknes et al., 2007
Exotic plant	(-) Hybridize with native plants	Levin et al., 1996
Exotic plant	(+) Be sources of resources for native pollinator populations when the resources of native plants are not sufficient	Bjerknes et al., 2007

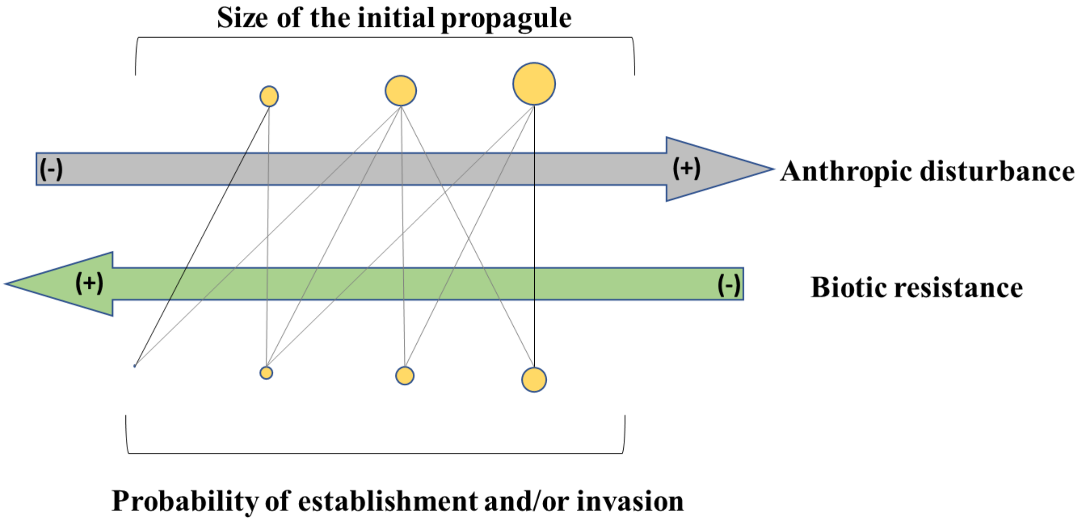

Figure 1. A general model of the invasion process. The probability of establishment or magnitude of invasion of the exotic species would depend on the initial size of the propagule, the anthropic disturbances, and the level of biotic resistance.

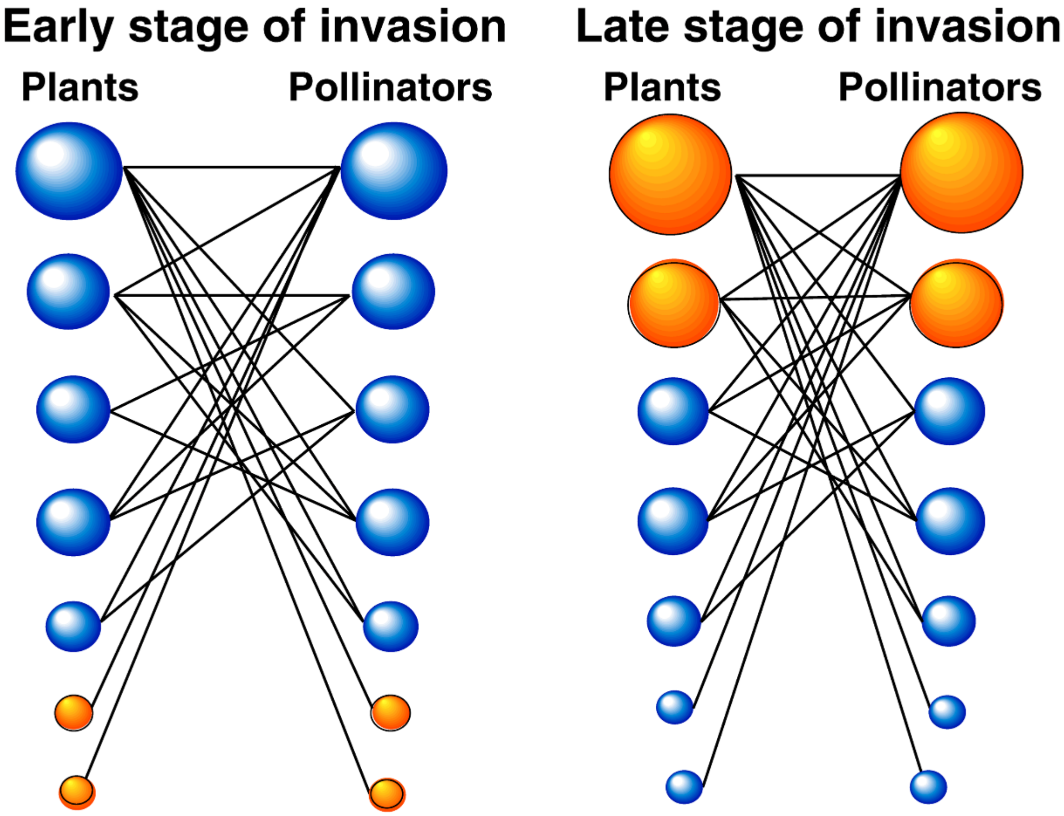

Figure 2. Plant–pollinator webs containing native (blue) and exotic (orange, dark outline) species, during the invasion process (Aizen et al., 2008; Tylianakis, 2008). The size of the circles is proportional to the interaction frequency of a species, which is highly influenced by its abundance. At the beginning of the invasion process (left web), exotic species are found in low abundance, interacting preferentially with native species. At the end of the invasion process (right web), the exotic species have become highly abundant. Exotic plants become highly attractive by virtue of their abundance, and exotic generalist pollinators are found to forage indiscriminately across plant species. Note that the “super-generalist” exotic species (top right) interact more frequently (have larger circles) than the native generalists (top left). (Figure courtesy of M. Aizen)

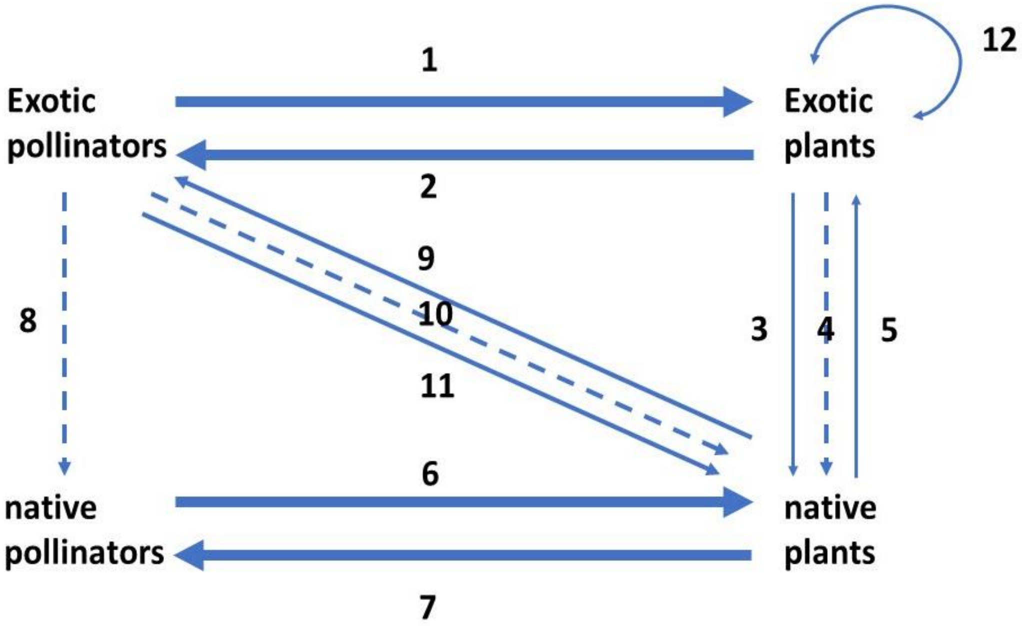

Figure 3. Different forms of interaction between invasive and native species in the pollination context, based on Simberloff & Von Holle1999 and Traveset and Richardson 2006. Arrows represent positive interactions while segmented arrows represent negative interactions. The thickness of an arrow indicates the magnitude of the action; 1and 2 is a mutual beneficial interaction between exotic pollinators and exotic plants, an invasional meltdown by Simberloff and Von Holle (1999), 3 and 5 is a beneficial mutualistic interaction between exotic plants and native plants, in some cases, some exotic plants could "maintain" several pollinators that at the community level would be beneficial for native plants; 4 is a negative interaction of an exotic plant species over native one, 6 and 7 is a mutually beneficial interaction between native pollinators and native plants, 8 is an interaction between exotic and native pollinators (documented only negative relationships), 9 and 11 is a beneficial interaction between exotic pollinators and native plants the

outcome of which would be an exotic pollinators would replace the native pollinators, 10 is an antagonistic interaction of exotic pollinators towards native plants which could disrupt pollination of native plants due to a morphological mismatch or resource robbery, and 12 is a beneficial interaction of exotic plants with other exotic plants.

