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Research Article

Silent takeover: How invasive bees reshaped plant-pollinator interactions in a biodiversity hotspot

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Abstract

Biological invasions are a major driver of biodiversity loss. Invasive pollinators can reshape native plant-pollinator networks. This study, taking Chile as an example, is divided into two parts. First, we assessed the impacts of three non-native pollinator species (*Apis mellifera*, *Bombus terrestris* and *Bombus ruderatus*) using over 2,100 records from scientific literature (including historical data) and citizen-science databases. Interactions were classified by plant origin (native or non-native) and analysed to characterise species roles. We found that *B. terrestris* dominated the interactions (73%), primarily with non-native plants and all three species exhibited generalist interaction patterns. Then, we evaluated the impact of *B. terrestris* on bee-plant interactions by building bipartite networks representing periods before and after 2005, when *B. terrestris* began to be used in open fields. We analysed network metrics including nestedness, specialisation, modularity and core-periphery structure, revealing that *B. terrestris* increased interaction frequency, displaced native species such as *Bombus dahlbomii* and contributed to a more nested, but less specialised network. Overall, our findings reveal that invasive bees silently, but profoundly reshape pollination networks – displacing native pollinators, reducing interaction specialisation and shifting systems towards homogenised structures that threaten native plant-pollinator mutualisms.

Key words: Biodiversity loss, biological invasions, citizen science, introduced pollinators, interaction networks, invasive species

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Introduction

Biological invasions pose a major threat to biodiversity, impacting native fauna through mechanisms, such as habitat disturbance, resource competition (Siddiqui et al. 2021) and the spread of pathogens and parasites (Goulson 2010), ultimately driving native species extinction (Clavero and García-Berthou 2005; Vieli et al. 2021). In particular, the introduction of non-native bees has resulted in indirect ecological consequences related to plant pollination (Vieli et al. 2021). Originally brought in to enhance crop productivity and honey production, exotic bees have spread beyond their intended use, establishing populations in new environments (Ghisbain et al. 2021), including species dispersing across large areas and widely affecting native ecosystems (Ruz 2002; Ortega et al. 2014; Valido et al. 2019). The balance between agricultural benefits and conservation concerns continues to be a critical challenge, as these introduced pollinators compete with native species (Prendergast et al. 2025) and modify local biodiversity (Ruz 2002). For example, native pollinators and their interactions with native plant species can be lost due to the introduction of honeybees *Apis mellifera*, which can significantly reduce the diversity of native pollinators and reshape plant-pollinator networks in their introduced ranges (Valido et al. 2019; Page and Williams 2023). Despite their value as effective crop pollinators, their excessive abundance can negatively impact general plant reproduction and even agricultural production (Aizen et al. 2020).

Both introduced honeybee and invasive bumblebees can alter ecological interactions by harming the pollination of highly specialised plants (Scaccabarozzi et al. 2024). Specifically, invasive bumblebees disrupt plant reproduction (Chalcoff et al. 2022), ultimately altering pollination services as they displace native bees (Rego et al. 2021). Similarly, *Apis mellifera* has led to monopolisation of floral resources, simplifying plant-pollinator interactions and reducing seed production in plants previously visited by native or endemic pollinators (Valido et al. 2019). These effects may be especially intense on islands or largely isolated ecosystems, which are particularly vulnerable due to their relatively depauperate and endemism-rich biodiversity (Valido et al. 2019). These studies highlight the need to prioritise isolated ecosystems as model systems for understanding the effects of exotic pollinators on native bees.

Chile (South America) can be considered a biogeographical island, with natural barriers, such as the Andes Mountains, the Atacama Desert and the Pacific Ocean heightening its biota isolation (Scherson et al. 2017), making its ecological dynamics somewhat similar to an "island". Moreover, Chile exemplifies the complex trade-off between agricultural expansion, economic development and conservation efforts. The introduction of *A. mellifera* in 1848 marked the beginning of a series of bee introductions in Chilean agriculture (Ruz 2002). Subsequent introductions, such as *Bombus ruderatus* in 1982, targeted to pollinate for specific crops like red clover (Ruz 2002; Ortega et al. 2014). Some years later, in 1997, the introduction of *Bombus terrestris* began with greenhouse tomato pollination and later in 2000, it started to be used also in open fields, initiating a biological invasion in central Chile that spread nationwide and to some parts of Argentina (Fontúrbel et al. 2021). This invasion process is reinforced every year through new introductions of this bumblebee species to Chile (Vieli et al. 2021). Within these three introduced bee species, *B. terrestris* stands out owing to its high tolerance to climate/environmental variations and harshness (Montalva et al. 2017).

