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Wild Floral Visitors Are More Important Than Honeybees as Pollinators of Avocado Crops

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Abstract: Wild insects provide pollination services in agroecosystems. Avocado is an economically important crop grown in the Chilean Mediterranean climate region and exported worldwide. Avocado pollination is managed using honeybee hives, while the role of wild insects as pollinators remains poorly known. We quantified the relative contributions of wild floral visitors and honeybees to the fruit set of avocados in two contrasting seasons (2015 and 2016) in Central Chile. Observations were made in 60 trees grown nearby (~300 m) to remnant patches of native sclerophyll vegetation. We found that honeybees and wild insects accounted for 48.6% and 51.4% of total floral visitation, respectively, with a 68% taxonomic similarity of floral visitors between seasons. The presence of honeybees significantly modulated the floral visitor composition and modified plant-pollination network parameters, which resulted in the biotic homogenization of the interaction network, through the increase of shared tree–floral visitor interactions, to the detriment of exclusive interactions. Finally, wild insects were more effective than honeybees in pollinating avocado trees and their contribution was greatest during the dry year. Thus, honeybees alone cannot be relied upon to deliver maximum pollination. We highlight ecological intensification practices to encourage wild insect visits and avoid native vegetation replacement with orchards. Therefore, we emphasize that future ecological intensification research should address agricultural practices to promote wild insects and evaluate the role of native vegetation as wild pollinator habitat in agricultural landscapes.

Keywords: ecological intensification; ecosystem services; *Persea americana*; pollination; wild floral visitors

1. Introduction

Human-managed crop systems often rely on ecosystem services provided by surrounding natural habitats, such as crop pollination by wild insects [1–4]. Insects increase yields of up to 68% of the world's major crops, and one third of our food is derived from pollination-dependent crops [5]. Therefore, safeguarding pollinators is key to the transition towards sustainable agriculture, as animal-mediated pollination contributes to global food security [6]. Commercial generalist insect species are frequently used to enhance crop production, as is the case of the European honeybee *Apis mellifera* [7,8]. Honeybees are generally assumed to have large positive effects on the fruit sets of cultivated plants; however recent and consistent field evidence have shown that wild insects may be playing a key role

in agricultural production [9] as maximum fruit yields are often achieved when flowers are visited by both honeybees and wild insects [10,11]. Although the area of pollinator-dependent crops continues to grow [7,12], the decline of pollinators worldwide [13,14] and reduced stocks of *Apis mellifera* do not allow for meeting the global demand for pollination services [8,12,15]. Therefore, managing wild pollinators to increase and sustain crop productivity through ecological intensification of agriculture [16], which refers to increasing productivity while minimizing negative environmental impacts by integrating the management of ecosystem services delivered by biodiversity into crop-production systems [17], presents an alternative to conventional agriculture with reduced negative externalities [17,18].

The Mediterranean climate region of Central Chile harbors the highest proportion of economically important crops with boreal winter production for off-season export to the northern hemisphere. However, this extensive cultivated area largely overlaps with native vegetation formations [19], considered as a global biodiversity hotspot due to their highly endemic and threatened biota [20]. This area hosts ~70% of the Chilean endemic bees, often inhabiting the native sclerophyllous forest [21]. However, those sclerophyllous forests are rapidly shrinking as a result of land-use change through the rapid expansion of intensive agriculture and forestry [19,22]. In particular, vineyards and avocado (*Persea americana*, Lauraceae) plantations have encroached into natural areas (Figure S1) [19,23]. Avocado plantations cover ~40% of the cultivable land in Central Chile and represent the third most important fruit crop in the country, making Chile the fifth largest avocado exporter worldwide [24].

Greater pollinator diversity, including wild pollinators, can promote improve fruit set and productivity by (i) increasing visitation rates by a larger pool of pollinator species that enhances the spatial and temporal distribution of visits to flowers [25–27], (ii) reducing the morphological mismatch between plants and pollinators by increasing generalist and specialist pollinator abundances [28,29], (iii) ensuring that pollination services are still delivered even under suboptimal or extreme weather conditions due to the broader tolerances of the ensemble [30,31], and (iv) reducing risks of temporal decoupling between flowering periods and pollinator availability over time [32]. When fruit sets are strongly dependent on a single pollinator species (e.g., *Apis mellifera*), these benefits can be lost. Therefore, combining both wild and managed pollinators, such as in the case of the almond in California, US, is likely to be the best strategy to enhance long-term productivity [11,16,33]. However, there are examples where abundant honeybees can even result in reduced activity of wild pollinators through competition and exclusion with detrimental implications for crop pollination [34].

