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The Impact of the Honeybee *Apis mellifera* on the Organization of Pollination Networks Is Positively Related with Its Interactive Role throughout Its Geographic Range

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Abstract: Studies at local spatial scales have shown that the generalist honeybee *Apis mellifera* L. can strongly affect the structural organization and properties of pollination networks. However, there is still little knowledge on how the connectivity of the honeybee within networks (i.e., interactive role) could affect pollination networks at a global scale. To fill this gap, we evaluated how the interactive role of *A. mellifera* could affect niche overlap, specialization, and robustness of pollination networks. We used 109 weighted pollination networks spread across about 94 degrees of latitude and 227 degrees of longitude. We developed a new standardized framework based on species removal to assess the impact of the honeybee on plant-pollinator networks. We found that when the honeybee was removed from the networks, plant species had less niche overlap (i.e., shared fewer interactions via their pollinators) and the networks became more specialized and more robust to species extinctions. Our findings indicate that *A. mellifera*'s effects on pollination networks vary geographically and could influence several ecological and evolutionary factors acting at local scales, including pollination services. We hope this contribution will stimulate new macroecological studies involving abundant and generalist species and their functional roles within ecological communities.

Keywords: ecological networks; floral visitors; functional role; keystone species; species centrality

1. Introduction

A central goal of ecology is understanding the mechanisms and drivers that determine the ecological dominance of species (i.e., high ability of one species to outcompete another due to its large size, population, or productivity) [1,2]. The honeybee, *Apis mellifera* Linnaeus 1758 (Hymenoptera: Apidae), a eusocial insect species, is a prime example of ecological dominance in plant and floral visitor interactions. *Apis mellifera* currently has a nearly cosmopolitan distribution, thriving in regions far beyond its native distribution (i.e., Africa, Europe, and parts of Asia) and occupies a broader range of climatic conditions than those encountered in its native range [3–5]. The ecological success of *A. mellifera* is linked to the species' capacity to adapt to new climatic environments, and because of its flexible foraging behavior, *A. mellifera* is capable of foraging for resources from a wide diversity of flowering plants [6,7]. Moreover, this species can digest a large range of nutrients and dilute toxins and unpalatable compounds due to social behaviors and stores [8–10]. Another aspect of the wide geographic distribution of *A. mellifera* is the diversity of its subspecies/breeds, species' domestication, and introduction by humans [11,12]. In fact,

honeybee keeping has steadily grown in recent decades worldwide, which is linked to the fact that *A. mellifera* is an effective pollinator of many crops and honey production is a profitable activity [13]. In this context, understanding how *A. mellifera* interacts with plants and influences other pollinators is an excellent study system to assess the effects of abundant species on biodiversity patterns and ecosystem functioning.

Studies have shown that generalist species such as *A. mellifera* have a major impact on pollinators in their native and introduced distributional ranges [14,15]. Overall, *A. mellifera* tends to be a locally abundant species and often dominates food and nesting resources [16,17]. Indeed, *A. mellifera* can aggressively and indirectly displace other species of pollinators from floral hosts and, consequently, lead to a reduction in foraging efficiency, fitness, and pollination services of those other species [18–20]. As a result of such exploitative and interference competition with other species, the presence of *A. mellifera* influences how pollinator communities are structured (e.g., abundance, richness, and interaction patterns) and patterns of pathogen transmission [14,21,22]. However, our theoretical and empirical understanding of how the presence of the honeybee influences such patterns, namely the interaction structure among plants and pollinators, remains to be thoroughly elucidated.