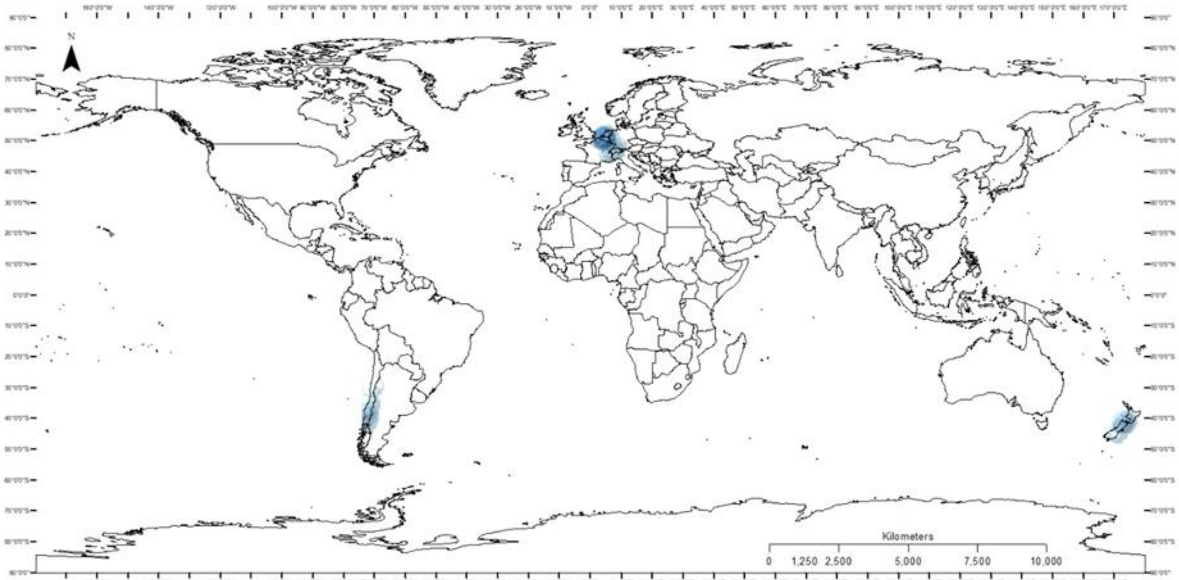

Figure 4. Global *Bombus ruderatus* distribution based on GBIF (2021) and Salvemos Nuestro Abejorro citizen science data.

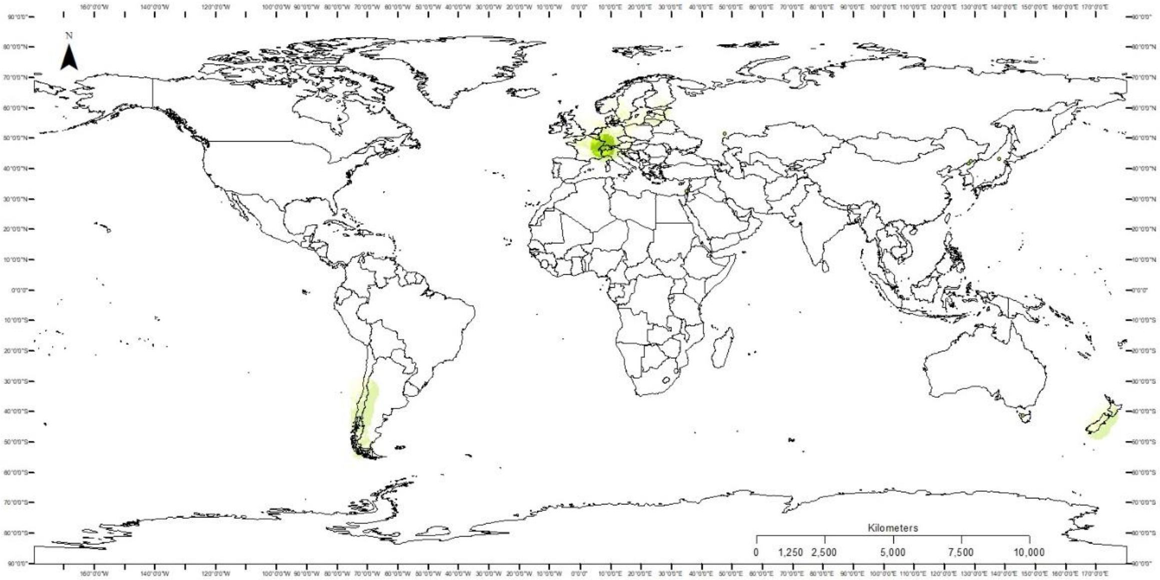

Figure 5. Global *B. terrestris* distribution based on GBIF (2021) and Salvemos Nuestro Abejorro citizen science data.

Figure 6. Left to right *Bombus terrestris* (European buff-tailed bumble bee) and *Bombus dahlbomii* (giant South American bumble bee). Picture Alvaro Becerra.

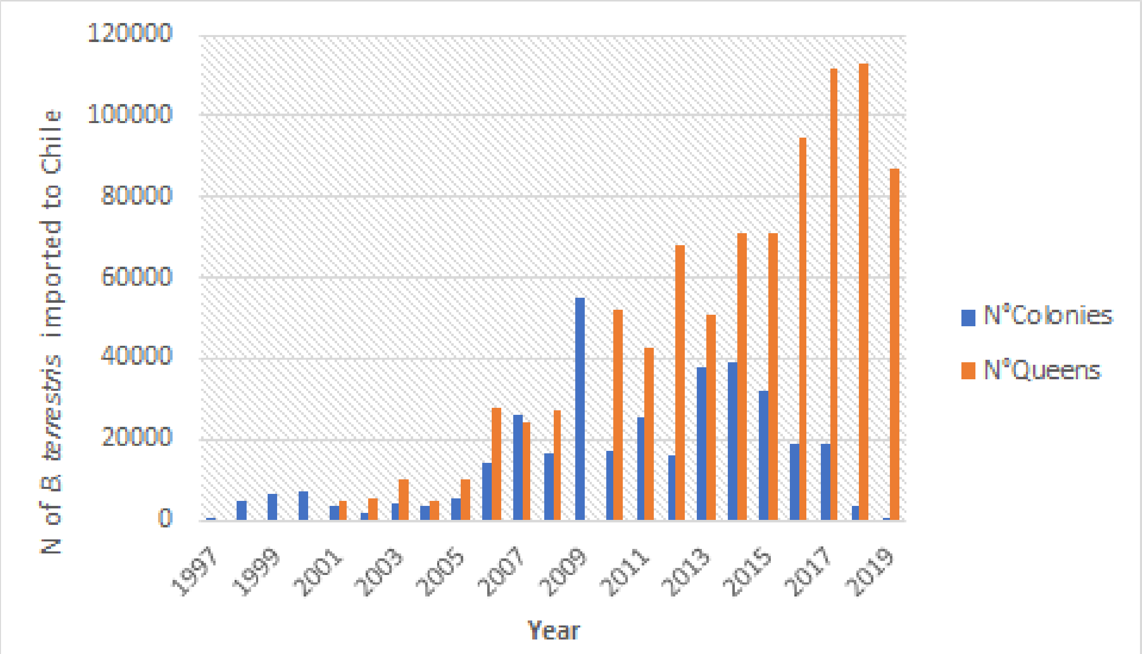

Figure 7. The number of colonies and queens of *Bombus terrestris* imported to Chile between 1997-2019. Edited from Aizen et al. 2019 and updated SAG 2019.

Chapter 2: Use of Citizen Science for data collection of the European bumble bees *Bombus terrestris*, *Bombus ruderatus*, and the endangered native species *Bombus dahlbomii* in Chile.

Abstract

In the past decade citizen science has become an essential tool for collecting data in research programs worldwide. Citizen scientists can collect significant quantities of data in a short period. Because citizen scientists are typically volunteers, this form of data collection is also cost-effective. And citizen scientists have proven effective in finding rare organisms, native or invasive species, and documenting declines in species populations. Although citizen science data can generate substantial quantities of data, it is not always quality data. Many online citizen science platforms accept photos as the primary data source, which requires careful vetting to assure accurate identification. Salvemos Nuestro Abejorro, is a citizen science project in Chile. Between 2014-2020 we collected over 5000 records of bumble bee species in Chile. Only 4302 were considered valid after vetting, but the result was 1875 records of the native bumble bee *B. dahlbomii*, and 2196 records and 231 records were for the introduced species *B. terrestris* and *B. ruderatus* respectively. Citizen science data was not consistently distributed geographically but trended to cluster in urbanized/highly populated areas. A drawback, however, is that the available citizen science records lacked density data, which is necessary for determining population trends. Our citizen science project is a successful tool for increasing collect data that will inform the conservation status of the native endangered species *B. dahlbomii* and the invasion rates of *B. ruderatus* and *B. terrestris*.

Keywords: Pollinators, community science, species distribution, invasion.

Introduction

Early ornithology and astronomy pioneered citizen science projects over a hundred years ago (Dickinson et al., 2010). In the last decade, however, the easy access to cameras, cellphones, apps, and social media, has helped numerous citizen science projects flourish (Conrad & Hilchey, 2011; MacPhail & Colla, 2020; Newman et al., 2012). These initiatives provide researchers data from locales that might not otherwise be accessible, such as private lands (Bonney et al., 2009; Chandler et al., 2017; Koffler et al., 2021; Olivier et al., 2016; Pocock et al., 2014; Tweddle et al., 2012), and potentially creates engagement between the public and professional scientists (Koffler et al., 2021; MacPhail & Colla, 2020; Pocock et al., 2014; Tweddle et al., 2012). Citizen science appears particularly effective at finding unique organisms such as previously unreported invasive species or rare native species (Chandler et al., 2017; Dickinson et al., 2010; MacPhail et al., 2020; Soroye et al., 2018; Tweddle et al., 2012). In general, a citizen science project follows a schema in which (1) citizen scientists take photographs and/or collects data for a target species, (2) images and data are uploaded to an online platform, (3) the identification of the photographed species is verified by a specialist, and (4) if the data are verifiable, they are uploaded into a database. Although this schema varies by project, each step presents unique challenges that require careful consideration.