Alongside invasive species, factors such as habitat loss, pollution and climate change are major contributors to pollinator declines, a phenomenon of worldwide concern (Dicks et al. 2021; Vieli et al. 2021). However, efforts to address these species are often hindered by a lack of comprehensive information needed for decision-making and effective problem-solving. Thus, citizen science emerges as a promising approach, involving public participation in various stages of scientific research and facilitating large-scale data collection (Hochachka et al. 2012; Poisot 2016; Eitzel et al. 2017; Fontúrbel et al. 2024), especially when providing valuable insights into bee community dynamics (Rondeau et al. 2023). Citizen-science contributions, often collected by volunteers, represent a promising resource for producing knowledge, raising ecological awareness and supporting conservation strategies (Bosenbecker et al. 2023; Rondeau et al. 2023). Therefore, integrating data from biological datasets (e.g. López-Aliste et al. (2021); Boyd et al. (2022)) with citizen-science initiatives (e.g. Bosenbecker et al. (2023); Fontúrbel et al. (2023)) is extremely valuable for assessing pollinator changes over time and space.

This study focuses on the impact of *B. terrestris*, the most recently introduced bee species in Chile, to examine its role in bee-plant interaction networks. We also assess the broader impacts of three invasive bees (*Apis mellifera*, *Bombus terrestris* and *Bombus ruderatus*), exploring their relationships with both native and introduced plants. Specifically, we seek to address the following questions: (1) What are the characteristics of the ecological interactions of the three main introduced bee species in Chile? (2) How do introduced bees interact with native and non-native plants and what implications does this have for the overall interaction patterns? (3) What is the impact of the introduction of invasive bees on the structure and dynamics of bee interaction networks in Chile? We hypothesise that *B. terrestris* will emerge as the most generalist and interactive species, outweighing the effects of *A. mellifera* and *B. ruderatus*. Then, we hypothesise that invasive bees would preferentially interact with non-native plants, potentially facilitating their establishment in urban areas, where non-native plant species are abundant. Finally, we hypothesise that *B. terrestris*, as a strong competitor, will disrupt the structure of interaction networks by becoming one of the species with the highest number of interactions and by altering the specialisation patterns of other bee species.

Materials and methods

Data sources

To evaluate the interactions of the invasive bees that were introduced in Chile (*Apis mellifera*, *Bombus terrestris* and *Bombus ruderatus*), we created two datasets, one (1) comprising only scientific literature data, considering every interaction between bees and plants from the central and south regions found in Muschett and Fontúrbel (2022); and another (2) uniting the records of exotic bees from the same scientific literature database and records of citizen science for *Bombus terrestris* and *B. ruderatus* provided by Fontúrbel et al. (2023). The full scientific literature database is freely available from GitHub (https://github.com/fonturbel-lab/pollination_catalogue). The *Apis mellifera* citizen-science data were acquired through personal observation and on the records of the iNaturalist project "Red Chilena de Polinización" (https://www.inaturalist.org/projects/red-chilena-de-polinizacion) following the same methodology described in Fontúrbel et al. (2023). This citi-

zen-science project included actions to encourage data collection on pollinators throughout the country, in which volunteers were rewarded for their participation. We began data analysis by characterising the plant interactions of invasive bees, exploring the number of plant families and species visited. Subsequently, we evaluated the number of interactions considering both native and non-native plants for each invasive bee species. Then, we classified plant species as native or introduced according to Rodriguez et al. (2018). We estimated the number of shared and unique plant partners for each case and measured overlap in plant species visited using the Jaccard index. Some studies from scientific literature report interactions where bees visit flowers, but effective pollination was not clearly described. For this reason, we refer to all flower-visiting bees as "pollinators", regardless of whether their pollinator effectiveness was evaluated.

Bipartite networks and metrics

We used the bipartite interaction network approach, building weighted networks and calculating the following metrics: weighted nestedness, modularity, specialisation and core-periphery structure (as described in Guimarães et al. (2025)). Nestedness describes the network structure where specialist species interact with a subset of the species with which generalist species also interact and was estimated, based on the wNODF index, which ranges from 0 (non-nested networks) to 100 (perfectly nested) (Almeida-Neto and Ulrich 2011). Modularity, which estimates the degree to which subgroups of the taxa (modules) interact more amongst each other than with others, was estimated with the DIRTLPAwb+ algorithm and expressed with Qw, with zero representing no modularity and 1 extreme compartmentalisation (Beckett 2016). Network specialisation indicates how much species partition their interactions overall and was estimated using the H_2' index that ranges from 0 (generalised) to 1 (highly specialised) (Blüthgen et al. 2006). Complementarily, we examined the core-periphery structure of the networks (cpness), which goes beyond nestedness to characterise the species subsets that were densely connected (i.e. the core) and the sparsely connected (periphery) to estimate a core-periphery index (cpness hereafter), which indicates the strength of the core-periphery partition, ranging from 0 (no core-periphery structure) to 1 (a well-defined core-periphery structure) (Martín González et al. 2020). We calculated the significance of those metrics, except for cpness, by using null models based on 1000 randomisations using the vaznull method (appropriate for pollination networks) that shuffles the matrix, maintaining its dimensionality (Fortuna and Bascompte 2006; Jordano 2016); randomised networks kept the number of interactions and connectance constant (Dormann et al. 2008). We conducted all network analyses and plotting in R 4.4.2 (R Development Core Team 2024) using the packages bipartite (Dormann et al. 2008), econetwork (Miele 2022), ggplot2 (Wickham 2016) and circlize (Gu et al. 2014).