Drought reduces floral resources for pollinators [35] and alters plant–pollinator interactions [36]. For instance, the ongoing megadrought in Central Chile strongly affected the sclerophyllous vegetation [37,38] which is reflected in the reduction of honey production by 80% [39]. Thus, the loss of pollinator diversity and functional redundancy due to prolonged droughts might simplify plant-pollinator networks with negative consequences on ecosystem resilience [40]. In this regard, pollinator networks can be a useful tool to understand the interactions between flower visitors and crop plants, giving us valuable insights into the pollination services delivered [41]. Managed pollinators, such as *Apis mellifera* and *Bombus terrestris*, are considered supergeneralist pollinators [42]. Therefore, their overabundance and spillover into natural ecosystems [43] have been documented to disrupt the network interactions between wild pollinators and plants [42,44–46], such as the case at Teide National Park, Tenerife, Canary Islands [46], and these effects may be amplified due to the monopolization of resources in drought conditions. Understanding the effects of honeybees on the overall plant–pollinator network structure within crops provide us with information for managing pollinators to increase productivity.

A novel framework to evaluate the provision of pollination ecosystem services to crops is under the mutualism 'effectiveness framework' [47,48]. In this case, the contribution of a floral visitor to the plant's fitness is defined by the multiplication of a quantity component

(e.g., visitation rates) and a quality component (e.g., a fruit set). These components form a two-dimensional abstract representation (called effectiveness landscape), in which each plant's location is determined by particular combinations of quantity (*x*-axis) and quality (*y*-axis) values, providing a useful conceptual framework to assess the outcome of plant-animal mutualisms, including crop pollination. This framework has been proposed to identify key crop pollinator species [49].

In this context, we hypothesized that wild pollinators would have a positive influence on the avocado fruit set, which could change under extreme weather conditions [36], such as the reduction of wild floral resources by drought [35], outweighing the relative contribution of the managed honeybee. The aims of this study were to (i) characterize the assemblage of insects that visit avocado flowers and determine the relative importance of honeybees and wild insects, (ii) determine if the presence of honeybees causes topology changes in individual-based pollination-interaction networks, and if these changes modify (iii) the relative contribution of wild insects and honeybees to the pollination of avocado trees, and (iv) assess how pollination in response to insects varies between a normal and a dry year.

2. Materials and Methods

2.1. Study Area

The field study was conducted in avocado orchards of the Quillota Province (Valparaíso), one of the most productive agricultural valleys within the Mediterranean-type ecosystems (hereafter MTE) of central Chile. Between 2015 and 2016, we surveyed floral visitors of 60 avocado trees (belonging to the Hass variety) of similar age (~20 years) and management regime, produced in the Quillota Province (32°51′ S, 71°12′ W). The study area is characterized by a 7-month dry–warm season, with rain falling exclusively during the cold austral winter (May to August). The native vegetation of the surrounding areas—hillsides and valleys—are dominated by evergreen sclerophyllous forests and scrublands, which characterize MTE in Chile and are the primary habitats for the highly endemic biota [20].

Avocado is a pollination-dependent crop since it does not self-pollinate [50]. Outside its original distribution range, such as in MTE in Central Chile, honeybees (*Apis mellifera*) are commonly recommended for use, at a density of between 4 to 10 hives/ha to assist in pollination [51–54]. In our study site, ten honeybee hives·ha-1 were distributed, following the arrangement recommended by De la Cuadra-Infante [52]. The distances from the sampled trees to the hives were kept relatively uniform (ca. 60 m). In addition, the avocado orchards used as study sites were located less than 300 m away from remnant areas of dense native sclerophyllous vegetation adjacent to La Campana National Park and Biosphere Reserve.

2.2. Study System

Avocado trees are native to Central America and Mexico. As male and female flowers open at different times, limiting self-pollination [51], this species is highly dependent on biotic cross-pollination (mainly by insects) [50,54]. As this subtropical species is non-native to MTE, the use of commercial pollinators, such as *Apis mellifera*, has been recommended to achieve higher yields [52,54]. However, in addition to honeybees, a large number of wild insects are often regular visitors to avocado flowers worldwide [50,55–57] and in Central Chile, those wild visitors mainly belong to the Orders Diptera, Hymenoptera, Coleoptera, and Hemiptera [56,58,59]. Bees and flies in particular are likely to be the most effective avocado pollinators given their morphology and behavior [50,58,60].