For all citizen science projects, step one is the most limiting. Many projects fail because they do not engage enough people (MacPhail & Colla, 2020; Pocock et al., 2014; Viana et al., 2020). Project managers often develop activities to overcome a deficiency in the number of observers (Viana et al., 2020). The remaining steps, however, face challenges that can consume the time of researchers. The success of citizen science has led to the proliferation of online platforms for submitting data, which is arguably a byproduct of step two. Specialized platforms can be more time effective for data collection but may not be attractive to users or prove less cost-effective. In recent years, iNaturalist has become the dominant platform for citizen science data collection (Chandler et al., 2017), though some argue it is crowdsourcing more so than citizen science (Pocock et al., 2014; Tweddle et al., 2012). Nevertheless, iNaturalist is engaging people by providing well-curated data (i.e., numerous specialists are engaged in the vetting of identifications), cost-free, and informative. Global Biodiversity Information Facility (GBIF) now accepts vetted iNaturalist records (Chandler et al., 2017; Koffler et al., 2021).

Vetting data and verifying identifications, as noted in step three, presents several challenges. The number of records being submitted far outweighs the number of experts available to verify identification. This situation is exacerbated by the decreasing number of taxonomic specialists (Coleman & Radulovici, 2020; Drew, 2011; Mace, 2004). For some taxa such as insects, not only is a group specialist required, but photos may not feature the characteristics necessary to confirm an identification (Falk et al., 2019; Kadoya & Washitani, 2010; Kremen et al., 2011; MacPhail et al., 2020; Suzuki-Ohno et al., 2017). Artificial intelligence may help with the verification and processing of this issue (Spiesman et al., 2021; Suzuki-Ohno et al., 2017).

The products of these efforts yield baseline data and raw data for analysis by researchers. Often data are gathered from multiple platforms that may have disparate goals and assumptions. Although data assembled from multiple sources may appear to adhere to comparable data standards, this may not be the case, so further vetting and normalization are required. For example, some databases ingest or aggregate data from multiple sources. When using data from an aggregated source, it is necessary to determine if and how many duplicate records are present. Poorly conceived data-mining projects can lead to inaccurate or misleading results. And all results must be interpreted in the context of species biology (Dickinson et al 2010).

Salvemos Nuestro Abejorro was initiated in 2014 and is one of the first citizen science projects in Chile (Fundacion Ciencia Ciudadana, 2018; Grez et al., 2020; Roy et al., 2017). With over 9000 members across different platforms (Facebook, Twitter, Flickr), the prime objective of Salvemos Nuestro Abejorro is to collect distribution records for three bumble bee species in Chile: *Bombus dahlbomii, B. ruderatus*, and *B. terrestris*. The latter two are non-native. The program is similar to projects like Bumblebee Watch (USA), Bumblebee Conservation Trust (UK), Hanamaru-Muruhana (Japan), and others.

Here we will analyze data obtained by Salvemos Nuestro Abejorro to determine the utility of citizen science data for monitoring these three bumblebee species. We compare the records derived via citizen science with traditional museum records to determine how citizen science complements the work of professional ecologists and taxonomists.

Material and Methods

Data Platform

Since its inception, Salvemos Nuestro Abejorro has collected citizen science data in the form of photographs from the social media platforms Facebook (https://www.facebook.com/groups/456701147797736) and Twitter https://twitter.com/SNAbejorro?s=20), which are then uploaded to Flickr (https://www.flickr.com/groups/dahlbomii/). Prior to upload, the photos were carefully vetted for correct identification and the inclusion of relevant data (date, place, coordinates, caste, predators, floral association, etc.). Fortunately, *Bombus dahbomii* possesses bright, orange-colored hairs covering the whole body that permits easy recognition and distinguishes it from the invasive bumble bees *B. terrestris* and *B. ruderatus*. *B. terrestris* can be differentiated from *B. ruderatus* by the pattern of color bands, and a heart-shaped (as opposed to long) face (Montalva et al., 2011). Once the identification was verified, the record was reviewed for the presence and quality of spatial data. Only records that were accompanied with coordinates pairs or possessed a locality description from which coordinates could be derived using google maps, were retained for further analysis.

The vetted data were used to map the distribution of the three species of bumblebees using ArcMap10.7.1. We then analyzed whether the records were distributed equally throughout Chile or whether they were clustered spatially. We then analyzed differences within regions and by regional population per capita. Data were analyzed using sp, spatstat, raster, maptools, rgeos, GISTools in RStudio (R Development Core Team 2018). To determine whether citizen science data contributed significantly to our knowledge of bumblebee distributions, we pooled all museum records and citizen science) and performed a $\chi2$ test using the package ggplot2 on RStudio. A $\chi2$ test was used to test if the records were collected equally between sources and among species or if they differed.

Results and Discussion

Pros of citizen science on the bumble bee data collection.

The citizen science data provided new and updated location information for the distribution of the three bumble bee species. The records corresponded with the known, historical distribution for the native *B. dahlbomii* (Montalva et al., 2011). Records for the introduced species *B. ruderatus* and *B. terrestris*, however, demonstrated how the distribution of these species has changed over time, and illustrated their spread in Chile (Figure 2).

From 2014 to 2020 Salvemos Nuestro Abejorro collected over 5000 bumble bee records of which 4302 were determined to be valid. The leading cause for rejecting a record was the absence of coordinates and the lack of sufficient locality information to geocode the data. Of the 4302 valid records, 1875 were for the native bumble bee *B. dahlbomii*, and 2196 for *B. terrestris*, and 231 for *B. ruderatus* (Figure 3). A comparison of the Salvemos Nuestro Abejorro records with the museum data reveals the efficacy of citizen science; 1875 *B. dahlbomii* records were collected in only six years as opposed to 1817 records of museums collected over 200 years (Figure 3). Also, the citizen science records yielded many new localities (Montalva et al 2017; Rendoll-Carcamo et al 2017). The $\chi 2$ analysis of citizen science data and museum records for *B. ruderatus* (112 museum versus 231 citizen science records, Figure 3) and *B. terrestris* (43 museum versus 2196 citizen science records, figure 4) revealed these differences to be significant ($\chi 2 = 1446.7$, df = 2, p-value < 2.2e-16). The disproportionate number of exotic species recorded by citizen scientists could be the product of 1) the relatively recent introduction of these species and/or 2) an attitude among some scientists that since the species are not part of the native fauna, collections should not be deposited in official repositories.

Engaging citizen scientists in data collection to understand environmental problems (e.g., water quality, noise pollution, plastic contamination, etc.) has developed rapidly (MacPhail & Colla, 2020; Pocock et al., 2014; Tweddle et al., 2012). The perceived advantage is that scientists gain broader coverage for data collection and citizen scientists are exposed to research methodologies. The outcome is tangible and may result in an informed populace (Koffler et al., 2021; MacPhail & Colla, 2020). For example, Salvemos Nuestro Abejorro records were used to petition the Ministerio de Medio Ambiente of Chile for inclusion of *B. dahlbomii* on its Red List in 2015 (Montalva et al., 2015). A campaign was also initiated to collect signatures in support of the listing, resulting in 2868 signatures in one month. In 2019 a similar campaign was started requesting that the Chilean government stop importations of *B. terrestris.* 5673 signatures were collected. There is also a lawsuit pending to force the Chilean government to stop the importation of *B. terrestris,* which is led by the Chilean scientist Dr. Smith-Ramirez and is supported by the Chilean Society of Ecology.

As noted earlier, there is a reciprocal exchange of knowledge between citizen scientists and professional scientists (Koffler et al., 2021; Pocock et al., 2014; Tweddle et al., 2012). Dedicated amateurs can develop explicit knowledge of populations and the ecology of organisms in their surrounding (Dickinson et al., 2010). It was through such reciprocity that Salvemos Nuestro Abejorro learned of local use and consumption of bumble bee honey from people that collected bumble bee honey in the forest. At first, these stories were considered anecdotal, but as reports continued, further investigation revealed that the Native Chilean Mapuche people harvested and used bumble bee honey as a source of food, medicine, and sacred rituals (Montalva et al, 2020).

Cons of the citizen science on the bumble bee data collection.

For a better understanding of the patterns revealed by the citizen science collection, we only selected photographs from 2010-2020. Citizen scientists started to submit fewer pictures of the more abundant species, *Bombus terrestris,* but started to submit more pictures of the rare species *B. dahlbomii* over time. We attribute this behavior to the fact that *B. dahlbomii* is a native and charismatic bee that draws the attention of citizen scientists. On the other hand, sharp decline in records for *B. terrestris,* the more abundant species, was because it is not a native or charismatic species (Figure 6).

These analyses confirmed another shortcoming of citizen science: the number of bumble bee observations corresponded positively with the number of observers in an area (Tracy et al., 2019). Although the density of the human populace alone does not account for these relationships, the resources, and technologies available in urban areas facilitate the submission of occurrence reports to online platforms (Tracy et al., 2019). This technology bias can create misleading interpretations. For example, visually the mapped records imply there is a greater density of individual bumble bees in urban environments, however, the data demonstrate an even distribution of bumble bees from the central to southern Chile. A disjunct record from the Atacama Desert, however, suggests that bumble bee populations may extend further north than anticipated. Further investigation revealed that the record was from an agricultural facility where the bees had been imported (Montalva et al., 2017) (Figure 7A). When we review citizen science records on a per capita basis, records are still focused on the central and southern portions of Chile, even though the capital Santiago has fewer records proportionally (Figure 7 B). Overall, our data do not show the pattern “more people more data” by region (Figure 7 A, B).

Conclusion

Overall, Salvemos Nuestro Abejorro proved successful in collecting valuable species distribution data. Since citizen scientists were not required to identify the species (Falk et al., 2019; Kadoya et al., 2009; MacPhail et al., 2020; Suzuki-Ohno et al., 2017), a greater number of records over a shorter period of time were gathered than available from museums, particularly for the introduced species (Figure 4). Unlike other citizen science platforms, the data gathered by Salvemos Nuestro Abejorro did not exhibit a relationship between human population density (Figure 7 A, B), implying a uniform level of engagement in the project by citizen scientists. In the future, new techniques are needed to census bumble bee populations that are accessible to citizen scientists. Despite these results, the citizen science records lack species abundance data.