Before and after *Bombus terrestris* introduction

To unravel the impact of the *B. terrestris* introduction on bee-plant interactions in Chile, we used the scientific literature database cited above. We used the year 2005 as a temporal cut-off to compare networks, as 2005 marks a critical point in the spread of *B. terrestris* across the country, following its release in open fields in

2000 (Fontúrbel et al. 2021). Accordingly, we constructed interaction networks for the periods preceding and following 2005. For the three invasive bee species, we calculated the normalised degree (n.d), the weighted betweenness (w.b) and species specialisation (d') as proxies of their invasiveness. The normalised degree is a standardised metric that represents the number of links per species. We measured the species centrality using the weighted betweenness for the possibility of identifying species that act as connectors in the network (Martín-González et al. 2010). The d' specialisation index measures how selectively a species interacts compared to random expectations, considering the available mutualistic partners and network size effects (Blüthgen et al. 2006).

Results

Identifying the plant-pollinator interactions of invasive bees

The complete database, combining scientific literature and citizen-science databases, comprised 2,164 plant-invasive pollinator interactions. The bumblebee species *B. terrestris* showed the most interactions (73.34% of interactions, n = 1587 interactions), followed by *A. mellifera* (17.65% of interactions, n = 382) and *B. ruderatus* (9.01% of interactions, n = 195). These three introduced bee species interacted with 89 plant families. The most representative plant families were Asteraceae (453 interactions), Lamiaceae (240 interactions), Fabaceae (199 interactions) and Rosaceae (122 interactions). In this general analysis, the three bees showed low specialisation (d'= 0.162 *A. mellifera*; *B. ruderatus* d' = 0.146 and *B. terrestris* d'= 0.084; Fig. 1).

Interactions were also more prevalent with non-native plant species (1079 species; 75.51%) than with native species (350 species; 24.49%) for the three bee species. *Bombus terrestris* was – by far – the most generalist species, visiting 301 plant species (30.9% of them were native plant species), followed by *A. mellifera* that visited 148 plant species (42.6% of them native) and then *B. ruderatus* visited 64 plant species (14.1% of them native). The number of unique plant partners (i.e. plant species being exclusively visited by a given bee species) followed the same trend (Table 1; Fig. 2). We found low similarity (12 to 20%) amongst invasive species regarding plant species visited (detailed Jaccard overlap results are presented in Suppl. material 1: table S1).

Changes in plant-pollinator interactions before and after *B. terrestris* invasion

Before the spread of *B. terrestris* (before 2005), we found records of 54 bee species interacting with 109 plant species in literature (Fig. 3a). The native bumblebee *B. dahlbomii* was the most connected species in the network (n.d = 0.44), followed by the invasive bumblebee *B. ruderatus* (n.d = 0.26) and *Megachile semirufa* (n.d = 0.17). *Bombus dahlbomii* also exhibited the highest betweenness centrality (w.b = 0.26), followed by *Megachile semirufa* (w.b = 0.11) and *Centris cineraria* (w.b = 0.11) (Suppl. material 1: fig. S1a). The most specialised pollinator species until 2005 was *B. terrestris* (d' = 1), which interacted only once with three plant species, *Liphanthus sabulosus* (d' = 0.798) and *Etcheverrius chilensis* (d' = 0.764). The most connected plants registered at this time were *Phacelia secunda* (Boraginaceae, n.d