2.3. Sampling of Insect Floral Visitors and Fruit Set

We established a grid with 20 × 20 m plots (making a sampling area of 400 m²·plot-1) along the study area. Then, we randomly selected 60 of these plots and identified one focal avocado tree within each plot for sampling floral visitors. Following Valdes [61], during

crop flowering (from October to November) each focal avocado tree was systematically subsampled using two quadrats of 1 m^2, located at the height of ~2 m above ground; one placed on the north-facing and a second one on the south-facing sides of the tree, to capture the variability, considering the sun's position in the southern hemisphere. We counted all flowers within each subsample and observed all floral visitors.

We recorded insect floral visitors at each quadrat by direct observation for 5 min at mid-day, between 11:00 to 13:00 h [62,63], since the optimum temperature is reached that allows activity in most pollinators. At this time, most flowers were in the male phase. Unknown floral visitors were captured using hand nets and later identified in the laboratory to the highest taxonomic resolution possible using field guides. Insects that could not be identified were classified into morphospecies. Insect abundance data obtained from the observation records from both quadrats were averaged per focal tree and this information was used to calculate floral visitation rates, taxonomic richness, and overall diversity of floral visitors for each one of the 60 sampled trees. Observations were conducted during two consecutive flowering seasons (i.e., 2015 and 2016). Although Central Chile has been experiencing a megadrought since 2010, both sampling years were contrasting in terms of precipitation, as 2015 was slightly less than a regular year, but 2016 was a very dry year (e.g., accumulated annual precipitation of 332 vs. 283 mm respectively) [38] with respect to the average accumulated annual precipitation of 407 mm. In the 2015 flowering season, field observations were made three times within the peak flowering period (i.e., in October and twice in November), while in the 2016 season, surveys were conducted twice, once in October and the other in November. However, due to climatic conditions and the absence of open flowers, we discarded the third observation of November 2015 and the second observation of November 2016 from our analyses. The total sampling effort was 1800 min. To assess the effects of floral resources on visitation rates, we counted the total number of flowers as well as the number that were open at the time of the survey. To assess fruit set, as a proxy of avocado yield, in January 2016 and 2017 we returned to the focal trees and measured the total initial avocado fruit set in the same 1 m^2 quadrats where flowers were counted earlier. We quantified the initial fruit set because it is an important determinant of yield but is independent of many other factors that may induce fruit fall subsequently [51].

2.4. Statistical Analyses

2.4.1. Spatial Autocorrelation among Sampled Trees

We performed the Mantel test to estimate the degree of spatial autocorrelation in the response variables (i.e., visitation rates of *A. mellifera* and wild insects) and the geographic position of the sampled trees, as we are aware of the spatial limitation of our study. We conducted Mantel tests using the ade4 package [64] with 9999 permutations to test for spatial autocorrelation.

2.4.2. Species Composition

We arranged the insect species composition and abundance field data into matrices for taxonomic similarity analysis. Aiming to contrast species composition, we grouped our data by year and by the presence or absence of *Apis mellifera*. Despite *A. mellifera* hives being present along the study site, we observed that some focal trees were visited by *A. mellifera* and wild insects, while other trees were visited only by wild insects. Thus, we referred to those trees as *A. mellifera* present or absent, respectively, but it is important to note that we did not conduct any pollination exclusion experiments. We made the species composition comparisons using an analysis of similarities (ANOSIM) test, which is a permutation-based nonparametric test [65]. Our ANOSIM tests used a Bray–Curtis similarity distance and 999 permutations to estimate *p*-values. Then, we used the nonmetric multidimensional scaling (nMDS) ordination to visualize those species composition comparisons based on Bray–Curtis dissimilarity distance. These analyses were conducted using the R package vegan 2.5.7 [66].