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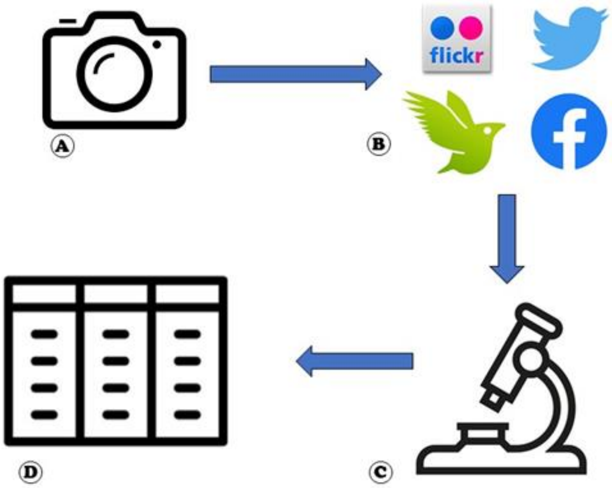

Figure 1. Diagram of the Citizen Science Model. A. Data collection by citizen scientists. B. Data upload to the different platforms. C. Data curation by experts. D. Data correctly curated are uploaded to the main database.

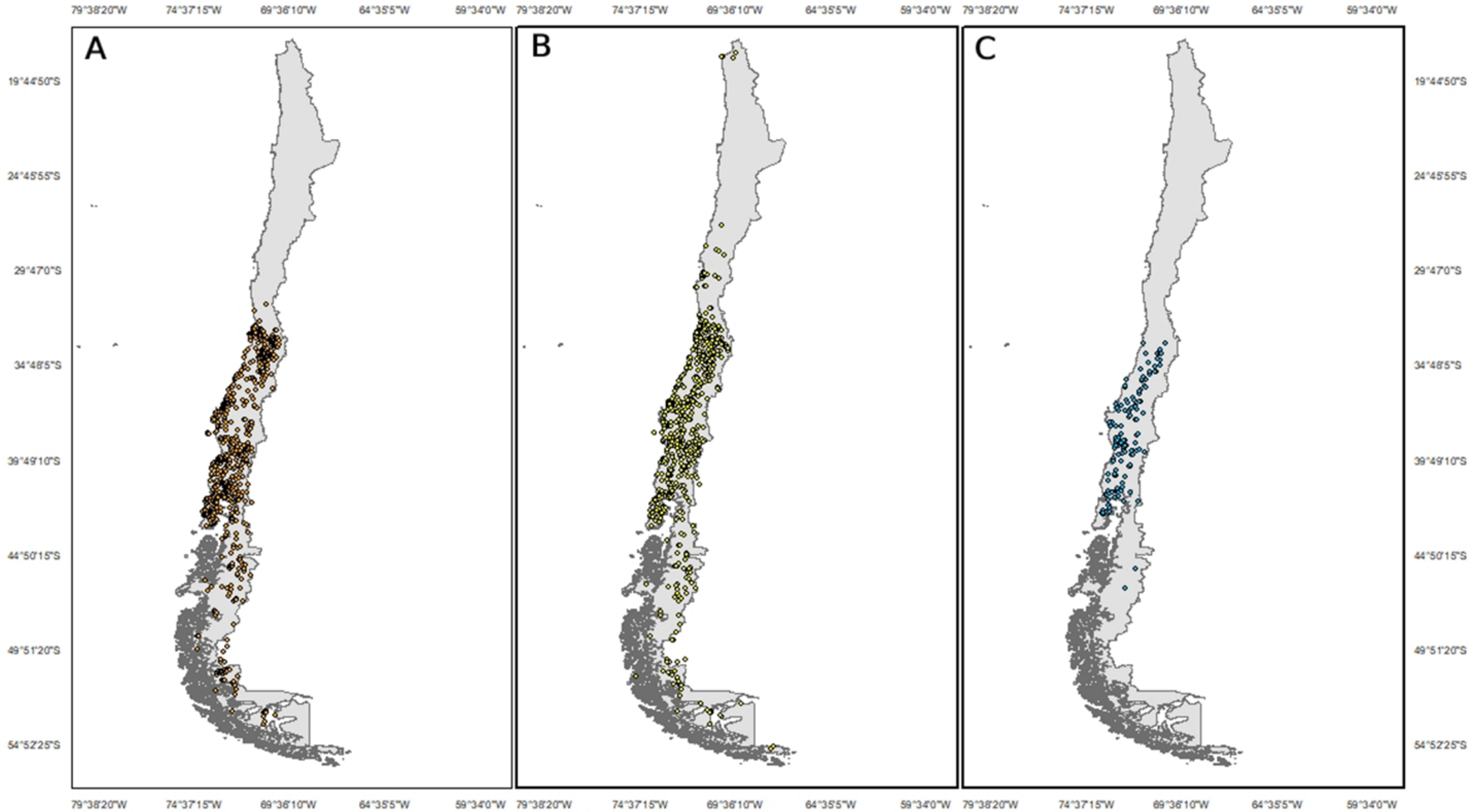

Figure 2. Distribution of the bumble bees present on Chile based in Citizen science reports. A.- *B. dahlbomii* B.- *B. terrestris* C.- *B. ruderatus*

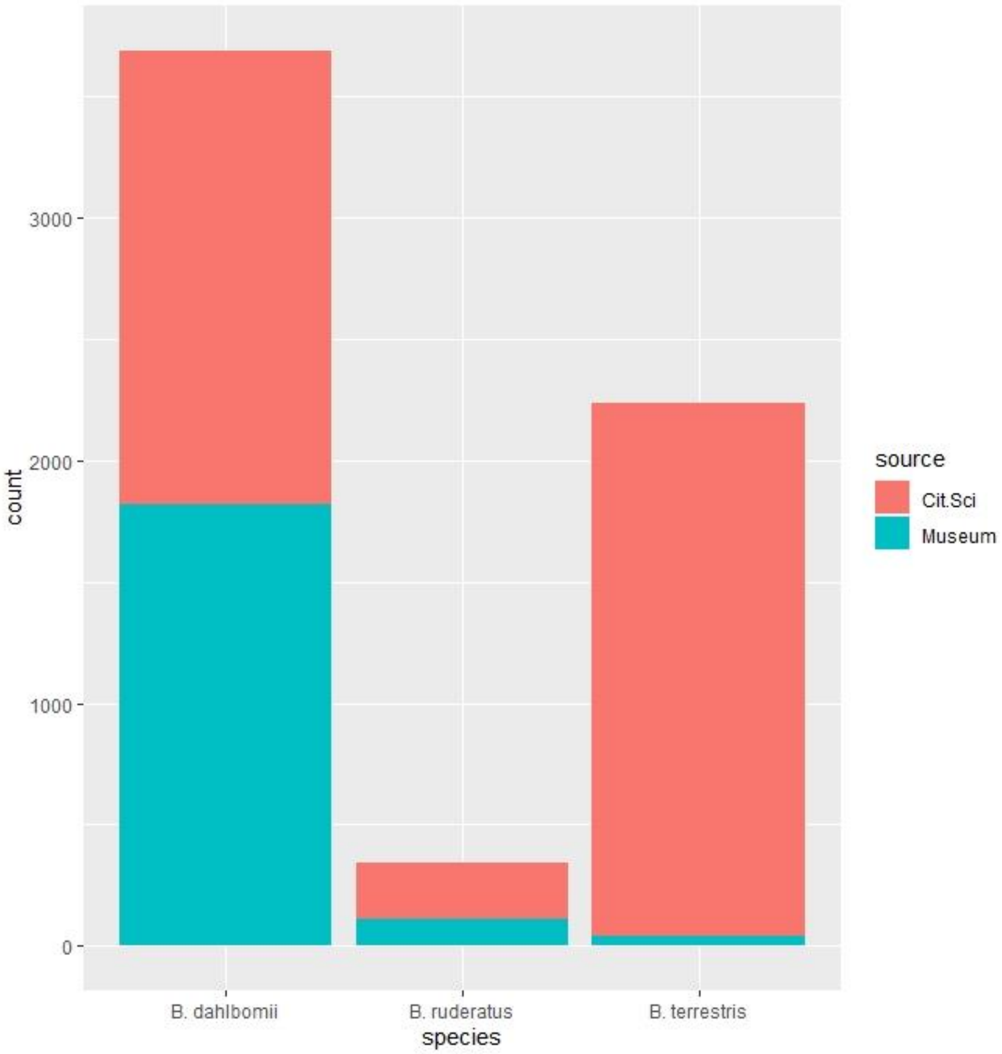

Figure 3. Comparison between the museum data and the bumble bee records from the citizen science project. *B. dahlbomii* 1875 citizen science records and 1817 museum records. *B. ruderatus* 231 citizen science records and 112 museum records. *B. terrestris* 2196 citizen science records and 43 museum records.