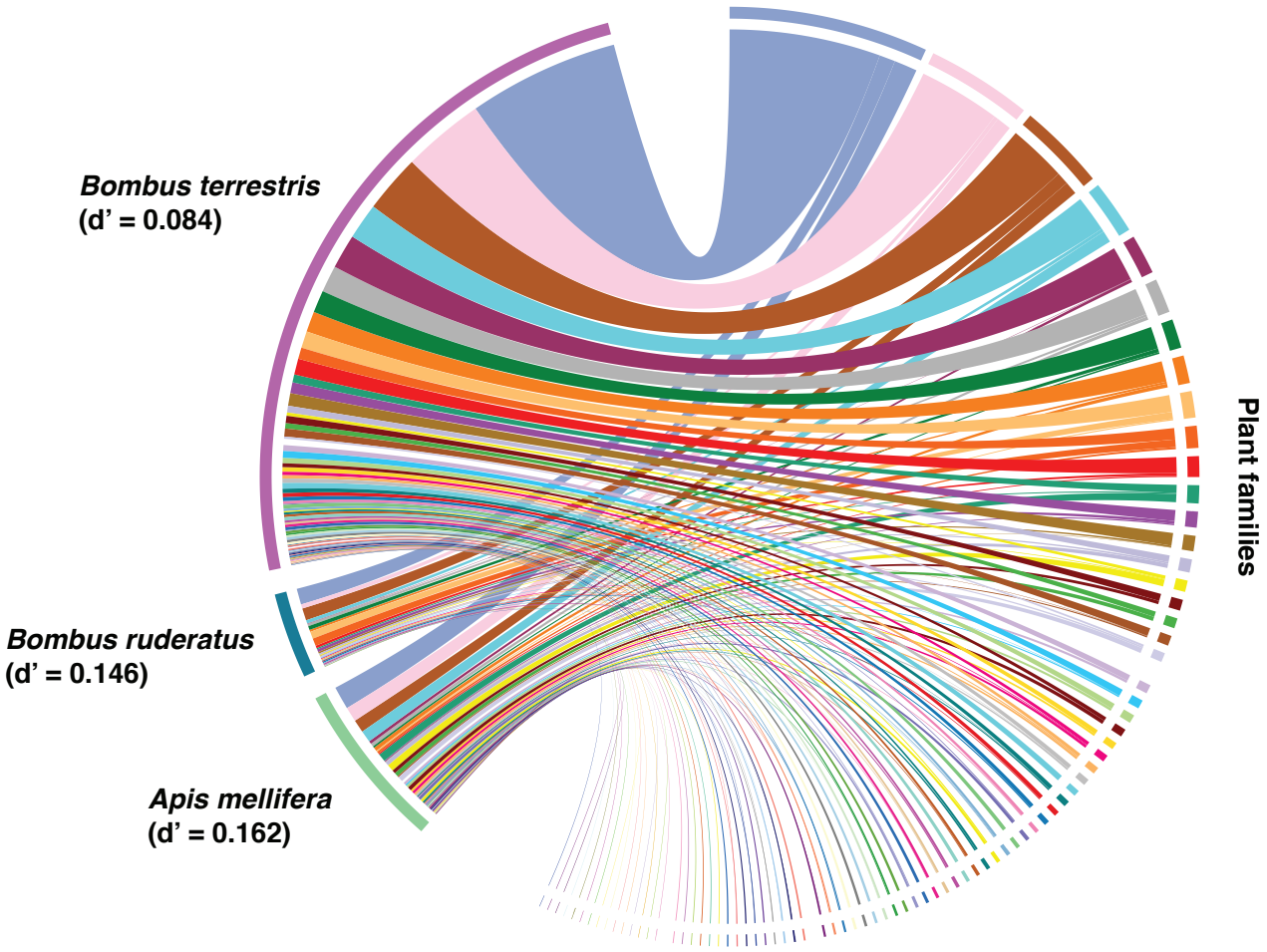

Figure 1. Circular graph showing interactions between the main invasive bee species and plant families across Chile, based on a combined database of scientific literature and citizen-science records. Each link represents an interaction between an invasive bee species and a plant species. *B. terrestris* is shown in purple, *A. mellifera* in green and *B. ruderatus* in blue. Species-level specialisation (d') values are indicated in parentheses.

Table 1. Number of plant species visited by the invasive bee species *Apis mellifera*, *Bombus ruderatus* and *Bombus terrestris* in Chile, detailed by native and non-native species and their respective percentages. In addition, the number of unique plant partners (i.e. plant species that are not visited by the other invasive bee species) and species-level specialisation (d') are indicated for each case.

Metric	*A. mellifera*	*B. ruderatus*	*B. terrestris*
Total plant species	148	64	301
Native plants	63	9	93
Native plants (%)	42.6	14.1	30.9
Non-native plants	85	55	208
Non-native plants (%)	57.4	85.9	69.1
Unique plant partners	69	15	199
Species-level specialisation (d')	0.162	0.146	0.084

= 0.35), *Stachys albicaulis* (Lamiaceae, n.d = 0.22) and *Adesmia conferta* (Fabaceae, n.d = 0.19).