2.4.3. Individual-Based Bipartite Networks

Finally, we used quantitative bipartite networks to assess the relationships between our focal avocado trees and the different floral visitors when *A. mellifera* was present or absent (as explained above), and its interannual variation. This approach has been widely used to document changes in pollinator communities caused by introduced species [44,46]. For this purpose, we built individual-based networks (using each avocado focal tree as a node [67], which are commonly used in pollination ecology to examine interaction variability among individuals of the same plant species (e.g., [68–71]. We estimated the following network metrics: connectance, links per species, web asymmetry, and nestedness (using NODF). Network analyses were performed using the R package bipartite 2.16 [72,73]. Then, we used the R package betalink 2.2.1 [74] to assess the network dissimilarly when A. *mellifera* is present or absent and between years.

2.4.4. Pollination Outcome

To compare pollination outcome between years and when *A. mellifera* was present or absent, we used the mutualistic interactions effectiveness framework proposed by Schupp et al. [47], which provides an abstract representation (called effectiveness landscape) of the interaction outcome for each focal plant by assessing the relative importance of quantitative and qualitative components. In this case, following Haedo et al. [49], we used visitation rates as the quantitative component and relative fruit set (estimated as the ratio between the number of fruits produced divided by the number of flowers) as the qualitative component, depicting means $\pm$ 1SE. We used the R package effect.lndscp 0.2.8 [75] to assess the pollination outcome and generate the effectiveness landscape plots.

3. Results

3.1. Spatial Autocorrelation

We found no spatial autocorrelation in the visitation rates of *A. mellifera* (Mantel test coefficient rM = -0.08; $p = 0.72$) nor of wild insects (rM = -0.07; $p = 0.72$). Thus, each tree was considered as an independent replicate (N = 60).

3.2. Floral Visitor Composition

Wild insects from the surrounding sclerophyll vegetation were common floral visitors to avocado flowers. We recorded 23 insect species in both sampling years, including managed honeybees. Floral visitors belonged to the orders Diptera, Hymenoptera, Coleoptera, and Lepidoptera (Table S1). Honeybees were the most frequent floral visitor, accounting for 48.6% of the total visits. Among wild species, Diptera was the most frequent Order, accounting for 43%, followed by Hymenoptera and Coleoptera (mainly Carabidae and Coccinellidae) with 36% and 17% of the visits, respectively. Another frequent visitor recorded was the butterfly *Vanessa carye*.

We found no significant differences in species composition between 2015 and 2016 (ANOSIM R = 0.06, $p = 0.06$; Figure S2) but we found that the composition of floral visitor species is significantly different between trees where *A. mellifera* was present or absent (R = 0.98, $p = 0.021$; Figure S3).

3.3. Individual-Based Networks

Examining the quantitative individual-based networks that we built, we found contrasting network topologies when *A. mellifera* was present or absent (Figure 1). The presence of *A. mellifera* reduced connectance, increased the number of links per species, increased web asymmetry, and increased network nestedness (Table 1). Those topology changes also showed an interannual variation between the regular (2015) and the dry (2016) years. Further, when we examined network dissimilarity within years (contrasting networks where *A. mellifera* was present or absent), we found that avocado trees interact with different floral visitors with a few interactions shared (Figure 2a,b). Then, when we compared the 2015 and 2016 networks when *A. mellifera* was present, we observed that most of the