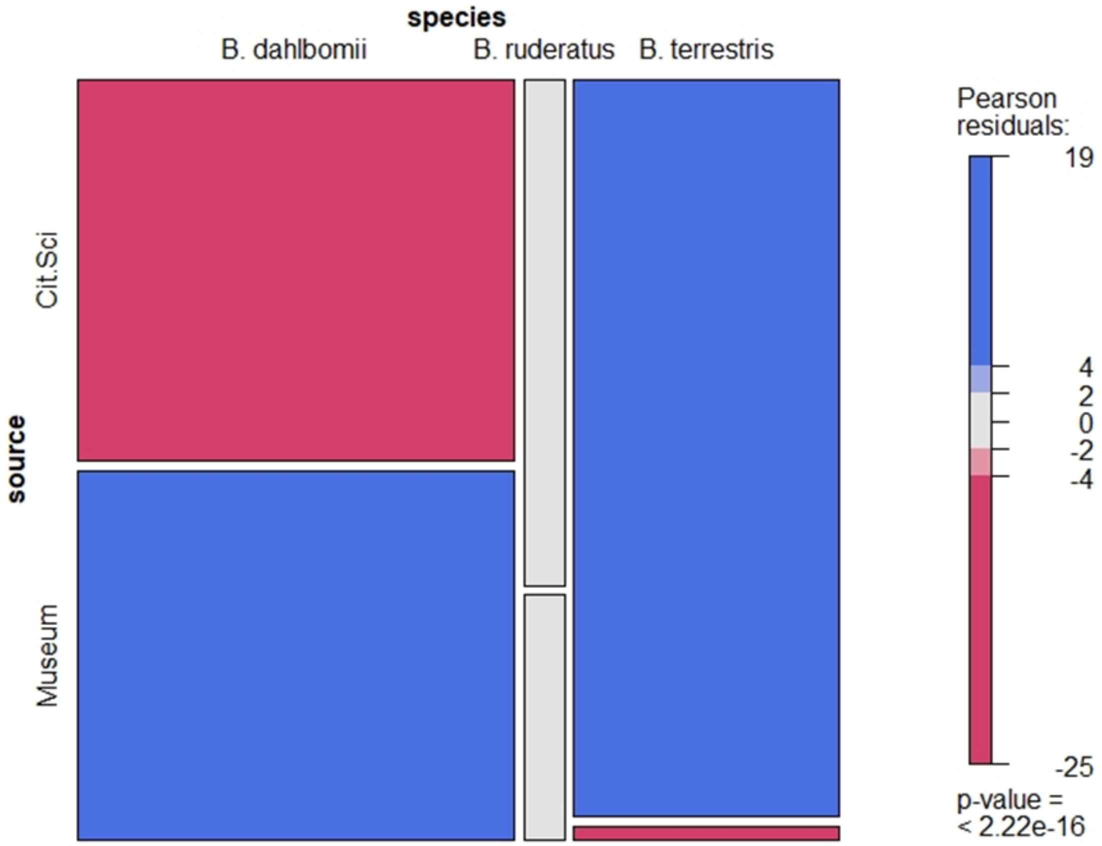

Figure 4. Mosaic plot comparing Citizen Science records vs Museum records for the three species of bumble bees present in Chile. The red cases mean that the observed frequencies are smaller than the expected frequencies, whereas the blue cases mean that the observed frequencies are more significant than the expected frequencies.

Figure 5. Salvemos Nuestro Abejorro at the first edition of “Dia de la Fauna Chilena” 2014.

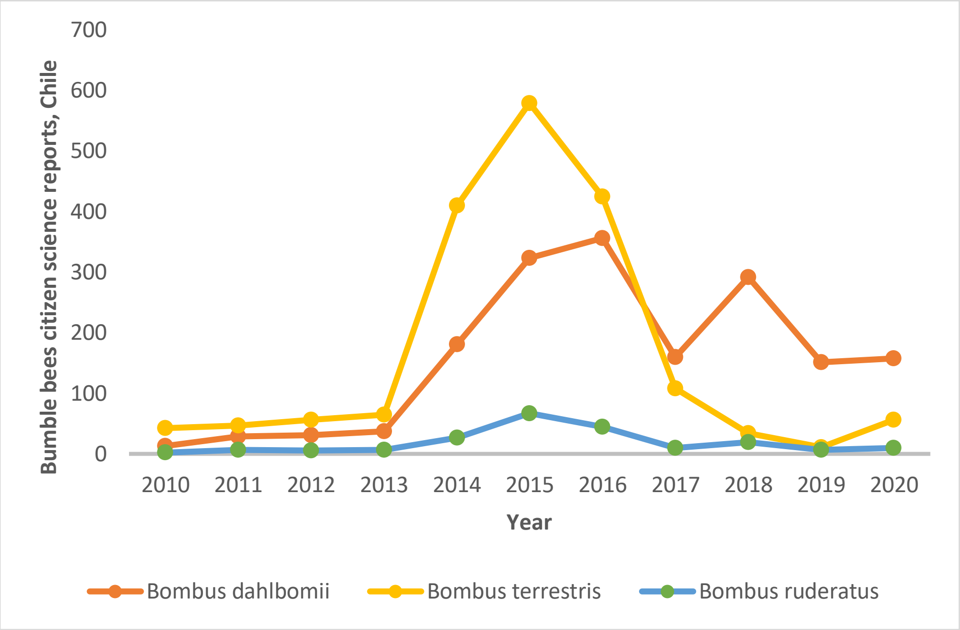

Figure 6. Bumble bee reports collected through Citizen Science between 2010-2020. A total of 44% of the reports in orange represent the native bumble bee *B. dahlbomii* (1875 records), 5% of the reports in blue represent *B. ruderatus* (231 records) and 51% in yellow represent *B. terrestris* (2196 records).

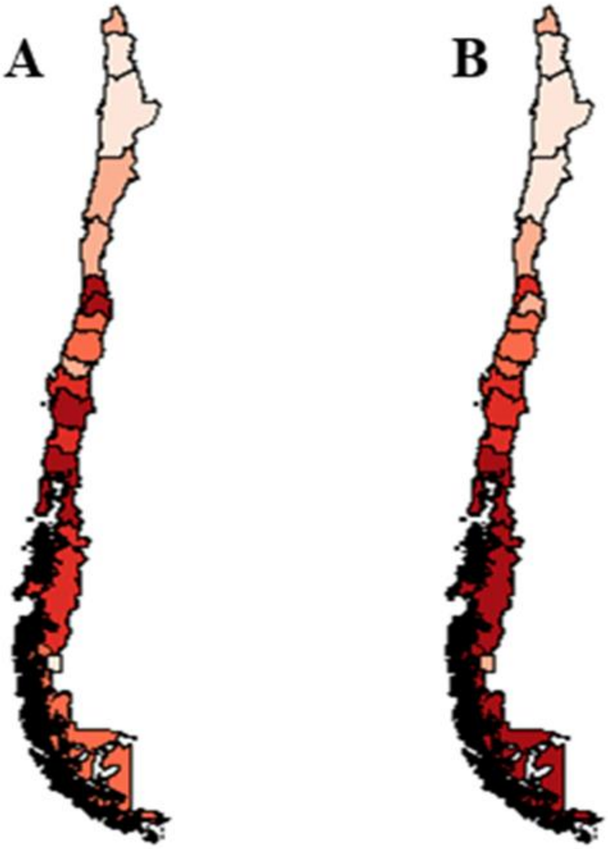

Figure 7. Bumble bee citizen science reports for the bumble bees present in Chile. A. by region. B. by region per capita.

Chapter 3: Modeling the distribution of native and invasive species of bumble bees (Hymenoptera: Apidae) in Chile, using citizen science data

Abstract

Bombus terrestris and *Bombus ruderatus* are invasive bumble bee species in South America. Several studies indicate that as a consequence of their introduction the populations of the Patagonian bumble bee *Bombus dahlbomii* are in sharp decline. Here, we gathered a comprehensive database of occurrence records from museum and citizen science sources. Multivariate bioclimatic niche analyses and species distribution models were used to determine if niche overlap occurred between the invasive and the native species. We also analyzed the potential effect of current and future climatic scenarios on the distribution of these bumble bees. From the results, we concluded that there was niche overlap between the three bumble bee species, and most significantly between *B. terrestris* and *B. dahlbomii* (61%). The current distribution for *B. terrestris* is extensive in South America but the models also show a shrinking distribution for *B. ruderatus* and *B. dahlbomii* in the pessimistic future scenario. We discuss the consequences of the niche overlap between the introduced bumble bee species and the endangered *B. dahlbomii*.

Keywords: Conservation biogeography, Distribution models, Pollinators, Niche overlapping.

Introduction

There are approximately 260 species of bumble bees (*Bombus*) globally (Michener, 2007). Although several provide essential pollination services (Cameron et al., 2011), most are experiencing declining populations (Arbetman et al., 2017; Cameron et al., 2011; Williams & Osborne, 2009; Goulson et al., 2008). One factor insinuated in the decline of bumble bees is the introduction of commercial congeners (Dafni et al., 2010; Williams et al., 2008). The worldwide trade in commercial bumble bee colonies for crop pollination has the potential for invasive, non-native bumble bees to adversely impact native pollinator populations (Dafni et al., 2010; Sutherland et al., 2017). Native bumble bees are biologically and ecologically more similar to introduced bumble bees than to non-*Bombus* native pollinators. Therefore, native *Bombus* species are expected to be more vulnerable to the potential negative impacts of the foreign species, either through disease transmission (Cameron & Sadd, 2020; Graystock et al., 2016; Meeus et al., 2011) or resource competition (Dafni et al., 2010; Morales et al., 2013).

In the past four decades, two European bumble bee species have been introduced in southern South America for crop pollination (Aizen et al., 2019; Montalva et al., 2011; Smith-Ramírez et al., 2018). *Bombus ruderatus* was introduced to pollinate *Trifolium pratense* (red clover), a livestock forage crop, during the 1982/1983 growing season. Approximately 400 queens were imported from New Zealand and released at two locations near Temuco (38^{o}S 72^{o}W), in southern Chile (Arretz & Macfarlane, 1986). In 1993, *B. ruderatus* was first reported in Argentina, and were likely the offspring of individuals in Chile (Roig Alsina & Aizen, 1996). *Bombus terrestris* is one of the leading commercially available species and has been introduced in several countries worldwide (Dafni et al., 2010; Kadoya & Washitani, 2010; Matsumura et al., 2004; Naeem et al., 2018). It was first introduced to central Chile in 1997 (Montalva et al., 2011), and more than a million individuals have been imported into the country since that time (Aizen et al., 2019; Smith-Ramírez et al., 2018). In 2006, it was reported as invading Argentina (Torretta et al., 2006). Both species now occupy an extensive territory in southern South American continent (Figure 1) and are associated with the sharp populational decline of the native and endangered bumble bee species *B. dahlbomii* (Montalva et al., 2015; Morales et al., 2013; Morales et al., 2016).