The conceptualization of ecological networks of interactions between species allows us to understand how interactive communities are structured and the roles of different species in structuring such communities [23]. In ecological interaction networks, species are represented by nodes and their interactions by links describing the ecological relationships between species. The number of studies using interaction network concepts is increasing and providing new insights into ecosystem functioning, stability, and coevolutionary processes [24–27]. Most of these studies addressed network structural properties covering the general organization of species interactions with biological significance: niche overlap (i.e., the similarity of the compositions of species interactions among species within a trophic level), specialization (i.e., the dependency between species based on the range of resources available), and network robustness (i.e., the ability of a network to avoid coextinctions after species loss) [28,29]. These network descriptors are biologically meaningful because together they describe the degree of niche partitioning and interaction similarity among species and evaluate potential coextinction cascades. Moreover, they are commonly used to describe the organization of bipartite networks, allowing direct comparisons with previous studies on species interaction networks. By using these network descriptors, we can evaluate how the presence or absence of a given species can change network organization. In this sense, empirical studies have shown that some species have high network importance and great influence on other species (i.e., a highly interactive role) [30]. These findings indicate that not all species contribute similarly to the ecological and coevolutionary dynamics of these interaction networks [31,32], and therefore some species are expected to be more influential than others in the organization of species interactions.

Studies have shown that the honeybee may strongly affects the structure and organization of plant–pollinator interaction networks at sites where *A. mellifera* is considered exotic [7,33–36]. In general, the presence of *A. mellifera* increases connectance and nestedness and decreases modularity and interaction links in these pollination networks. Such effects are associated with the foraging behavior of the honeybee which interacts with multiple types of flowering resources, leading to biotic homogenization of interactions in networks with negative impacts on pollination services [7,33–36]. However, these studies have been mainly focused on local spatial scales and consider small regions (e.g., Brazilian biomes, Canary Islands, and the Italian Alps). Therefore, our knowledge and accumulated information on the effect of *A. mellifera* on pollinator networks does not represent the global extent of its current distribution. Consequently, the impacts of the interactive role of honeybees on pollination network organization at the global scale, including both its native and introduced range, remain to be determined.

In this study, we evaluated how the interactive role of *A. mellifera* impacts the niche overlap, specialization, and robustness of pollination networks. For this, we developed

a standardized framework based on in-silico species removal from networks to assess the potential impact of *A. mellifera* in over 109 pollination networks across the globe. In general, we postulated that the impact of *A. mellifera* on the organization of pollination networks should be positively correlated with its interactive role within such networks. This is because Cruz et al. [37] recently showed that *A. mellifera* has a highly interactive role in global pollination networks. However, this role varies geographically and is shaped by environmental (e.g., temperature and precipitation) and anthropogenic factors (e.g., disturbance). Therefore, despite some studies showing that A. mellifera establishes a large number of interactions within pollination networks [7,33–36], it is expected that in those sites where *A. mellifera* is more connected to other species by multiple direct and indirect pathways (i.e., higher interactive role), its removal from these sites should have a greater simulated effect on the organization of these networks. Here, we calculated the potential impact of *A. mellifera* on the values of network metrics by removing this species from the networks and compared them to random species removal simulations (i.e., standardized effect). It is very important to note that removal simulation studies may not represent the real experimental conditions in the field but help us produce theoretical outcomes that improve our ability to predict potential changes under controlled conditions. Overall, we advanced the knowledge of macroecological patterns of plant-pollinator interaction networks, demonstrating how the interactive role of *A. mellifera* across its geographic range directly impacts the organization of plant-pollination networks. We hope this contribution will stimulate new macroecological studies involving abundant and generalist species and their functional roles within ecological communities.

2. Materials and Methods

2.1. Interaction Network Dataset

We compiled species interaction networks available in the literature from 1976 to 2021 that contained information on floral visitor species (including *A. mellifera*) foraging on plant species (Figure 1 and Supplementary Materials Table S1) [38–63]. Such information was obtained by using the scientific web search engines Google Scholar, Web of Science, and Scopus using the keywords "pollination networks", "plant–floral visitor networks", "floral–visitor networks", and "flower-visitor networks". Moreover, we also compiled interaction networks available in the online repositories Web of Life (http://www.web-of-life.es) and Dryad (https://datadryad.org/stash) (accessed on 24 January 2022). Note that we only used weighted networks as metric estimates are less susceptible to sample effort biases than binary networks [64]. Plant-hummingbird networks, plant-bee networks, plant-bat networks, and other taxonomically restricted networks were excluded. Detailed information on the exclusion and inclusion criteria of the interaction networks used in this study is shown in Figure S1. Of the 109 networks compiled, only three (2.75%) were obtained from thesis. All other networks were taken from papers and online datasets.