avocado tree–floral visitor interactions were shared (Figure 2c) but the proportion of shared interactions is lower when *A. mellifera* was absent (Figure 2d).
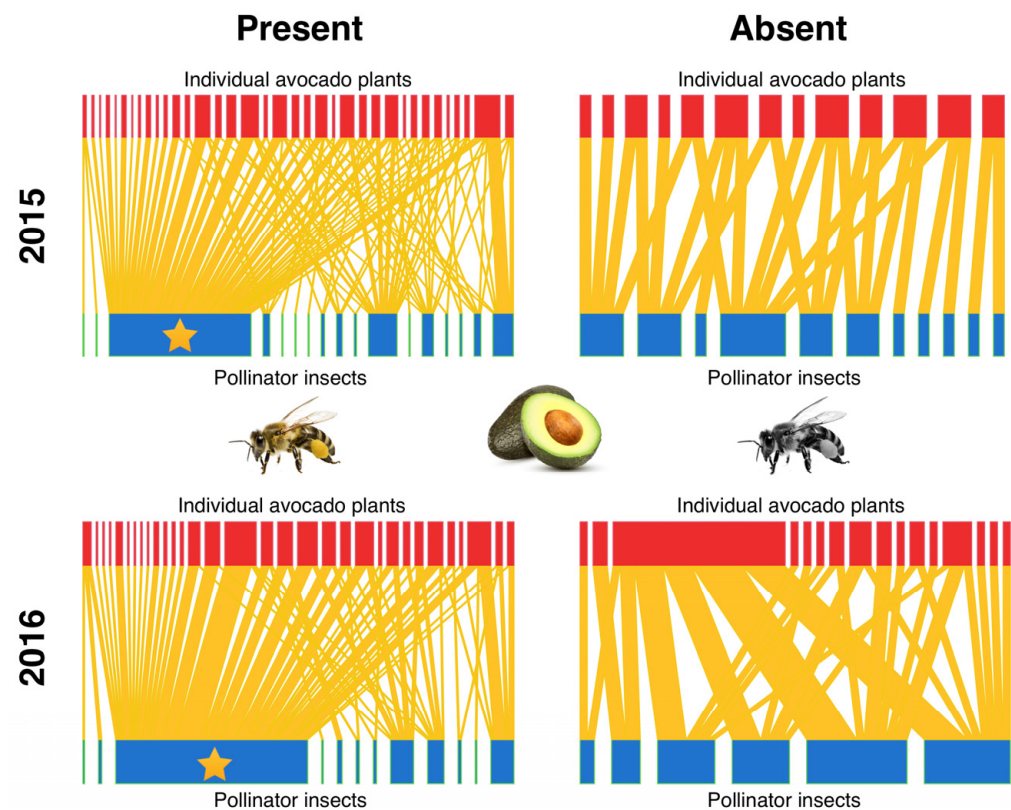

Figure 1. Individual-based quantitative networks (using visitation events as a quantity measurement) built for avocado trees where *Apis mellifera* (marked with a star) was present or absent, in two sampling years (2015 and 2016). The blue bar at the bottom represents different floral visitors, while the red bar at the top represents each sampled avocado trees.

Table 1. Network topology variation between sampling years, comparing avocado trees where *Apis mellifera* was present or absent.

Metric	2015		2016	
	Absent	**Present**	**Absent**	**Present**
Connectance	0.182	0.157	0.271	0.164
Links per species	1.083	1.811	1.182	1.432
Web asymmetry	0.083	0.358	0.455	0.455
NODF	18.672	58.978	33.025	58.322