The objective of this research is to ascertain the ecological interactions of these three species over space and time. Specifically, we seek to answer the questions 1) is there extensive niche overlap among these *Bombus* species, 2) how might these relationships change based upon future climate scenarios, and 3) how might the results of these analyses inform us about the persistence of *B. dahlbomii* and the invasive behavior *B. terrestris* and *B. ruderatus*, To address these questions, we applied multivariate bioclimatic niche analyses (Broennimann et al., 2012) and species distribution models to evaluate the relationship between the distributions of the two European bumble bee species and the native *B. dahlbomii* and potential alteration of their ecological niche. Specifically, we calculated species pair-wise niche overlap in both geographic and climatic space to determine the threat posed by the European species on the native endangered species. Also, we used species distribution models to predict the current and future distribution for the three bumble bee species in South America.

Methods

Occurrence dataset

We gathered a comprehensive database of occurrence records for *B. dahlbomii, B. ruderatus* and *B. terrestris* from the Global Biodiversity Information Facility https://www.gbif.org/ (GBIF) and records from the Citizen Science initiative “Salvemos Nuestro Abejorro” (Save our Bumble bee; https://salvemosnuestroabejorro.wordpress.com/). From the GBIF dataset, we only used the museum records. We felt confident in adopting the citizen science data because the three species possess morphological characteristics that facilitate accurate identification by citizen scientists. For example, *B. dahlbomii*, the native species, is covered with bright orange-colored hairs, and can be recognized by Citizen Scientists with little or no training in bumble bee taxonomy (Falk et al., 2019; Montalva et al., 2011).

The existence of, or ability to attribute these to coordinate pairs is crucial for successful analysis. An occurrence record in our preliminary dataset was retained for further analysis if the record provided coordinates or if the locality string was sufficiently detailed to geocode a record using Google Earth. Dubious, unreliable, and duplicate occurrence records were discarded from the dataset. This process yielded 251 records for *B. ruderatus*, 885 for *B. terrestris*, and 321 for *B. dahlbomii* (Fig.1), for the preliminary dataset of 5307 records.

Data Analysis

Ecological niche overlap

To determine if and the extent to which similarities existed in the environmental space occupied by the three bumble bee species, we applied the analysis framework of Broennimann et al. (2012) to calculate potential niche overlap. The dataset for this analysis consisted of the 19 Wordclim bioclimatic variables (www.worldclim.org) for temperature and precipitation from 1950 to 2000 (Hijmans et al., 2005). We extracted a subset of these data by placing a buffer of ~ 100 km around the occurrence records for each species as a representation of their current bioclimatic setting. The data were compiled into a matrix and analyzed using a PCA to generate an environmental space (PCA-env in Broennimann et al. (2012)). For each species, we calculated the occurrence density within each cell of the environmental space grid. the occurrence density was then modeled using a smooth kernel density function that analyses the geographical conditions for each species (Broennimann et al., 2012). The species pair-wise niche overlap was then calculated using Schoener's D metric between the modeled occurrence density in the PCA ordination space (Broennimann et al., 2012; Schoener, 1970; Warren al., 2008). We tested for the significance of D by calculating the niche equivalency and similarity between the pairs of species (Broennimann et al., 2012) using the ecospat package (Di Cola et al., 2017) in R (R Development Core Team 2018) with code modifications in Silva et al. (2016).

Species distribution modeling

We adopted the methodology of Silva et al. (2019) for the analysis of current and future distribution scenarios for the bumble bee species. We used six different models in an ensemble approach: Generalized Linear Model (GLM), Random Forest (RDF), Maximum Entropy (MAX), Gaussian Model (GAU), Support Vector Machines (SVM), and Maximum Likelihood (MLK) (Silva et al., 2019). Models were evaluated using the Jaccard similarity index metric (Leroy et al., 2018), which measures the similarity between predictions and observations on a scale of 0 to 1 (where a value of 1 indicates that the model predictions are perfectly matched with the known observations of the species, and a value of 0 indicates that the models do not correspond to actual observations; Leroy et al., 2018). We used a threshold that maximizes Jaccard values in relation to the sensitivity and specificity values. Since similarity indices do not include true negative values, they are not biased by a disproportionate number of pseudo-absences. Also, we calculated the Area under the Curve (AUC) and True Skills Statistics (TSS) (Table 2).

Results

The first two axes of the PCA captured 71.39% of the variation in the climate dataset. The first axis (43.5%) corresponded to temperature variables and the second (27.89%) to precipitation. Considering that *B. terrestris* and *B. ruderatus* are native to Europe (Michener, 2007), the high niche overlap between these species (D*:* 0.672, Table 1) was anticipated. European bumble bee species, however, also exhibited niche overlap with the native species *B. dahlbomii*; 46% (D: 0.46) overlap with *B. ruderatus*, and 61% with *B. terrestris* (Figure 2, Table 1).

The models for *B. ruderatus*, *B. terrestris* and *B. dahlbomii* reached mean Jaccard values of 0.8544 ± 0.048, 0.8936 ± 0.03, and 0.9279 ± 0.008 respectively (mean ± standard deviation). For *B. ruderatus* MAX had the highest Jaccard value (0.918 ± 0.07), and RDF for *B. terrestris* (0.906 ± 0.009, Table 2). For *B. dahlbomii*, GAU (0.94 ± 0.008), RDF (0.943 ± 0.013) and SVM (0.943 ± 0.004) had comparably high Jaccard values. MLK performed poorly for all three species (Table 2).

In the current climate scenario, considering the final ensemble for the three species, the distribution of *B. ruderatus* extends mainly in the Mediterranean zone of Chile and parts of Patagonia (Figure 3, 4). The distribution of *B. terrestris* in the current climate scenario almost reaches the southern tip of continental South American (Figure 4), which covers a significant portion of the Chilean Mediterranean and most Patagonia, Argentina and Chile. The model also indicates expansion into Peru and Bolivia (Figure 4). For the future distribution ranges the three species show a similar pattern; all species would move toward southern Chile and Argentina (Figures 3, 4).

Discussion

Here, we showed that the potential distribution for three bumble bee species (two introduced, *B. ruderatus* and *B. terrestris,* and one native species, *B. dahlbomii*). Specifically, we evaluated both the spatial and multivariate overlap of both introduced and native bumble bee species using species distribution models and multivariate analyses. Our results show a high niche overlap between *B. ruderatus* and *B. terrestris* (D*:* 0.672, Figure 2, Table 1) which was expected given their geographic origin (Michener, 2007). Of concern, however, was the niche overlap between each of these species and *B. dahlbomii* (Figure 2, Table 1). These values indicate possible competition for resources between these species and *B. dahlbomii*, with *B. terrestris* as the likeliest threat (Arbetman et al., 2013; Arismendi et al., 2016; Madjidian et al., 2008; Morales et al., 2013; Schmid-Hempel et al., 2014). In some areas where the species distributions are allopatric, populations of *B. dahlbomii* exhibited a sharp decline (Morales et al., 2013; Morales et al., 2016). For this reason, a high niche overlap signals an increased threat to the persistence of *B. dahlbomii* (Morales et al., 2016).

The distribution maps implied that both introduced species, in the current scenario, could potentially migrate to and occupy an extensive area in South American (Figure 3, 4). Although *B. ruderatus* was more restricted to Patagonia, the distribution of *B. terrestris* moved north into Peru and Bolivia. Should this scenario unfold, *B. terrestris* would come into contact with populations of *B. funebris* and other pollinators with possible adverse outcomes for natives (Morales et al., 2017; Vanbergen et al., 2018). The models indicated areas suitable in the Mediterranean region of Chile for *B. terrestris* (Figure 4), which Acosta (2016) reported as a low probability likelihood.

The future scenario shows a decrease in the area occupied by the bumble bee species (Figure 4), especially *B. ruderatus* and *B. dahlbomii*. The models indicated that *B. ruderatus* will probably move toward southern Patagonia, while *B. dahlbomii* will likely disappear near the northern Mediterranean region of South America. This is consistent with the trend of European and North American bumble bee species that have experienced northward or high elevation shifts in distribution (Kerr et al., 2015). Also, in South America, *B. bellicosus* has shown declines in distribution due to climatic conditions (Martins & 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). Again, *B. dahlbomii* is already an endangered species facing competition for resources with their exotic congeners. For these reasons, *B dahlbomii* conservation programs and ban the importation of *B. terrestris* are essential.

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Table 1. Main results of the multivariate analyses, considering Schoener's D metric, and the p values obtained using the similarity test (I) of the climatic niche of the species. Bold values are statistically significant.

	B. ruderatus		*B. terrestris*		*B. dahlbomii*	
	D	*I*	*D*	*I*	*D*	*I*
B. ruderatus			0.67	**0.01**	0.46	0.059
B. terrestris	0.672	**0.01**			0.61	**0.02**
B. dahlbomii	0.46	0.059	0.61	**0.02**		

Table 2. Summary of the species distribution models obtained for GAU, GLM, MLK, MAX, RDF, and SVM algorithms. Values has standard deviation.