2.2. The Interactive Role of Apis mellifera

To measure the interactive role of *A. mellifera* within each pollination network, we considered four species-level descriptors: species degree, betweenness centrality, species strength, and Katz centrality using the bipartite package [65] implemented in R [66]. We chose these descriptors because they provide complementary biological information on species centrality within interaction networks. Therefore, estimates of the interactive roles of species in interaction networks are expected to be more robust when based on complementary information than on a single measure. Species degree (k) is the number of plant species with which *A. mellifera* interacts [67]. Betweenness centrality describes the shortest paths connecting pairs of floral visitor species using *A. mellifera* as a potential bridge [28–68]. Species strength quantifies the cumulative importance of *A. mellifera* using the sum of dependencies across all the flowering plants visited by this bee species [69,70]. Katz centrality calculates the number of immediate neighbors and the direct and indirect paths of *A. mellifera* to other species in the network, either plants or floral visitors [71]. All

equations and data distributions of the four species-level descriptors are shown in File S1 and Figure S2, respectively.
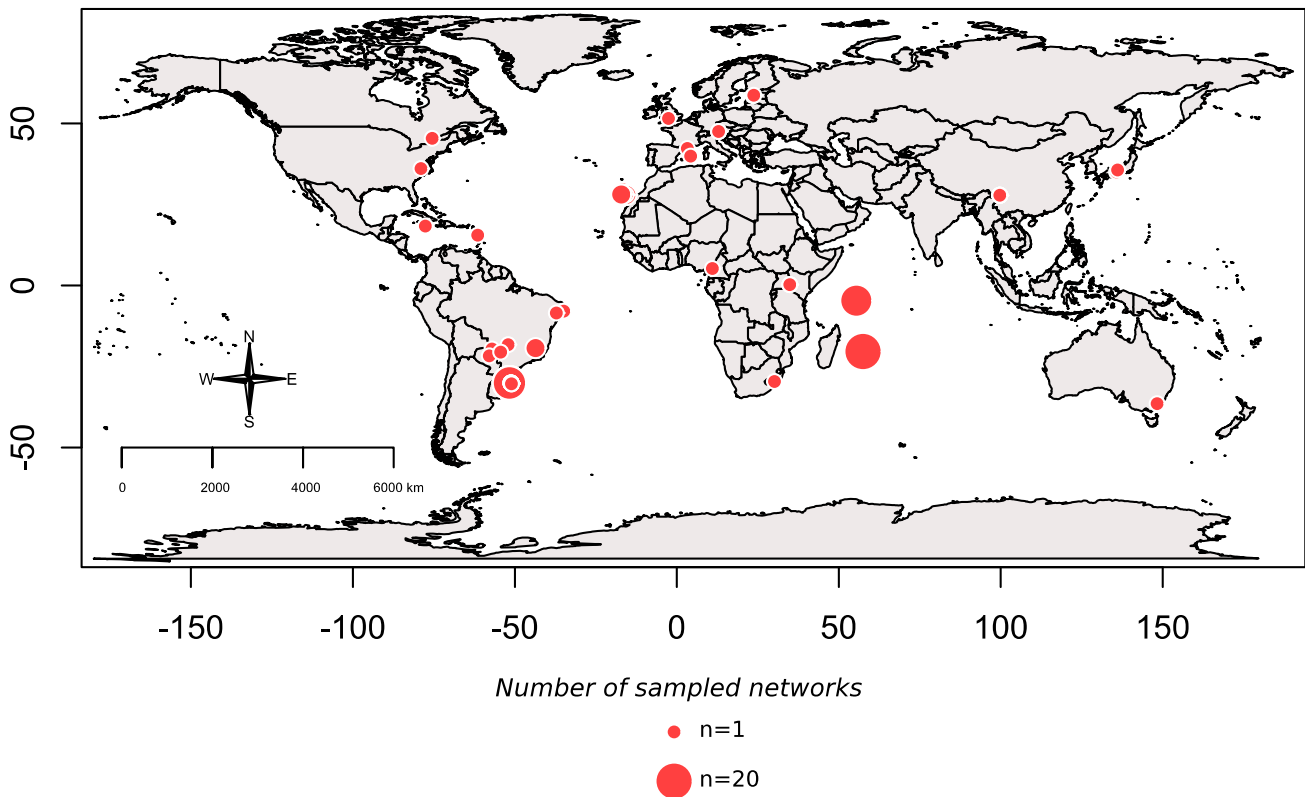