After 2005, the network comprised 90 bees and 112 plant species (Fig. 3b). There was a change in the composition of the most connected bees, as *Apis mellif-*

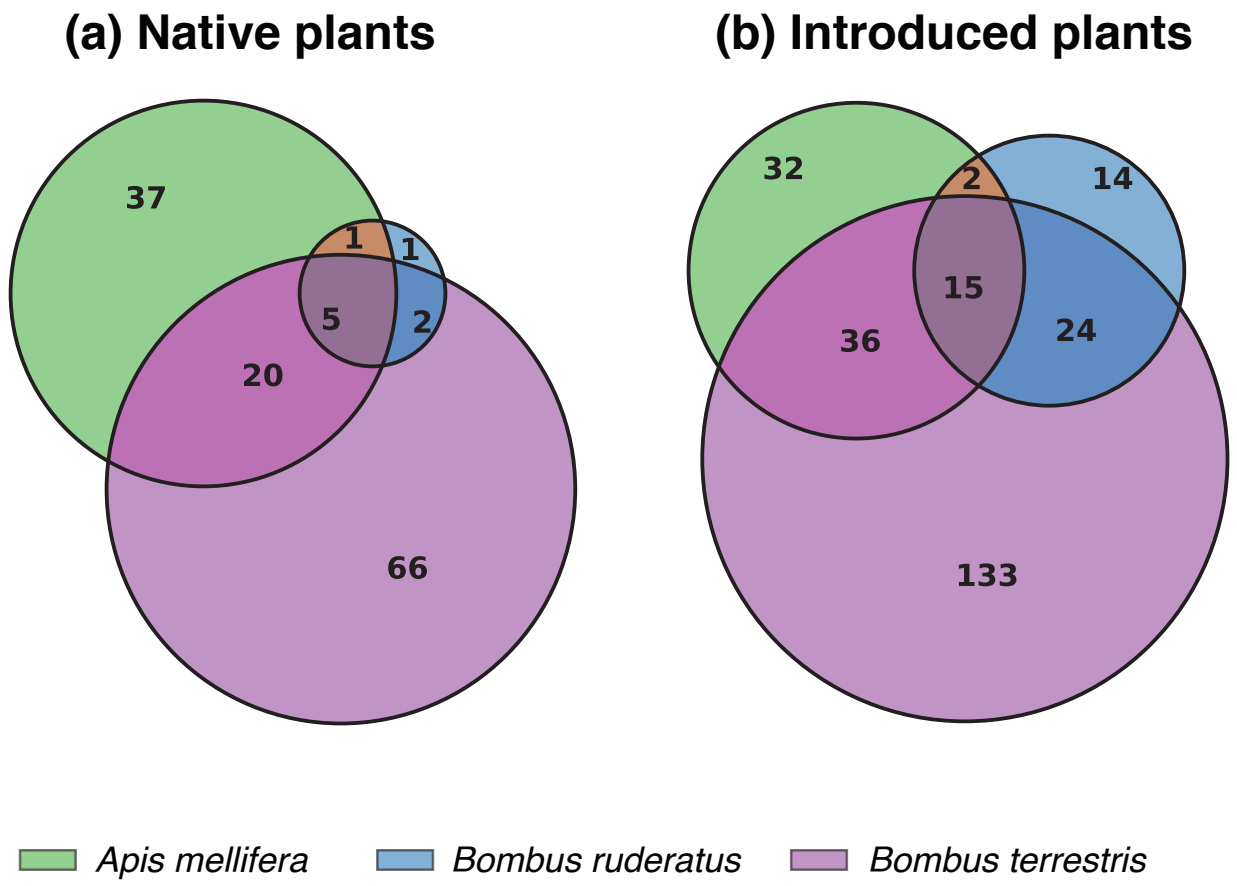

Figure 2. Number of (**a**) native and (**b**) introduced plant species visited by the invasive bees *Apis mellifera*, *Bombus ruderatus* and *Bombus terrestris* in Chile, based on a combined database of scientific literature and citizen-science records. Circle overlaps denote shared plant species between bee species.

era led the number of links with a normalised degree of 0.56, followed by *B. dahlbomii* (n.d = 0.39) and *B. terrestris* (n.d = 0.16) (Suppl. material 1: fig. S1b). The Chilean-native bumblebee *B. dahlbomii* (w.b = 0.242) was no longer the bee with the greatest centrality of interactions, becoming the second most central after *A. mellifera* (w.b = 0.348) and then followed by *C. nigerrima* (w.b = 0.130). The most specialists were *Chalepogenus caeruleus* (d' = 0.868), *Alloscirtetica gazullai* (d' = 0.865) and *Leioproctus andinus* (d' = 0.865). There was also a shift in the most connected plant species, which were *Alstroemeria ligtu* (Alstroemeriaceae, n.d = 0.20), *Echinopsis chiloensis* (Cactaceae, n.d = 0.18) and *Eucryphia cordifolia* (Cunoniaceae, n.d = 0.18).