		B. ruderatus	*B. terrestris*	*B. dahlbomii*
GAU	AUC	0.951 ± 0.031	0.979 ± 0.005	0.991 ± 0.008
	TSS	0.808 ± 0.08	0.874 ± 0.012	0.938 ± 0.09
	Jaccard	0.819 ± 0.07	0.882 ± 0.011	0.94 ± 0.008
GLM	AUC	0.887 ± 0.03	0.891 ± 0.005	0.905 ± 0.01
	TSS	0.71 ± 0.032	0.765 ± 0.151	0.753 ± 0.058
	Jaccard	0.736 ± 0.026	0.787 ± 0.128	0.775 ± 0.047
MLK	AUC	0.5	0.5	0.5
	TSS	0	0	0
	Jaccard	0.5	0.5	0.5
MAX	AUC	0.977 ± 0.015	0.977 ± 0.0004	0.983 ± 0.007
	TSS	0.913 ± 0.003	0.874 ± 0.022	0.914 ± 0.043
	Jaccard	0.918 ± 0.07	0.88 ± 0.017	0.918 ± 0.039
RDF	AUC	0.955 ± 0.003	0.983 ± 0.003	0.984 ± 0.014
	TSS	0.851 + 0.084	0.905 + 0.01	0.941 + 0.014
	Jaccard	0.859 + 0.07	0.906 + 0.009	0.943 + 0.013
SVM	AUC	0.955 ± 0.02	0.962 ± 0.011	0.984 ± 0.007
	TSS	0.851 ± 0.082	0.857 ± 0.007	0.941 ± 0.004
	Jaccard	0.8594 ± 0.077	0.868 ± 0.007	0.943 ± 0.004

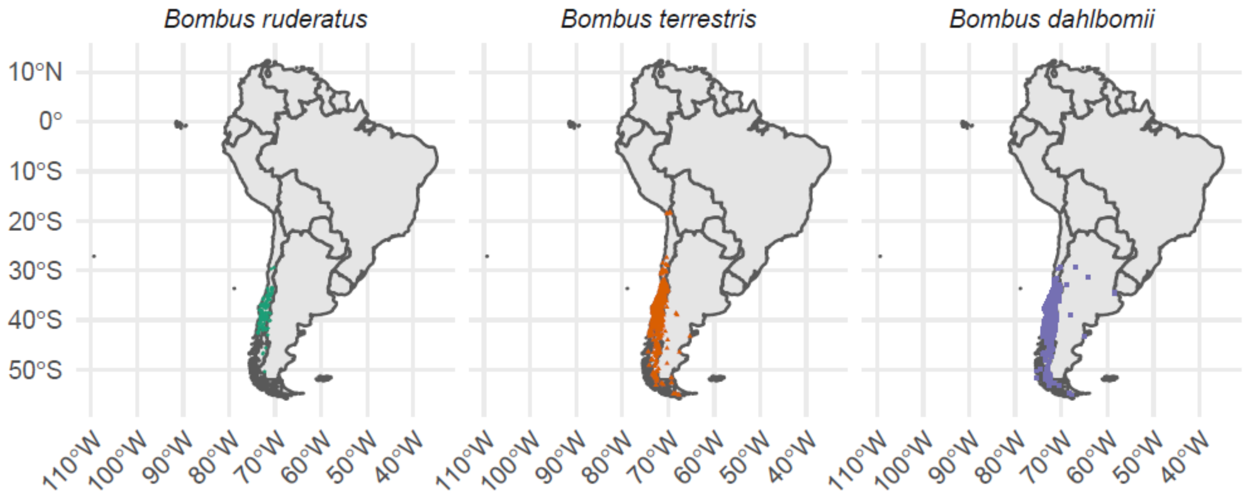

Figure 1. Geographic occurrences of *Bombus ruderatus*, *Bombus terrestris* and *B. dahlbomii* in South America.

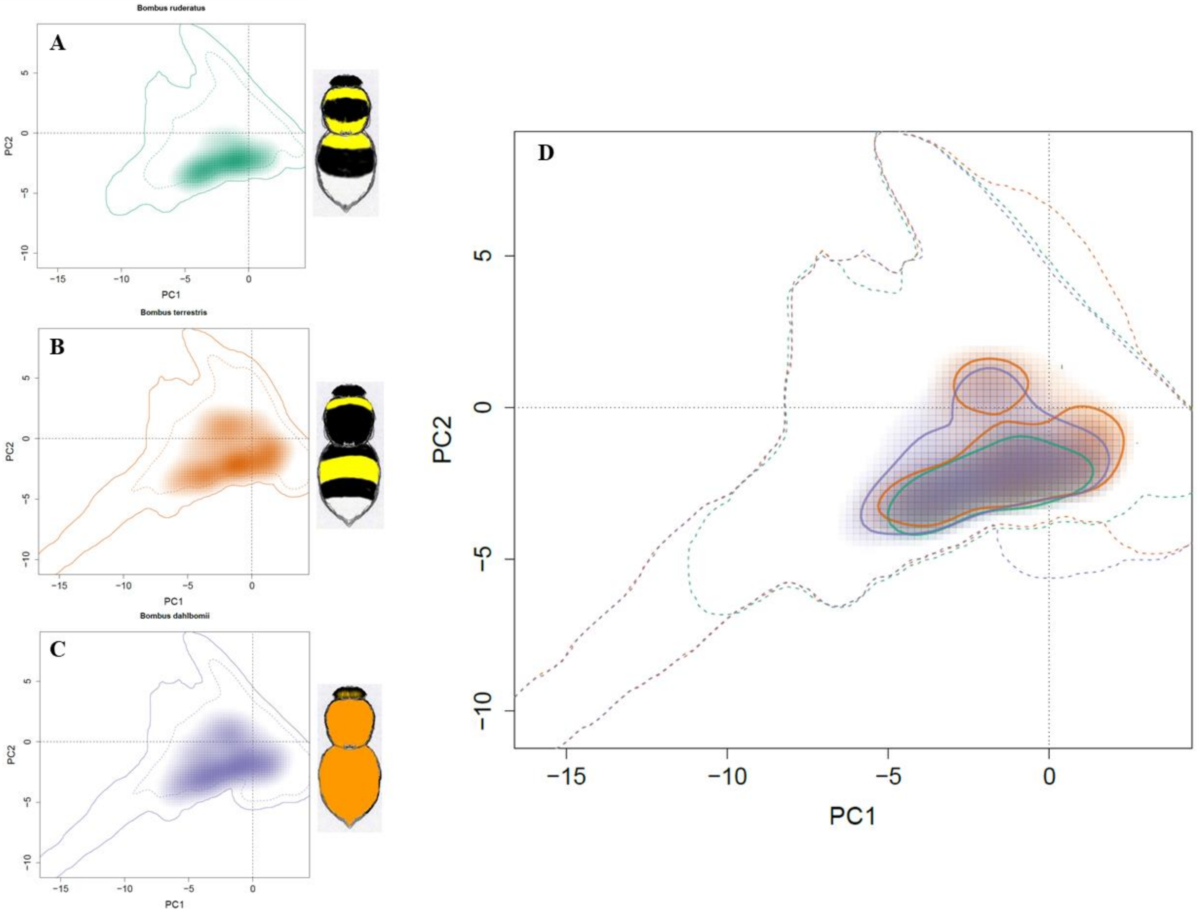

Figure 2. Climatic conditions occupied by A. *B. ruderatus* B. *B. terrestris* C. *B. dahlbomii* D. overlapping of all the three bumble bee species. Results obtained from the environmental niche analysis. The solid and the dashed lines illustrate, respectively, 100 and 50 % of the available (background) climate for each of the bumble bee species in each one of its ranges.