3.4. Pollination Outcome

The pollination outcome obtained from our data was represented in an effectiveness landscape plot (Figure 3) that showed a marked difference in pollination effectiveness between 2015 (a regular year) and 2016 (a very dry year). In both years, visitation rates (i.e., the quantitative component) were much larger when *A. mellifera* was present but it did not improve pollination quality (i.e., fruit set). In 2015, despite visitation rates being significantly larger when *A. mellifera* was present (0.01 versus 0.10 visits·flower^{-1}), we observed an increase of only 20–25% in the fruit set. In 2016, however, visitation rates were again much larger when *A. mellifera* was present (0.03 versus 0.08 visits·flower^{-1}) but fruit set decreased by 25% compared to those trees only visited by wild insects.
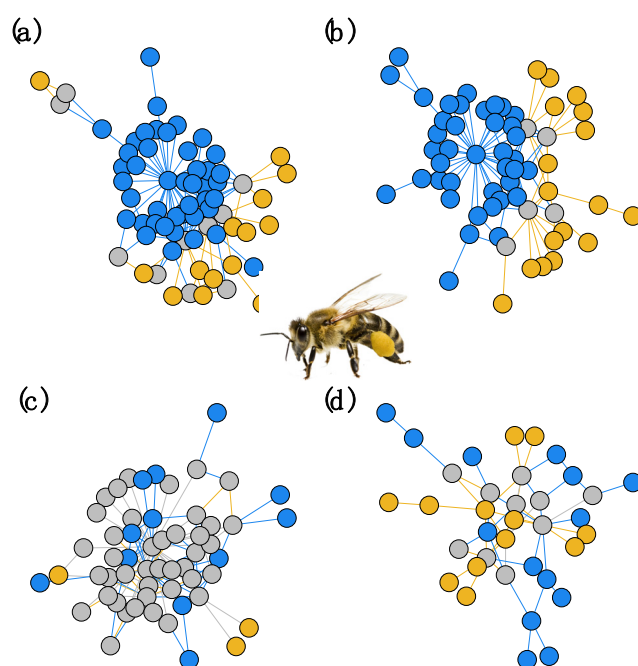
Figure 2. Network dissimilarity pairwise comparisons: (**a**) for 2015 when *Apis mellifera* was present or absent, (**b**) for 2016 when *A. mellifera* was present or absent, (**c**) comparing 2015 and 2016 when *A. mellifera* was present, and (**d**) comparing 2015 and 2016 when *A. mellifera* was absent. Blue and yellow circles correspond to exclusive interactions while gray circles represent shared interactions for each comparison.
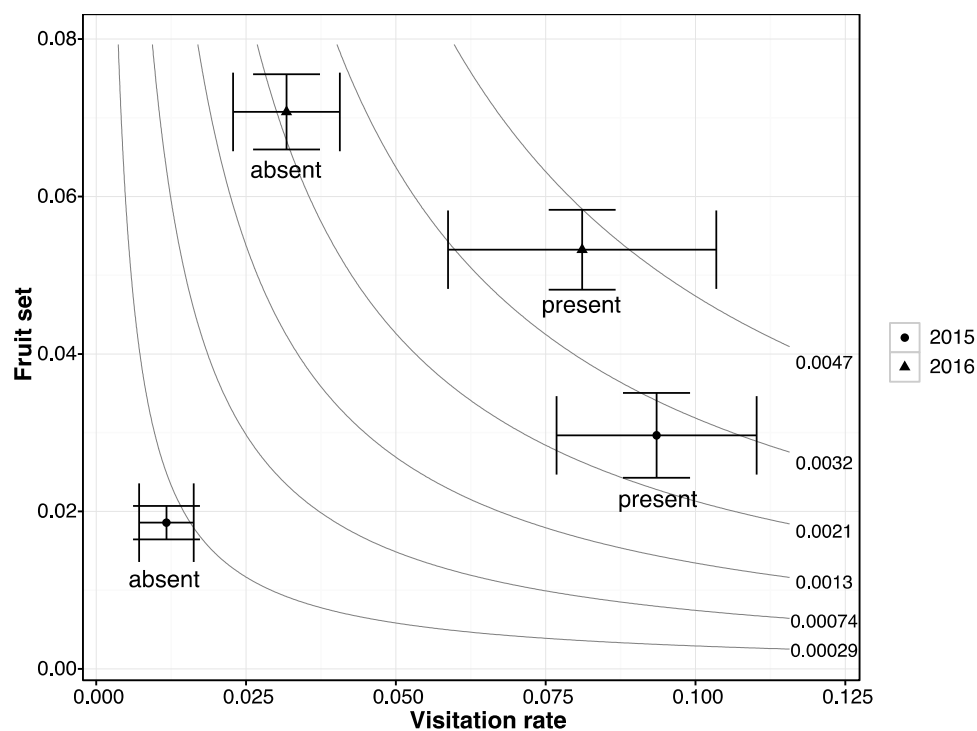

Figure 3. Pollination effectiveness for avocado trees where *Apis mellifera* was present or absent, in two sampling years (2015 and 2016). Visitation rates are measured as visits per flower. Values are presented as mean ± 1SE.

4. Discussion

A diverse assemblage of wild insect species were common visitors of avocado flowers, although honeybees were more abundant (~50% of the observed visits). Despite that fact, several focal trees were visited only by native insects, allowing us to compare pollination outcomes when *A. mellifera* is visiting an avocado tree or not. However, we observed that honeybees altered the structure and functionality of plant–pollinator networks, including connectance, number of links, web asymmetry, and nestedness, similar to previous studies [44,46]. As a result, pollination of our avocado trees was better linked to visitation by wild insects, particularly in a dry year where better pollination was achieved in the absence of honeybees. The hoverfly *Allograpta* sp. (Diptera: Syrphidae) was the most frequent wild floral visitor in both flowering seasons (Table S1) followed by Hymenopterans, similar to most regions where it is grown [50,55,57,58,60].

We observed that the introduction of honeybees into avocado farms had a significant effect on the taxonomic composition of floral visitors, becoming the dominant species. Therefore, the introduction of honeybees results in the biotic homogenization of plant–pollinator interactions [44] through the increase of shared plant–pollinator visitor interactions to the detriment of exclusive interactions.