Exploring species metrics of the invasive bees, we observed many changes in plant-bee interactions before and after 2005 (Fig. 4). The exotic bumblebee *B. ruderatus*, one of the most interactive bee species before 2005, became the least interactive amongst the invasive ones. *Bombus terrestris* increased in importance, with its normalised degree rising nearly six-fold. The increase in the normalised degree of *A. mellifera* was less pronounced. Regarding betweenness centrality, the honeybee showed a greater increase. For specialisation, these bees showed a decrease, with the major effect on *B. terrestris*, which became three times less specialised. Network topology changed after the year 2005, as nestedness and specialisation increased while modularity did not present significant changes (Table 2). Despite

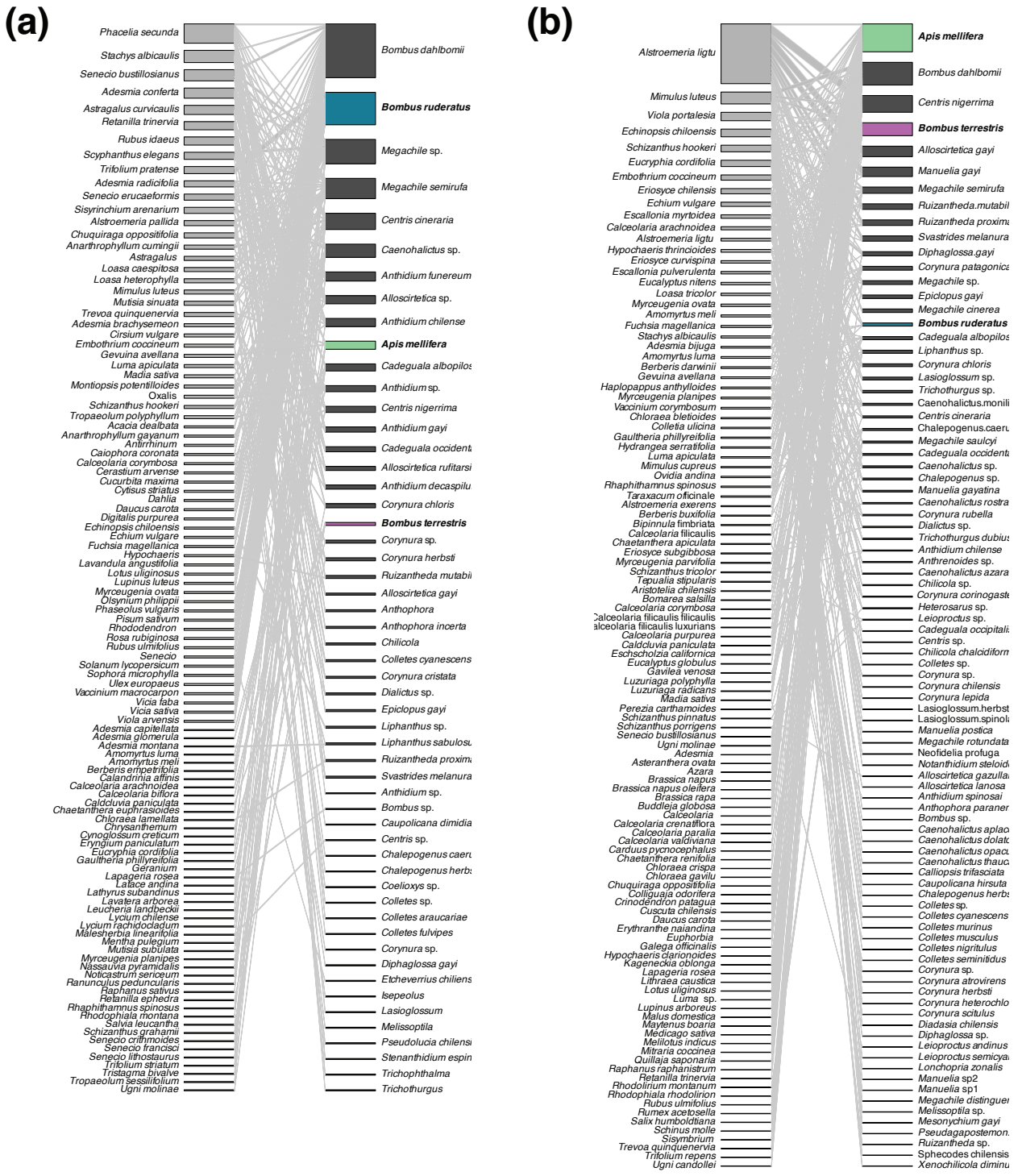

Figure 3. Bipartite plant-bee interaction networks in Chilean ecosystems before (**a**) and after (**b**) the open-field introduction of *Bombus terrestris* (year 2005), based on a scientific literature database. Each node represents a plant species (on the left) or a bee species (on the right) and their interactions. Invasive bee species are denoted by colours: *B. terrestris* in purple, *A. mellifera* in green and *B. ruderatus* in blue.

the increase, nestedness and specialization remained low. According to the z-scores, the wNODF values were always lower than expected by chance, while the specialisation was lower only before 2005. The core-periphery index showed a highly connected network and was higher before 2005 (cpness = 0.760) than afterwards (cpness = 0.680; Table 2).

Table 2. Bee-plant network metrics before and after the year 2005, based on data from scientific literature. Statistical significance was assessed for nestedness (wNODF), modularity (Q) and specialisation coefficients (H_2') comparing results with null models. cpness: core-periphery index coefficient. Significance codes: ^{ns} P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

	Overall		Before 2005		After 2005	
Metric	**Value**	**z-score**	**Value**	**z-score**	**Value**	**z-score**
wNODF	4.503***	-2.681	1.322***	-4.630	5.299***	-4.030
Qw	0.544^{ns}	-17.816	0.594***	9.800	0.553***	28.670
H_2'	0.233***	6.895	0.049***	-3.600	0.280***	6.610
cpness	0.782	-	0.760	-	0.680	-

Discussion