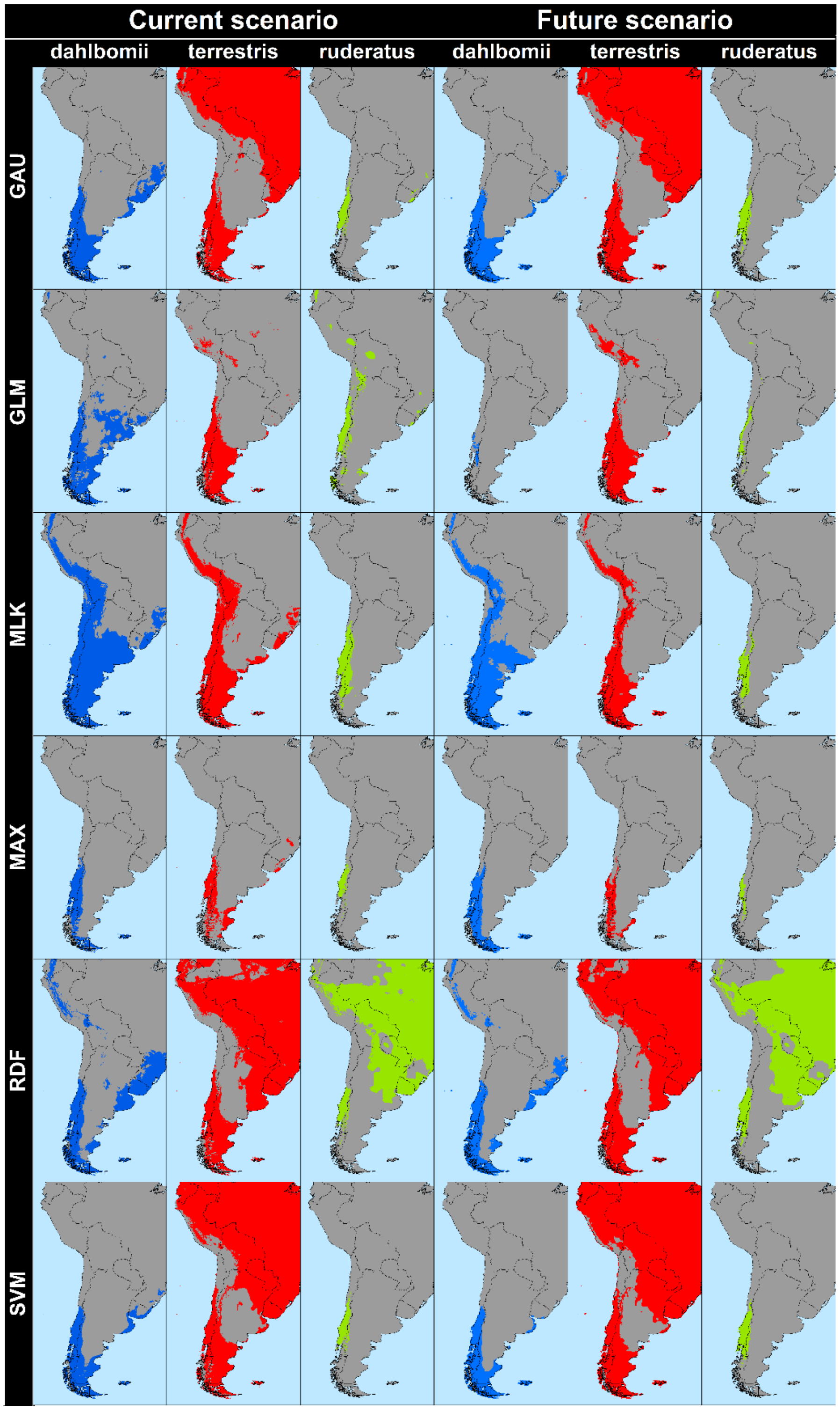

Figure 3. Species distribution models current and future scenario for the three bumble bees species based on GAU, GLM, MLK, MAX, RDF, SVM algorithms.

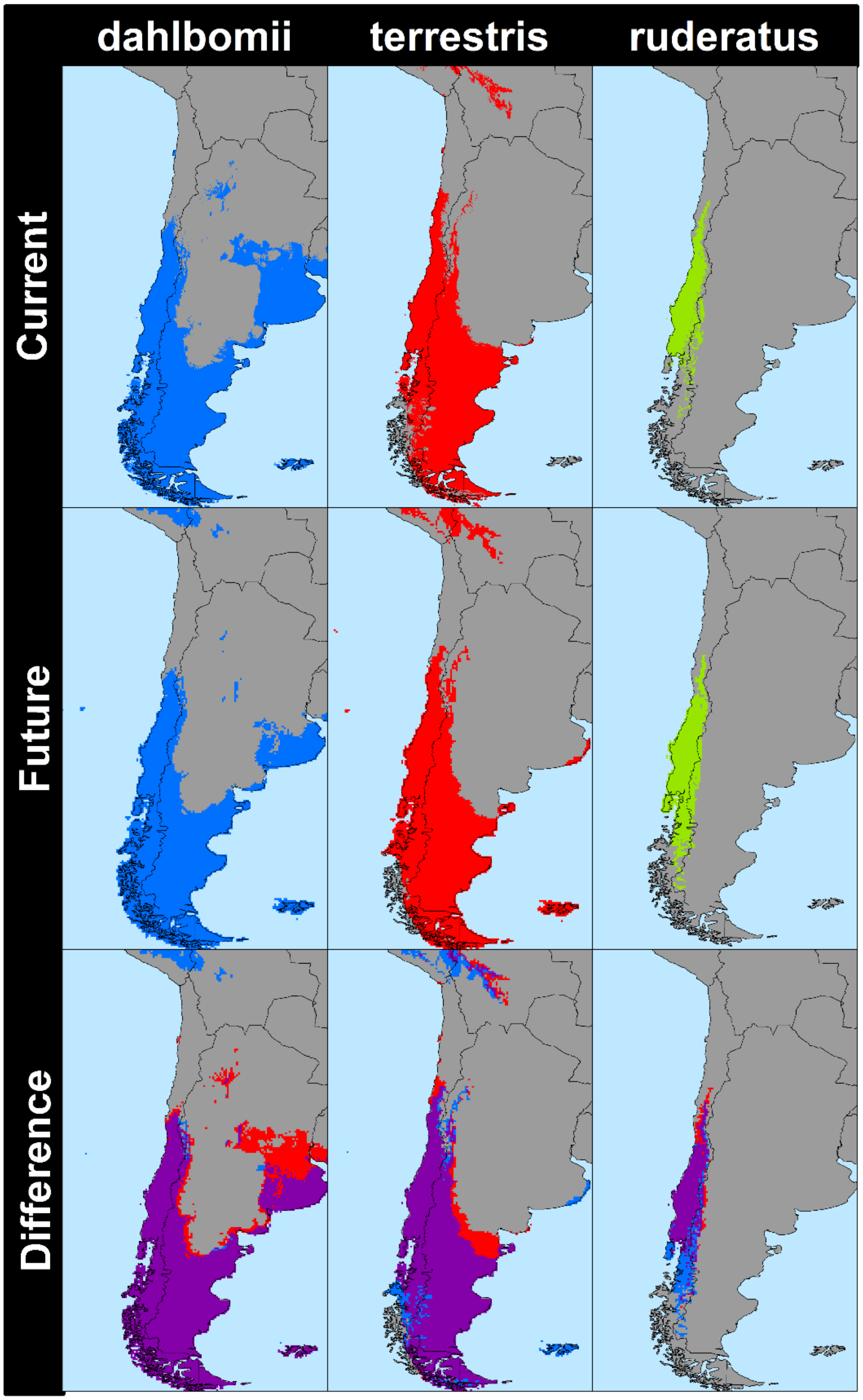

Figure 4. Summary of the species distribution models showing current, future and difference scenario for the three bumble bees species

Chapter 4: Conclusions

Despite decades of ecologic and biogeographic research, glaring gaps still exist in the types and quantity of data. Hortal et al. (2015) identified seven data “shortfalls” that challenge progress in ecologic and biogeographic research. This research has addressed two of those shortfalls. The Wallacean shortfall is the lack of data for the geographic distribution of a species or taxon (Whitaker 2005). Depending upon the extent of missing data, the repercussions for 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). The Hutchisonian is a “lack of knowledge about the response and tolerances of species to abiotic conditions” (Hortal et al. 2015). This thesis addressed these two shortfalls as related to three species of bumblebees: *Bombus terrestris* and *B. ruderatus,* both introduced species in Chile, and *B. dahlbomii,* a native species in jeopardy.

The traditional data sources for describing species distributions have been museum records, scientific observations, and published literature. But as noted by Hortal et al. (2015), as valuable as these sources are, they alone have not or cannot provide sufficient data for comprehensive distribution mapping. This research evaluated the veracity of citizen science data and examined its utility for mapping the distribution of these species and the impact of environmental change. The first research chapter utilized citizen science data collected by Salvemos Nuestro Abejorro, and represented over 5000 records of bumble bee species at different localities throughout Chile. The number of citizen science records surpassed the quantity of the museum records (n= 1972). Although museum records cover a longer temporal extent, the Salvemos Nuestro Abejorro provided a greater number of interannual records. The number of reports for the *B. terrestris* and

B. ruderatus, were 2196 and n=231 respectively. It was concluded that citizen science is particularly effective at documenting the occurrence in new or remote locales of both invasive organisms (in this case *B. terrestris* and *B. ruderatus*) or declining populations of the native species (*B. dahlbomii*), as reported in other studies (Chandler et al., 2017; Dickinson et al., 2010; MacPhail et al., 2020; Soroye et al., 2018; Tweddle et al., 2012).

The Hutchisonian shortfall can be addressed by experimental approaches or the use of multivariate tools to model the response of species to the abiotic environment. In the second research chapter, principal components analysis and species distribution models (SDMs) were employed to evaluate niche overlap and the impact of environmental change on *B. dahlbomii, B. ruderatus,* and *B. terrestris*). These models have proven effective for 1) spatial conservation prioritization (de Marco and Nóbrega 2011), 2) biogeographic analyzes (Siqueira and Durigan 2007), 3) measurement of Climatic change effects on biodiversity (Peterson et al. 2002; Martins et al. 2015; Silva et al. 2015), 4) conservation of rare and threatened species (Araujo & New 2007), and 5) the detection of areas suitable for occupation by exotic species (Silva et al. 2014; Acosta et al. 2016).

The results showed a high degree of niche overlap for the three species, with the implication that resource competition between the three species is intense and with the concern that *B. dahlbomii* could be displaced. Besides direct displacement for resources (e.g., nectar bearing plants, etc.) (Morales et al 2013; Smith-Ramírez et al 2018), exposure to pathogens due to the increased abundance of the invasive bumble bees is also a threat (Arbetman et al 2013; Schmid-Hempel et al 2014).

The SDMs revealed the likelihood that the three bumblebees could experience a decrease in range size and a shift southward in distribution due to warming conditions. In the worst case, populations of *B. dahlbomii* will be extirpated by environmental change, such as postulated for *Bombus bellicosus*, also a species of South American bumblebee (Martins & Melo, 2010; Martins et al., 2015). The shift in geographic range toward cooler conditions has been documented in North American and European bumble bees (Kerr et al., 2015).

The use of citizen science was highly effective in overcoming a dearth of distribution data and thereof proved to be of great utility in the analyses conducted in this thesis. In fact, the Salvemos Nuestro Abejorro approach is being expanded to track the distribution of *Hylaeus euxanthus* (Montalva et al 2019), *Xylocopa augusti* (Montalva et al 2013) and *Anthidium manicatum* (Montalva et al 2015), all recently introduced to Chile.

Citizen science in combination with SDMs were effective tools for tracking the distribution patterns of the endangered *B. dahlbomii* and the introduced species *B. ruderatus* and *B. terrestris*. The information gathered here could and should be used in future International Union for Conservation of Nature (IUCN) Red List assessments for the *B. dahlbomii.* In addition to contributing to the IUCN assessment, a GAP analysis of protected areas for *B. dahlbomii* based on citizen science data would assist in the identification and protection of crucial habitats.

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