The disruption of the hierarchical structural organization of plant–pollinator networks induced by the introduction of honeybees, has had negative consequences on the reproductive success of plant species in natural ecosystems [76]. Furthermore, as Garibaldi et al. [77] reported for the invasive African honeybees in Brazil, the dominance of a single species could be an indicator of the degradation of the bee community and, in general, the severity of ecological invasions could have negative consequences for the native bee community [44]. In fact, the presence of honeybees results in an impoverished pollinator taxa diversity and interaction richness [46].

Being aware of the limitations in the spatial representation of our study, we observed that pollination outcome was mainly modulated by the presence of managed honeybees, even more than by climatic variation. Similar to Haedo et al. [49], the contribution of both components and the resulting pollinator effectiveness varied between honeybees and wild floral visitors, indicating a contrasting effectiveness of both groups. We found that wild insects were more effective in pollinating avocado trees than *A. mellifera*, resulting in a higher fruit set as a proxy of avocado-fruit yield. Moreover, their role was more evident during extreme weather conditions, highlighting the importance of wild insects for crop pollination and production [9,78]. We suggest that the increase in the qualitative component of the interaction outcome in the dry year (2016) was due to drought's impact on native vegetation [37,39]. The flowering bloom of an irrigated crop represented an essential resource for a higher diversity of floral visitors, which is ultimately translated into a higher fruit yield. Finally, despite the recent debate on the contribution of Apis and non-Apis bees to crop production [79], based on our results, we recommend, on a larger spatial scale, further studies on honeybee hive density in agricultural landscapes to ensure basal pollination in crops but avoiding undesirable effects on wild floral visitor communities and crops [34].

In our studied crop system, the diversity of floral visitors recorded represented a subset of visitors from native trees from the adjacent sclerophyllous vegetation. For example, 42 and 95 insect species were observed visiting the flowers of two native species of Central Chilean trees over one season in *Quillaja saponaria* (Quillajaceae) [62] and over three seasons in *Escallonia pulverulenta* (Ecalloniaceae) [63]. This is evidence of potential spillover as our study areas were located less than 300 m away from remnant areas of native sclerophyll forest, which likely act as a source habitat for wild insects. That only a subset of insects visit flowers of avocado in the same geographical area could be because (i) avocado flowers have lower attractiveness to local bees [80] or (ii) that the agricultural landscapes and/or conventional management have a negative impact on wild pollinator diversity [81,82]. Therefore, conserving natural areas, hedgerows, or implementing floral strips in crops, could have a positive impact on wild pollinators [83–89]. However, the distance from natural habitats

to crop vicinity has a negative relationship with pollinator diversity [1,2,90], although further studies are required for the southern hemisphere Mediterranean areas. Moreover, land-sharing and conservation strategies could transform pollinator-limited landscapes into more suitable ones by promoting the maintenance of remnant native vegetation within the landscape and even within the crops. Since the use of native vegetation strips within avocado crops has increased the diversity of beneficial insects, including pollinators, with positive consequences for productivity [59,88]. The current stock of honeybee colonies is insufficient to supply the agricultural pollination demand worldwide [12]. Therefore, increasing the contribution of wild insects will improve pollination efficiency and food security.

This is particularly relevant for our studied systems, since ecological intensification encourages management strategies that favor the coexistence of crop fields with biodiversity-rich areas, as these actions translate into a steady provision of wild pollinators and the transference of other ecosystem services (e.g., biological pest control) to the productive land [17,83,88,89,91]. Moreover, the widespread adoption of an ecological intensification framework in the MTE of Central Chile should reduce the negative impacts of high-density monocultures and counteract landscape homogenization [24,92], which completely removes biodiversity-rich native woodlands as exemplified in Figure S1 [19] thereby simplifying the landscapes and decreasing wild-pollinator diversity [81,82]. The use of alternative pollination strategies for avocado production in Central Chile is especially critical during early spring (October), when the flowering period begins, and low spring temperatures are still limiting the activity of honeybees [51]. At that time, many native plant species of the surrounding sclerophyllous forest begin to flower (i.e., late winter and early spring bloom; [93]) and wild floral visitors seem to be better adapted to cope with cool conditions than managed honeybees.

In conclusion, we emphasize the critical role of wild pollinators, alongside *Apis mellifera*, in enhancing crop production. Promoting the conservation of wild pollinators through biodiversity friendly farming practices and raising awareness about their importance is key to safeguarding biodiversity and food security.

Conflicts of Interest: The authors declare no conflict of interest.

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