Our results revealed shifts in the structure and composition of plant-pollinator networks following the introduction of *Bombus terrestris*, the most recent alien bee invader in Chile. Native bee species, once central in these interactions, have been partially displaced by invasive bees. Invasive bees dominate the most frequent interaction records, especially with introduced plants and show generalist behaviour that reshaped network architecture. These changes indicate a trend towards more homogenised and less compartmentalised systems. The broad geographical coverage of the dataset, spanning diverse ecosystems, such as the Atacama Desert, Mediterranean-type region and temperate forests, makes the findings of this study relevant to other regions. The implications of these patterns are examined in detail below.

Interactions of invasive bees

Apis mellifera, *B. ruderatus* and *B. terrestris* – three generalist and widespread species – are part of interaction dynamics throughout Chile, with *B. terrestris* predominating in the number of interactions (73% of recorded interactions). These introduced bees interact with a considerable number of plant families (89 out of 167 vascular plant families from Chile; Rodriguez et al. (2018)) and most of plant species visited by invasive bees are non-native. The integration of these bees into Chilean pollination networks reflects a substantial ecological shift. Its ability to thrive across the country, facilitated by traits, such as variable tongue lengths and tolerance to adverse weather (Dafni and Shmida 1996), has enabled its widespread establishment and central role in the networks and widespread distribution throughout the Chilean territory. Moreover, the continuous import of *B. terrestris* to Chile, more than 60,000 individuals every year for pollination purposes (Vieli et al. 2021), reinforces the invasive process of this species.

Functionally, a shift in dominance is evident. *Bombus dahlbomii*, historically the most central native species in Chilean networks (Carvallo et al. 2023; Guimarães et al. 2025), has been partially displaced by *A. mellifera* and *B. terrestris*. In contrast, *B. ruderatus*, introduced for agricultural use (Arretz and Macfarlane 1986), shows limited spatial distribution and low interaction frequency, possibly due to competitive exclusion by more adaptable species. *Bombus ruderatus* was introduced into southern Chile during the 1980s from New Zealand stock (Arretz and Macfarlane 1986). This species of bee visits cranberries, raspberries and various weeds, such as *Echium vulgare*, contributing to the reproduction and spread of

these plants. *Bombus ruderatus* populations appear to have declined, possibly due to changing climatic conditions or the increased presence of *B. terrestris* (Morales et al. 2013; Aizen et al. 2019). This could explain the restricted spatial distribution and the lowest number of interaction records.

Impact of invasive bee species on interaction networks

The introduction of *B. terrestris* into Chilean ecosystems has triggered a marked restructuring of plant-pollinator interaction networks. Following the introduction of *B. terrestris*, a broader range of bee species interacting with a greater variety of plants was recorded. Notably, during this period, the honeybee emerged as the species with the highest centrality, playing a dominant role within the network. *Apis mellifera* was introduced more than a century ago because it is easily managed and widely distributed throughout the world. It has been used to improve pollination and produce honey and, despite being less efficient in some crops, honeybees compete for the niche of some native bees (Ruz 2002; Valido et al. 2019; Page and Williams 2023). At the same time, the native *B. dahlbomii* maintained a significant position within the network, reinforcing its importance in the structure of bee-plant interactions in Chile. A recent review of pollination in wild ecosystems in Chile corroborates that *B. dahlbomii* is the most important bee for these systems, with the highest number of interactions, followed by *A. mellifera* (Carvallo et al. 2023). By analysing a comprehensive dataset encompassing interactions with native, non-native and cultivated plants, our study highlights the continued importance of both the native bumblebee and the honeybee after 2005.

The increase of invasive species also contributed to the shifts in plant composition within the pollination network. Nonetheless, interactions with native plant species remained predominant both before and after the introduction of *B. terrestris*, as evidenced by early records of *Phacelia secunda*, *Stachys albicaulis* and *Adesmia conferta* and more recent records featuring *Alstroemeria ligtu*, *Leucostele* (=*Echinopsis*) *chiloensis* and *Eucryphia cordifolia*. However, several studies in Chile focus only on native plant species (e.g. *A. ligtu*, *E. cordifolia*) or ecosystems dominated by native plants (e.g. Andean ecosystems; central Chile: Medel et al. (2018); Muschett and Fontúrbel (2022); Carvallo et al. (2023)), which skews the observed results. As more records become available that include non-native species and disturbed ecosystems (e.g. urban environments), the overall picture of pollinator change will become clearer.

Networks in forest areas may reflect restructured assemblages of opportunistic species rather than functionally resilient systems. As Oliveira et al. (2025) pointed out, the continuity of interactions in such environments relies more on the flexibility of generalists than on the persistence of co-evolved partnerships. In our study, *B. terrestris* exemplifies this trend, thriving in modified habitats due to its behavioural adaptability. However, its success may potentially contribute to the exclusion of native pollinators and may favour the reproductive dominance of invasive plants, which could lead to biotic homogenisation and long-term ecological simplification. The introduction of *B. terrestris* has not only altered the numerical composition of the interaction network, but has also redefined its architecture. This happens particularly in converted habitats where human-induced changes facilitate biological invasions.

Several cases presented by Simberloff and Von Holle (1999) illustrate that non-native species can promote the establishment and spread of other introduced species, a phenomenon referred to as invasional meltdown. These facilitative interactions may occur through direct mechanisms, such as interactions between introduced species (as pollination) or indirectly through habitat alterations that create favourable conditions for additional invaders. A well-documented example involves the fig tree *Ficus microcarpa*, whose spread in regions like Florida became possible only after the introduction of its specific pollinator, the wasp *Parapristina verticillata* (Zhang et al. 2021). Once this mutualistic relationship was established, the plant rapidly expanded, aided by non-native frugivores. This highlights instead the frequent mutual reinforcement amongst introduced species, which increases the chances of invasional meltdown and amplifies possible ecological impacts. In this case, the integration of *B. terrestris* into the pollination network has a positive impact on some exotic plants that are more frequently visited than native ones (Fontúrbel et al. 2023), favouring their reproduction and spread.

Conclusions

The case of *Bombus terrestris* in Chile exemplifies a "silent takeover" of native ecosystems, where this invasive bee has stealthily, but decisively reshaped plant-pollinator networks. By outcompeting native species and forcing a shift towards generalised, less specialised interactions, it has secured ecological dominance. This restructuring, while boosting pollination for some commercial plants, comes at a high cost: it undermines the reproductive success of native flora and increases biodiversity risks like harmful pollen transfer. The study underscores that such biological invasions demand a vigilant, proactive response. To safeguard biodiversity hotspots worldwide, conservation must prioritise early detection, science-based management and policies that weigh the full ecological costs against any narrow agricultural benefits. By democratising data collection and expanding geographic coverage beyond the capabilities of regular research projects, citizen science proves to be an indispensable tool for detecting and tracking the expansion of invasive species across ecosystems, directly providing information for conservation actions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

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Use of AI

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Data availability

Data and code associated with this submission are available from the figshare repository: http://doi.org/10.6084/m9.figshare.29824928

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Supplementary material 1

Supplementary information

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Data type: docx

Explanation note: **fig. S1.** Species level metrics (normalized degree, species specialization and weighted betweenness) for the 15 most connected bee species (a) before and (b) after *Bombus terrestris* spread in 2005. **table S1.** Pairwise similarity among plant species visited by the invasive bees *Apis mellifera*, *Bombus ruderatus*, and *Bombus terrestris*, measured using the Jaccard index.

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