Figure 1. World map showing the spatial distribution of the 109 weighted pollination networks compiled in this study. Although some networks were sampled within the same or nearby sites, they are at 68 different geographic coordinates.

Because centrality measures are highly correlated (Figure S3) we used a principal component analysis (PCA) to reduce the four-dimensional space to a single generalized centrality index represented by the scores on the first principal component as often used in specialized literature [30,72,73]. This generalized index summarized the information on the interactive role of *A. mellifera*. The first principal component (PC1) accounted for 68.2% of the variability, indicating complementarity among the four metrics of centrality despite being correlated (Figure S1). Then, we rescaled this PC1 axis by adding up the absolute value of the minimum PC1 score plus one ten-thousandth of a unit. Therefore, all PC1 scores were greater than zero, but the order and distance among them remained the same. Because the four-centrality metrics correlated positively with PC1, high PC1 scores indicated that *A. mellifera* has a highly interactive role and is connected to other species by multiple direct and indirect pathways.

2.3. Estimating Specialization, Niche Overlap, and Robustness

Each pollination network was built by an interaction matrix A with r floral visitors and c plant species. The matrix body, $A_{r,c}$ contained the number of times the plant species c interacted with the floral visitor species r. We calculated the plant's niche overlap, specialization, and robustness for each pollination network using the bipartite package [65] in R [40].

We calculated the plant's niche overlap using Horn's index (*NO*), which provides information on the similarity of plant species' interactions [74]. This index ranges from 0 to 1, where lower values indicate no common use of partners and higher values indicate high similarity in plant interactions. We focused only on the plant's niche overlap to assess

how *A. mellifera* could influence the similarity of floral visitor composition shared between plants. Network specialization was estimated using the complementary specialization (H_2') index. This index quantifies the extent to which interaction frequencies deviate from an expected random probability distribution of interactions. This probability is based on random encounters between trophic levels and is weighted by the total frequency of each species using Shannon entropy [75]. The values of complementary specialization H_2' range from 0 (complete generalization) to 1 (complete specialization) [75].

We calculated the robustness of pollination networks to floral visitor extinction based on simulating cumulative removals of species from the network using their number of links (i.e., species degree) as an extinction criterion [76]. We used a systematic removal from the most to the least connected species as expected in a catastrophic scenario, where the most connected species have a higher extinction risk. Specifically, we removed one floral visitor species and those plant species connected to it, indicating secondary losses. Afterward, we removed all remaining species based on their degrees until all floral visitor species were removed. Then, we calculated the area under the coextinction curve to estimate the network robustness (R) [76]. Here, $R = 1$ corresponds to a very slight decrease in the extinction curve until the point at which almost all species were removed (i.e., a more robust network), and $R = 0$ corresponds to a swift reduction in the extinction curve and, therefore, represents a less robust network.

2.4. Weighted Impact of Apis mellifera on Pollination Networks

Some studies have calculated the impact of *A. mellifera* on network metrics by removing this bee species from the network [33,77]; that is, all the honeybee interactions and those plant species exclusively connected to this species. Then, they estimated the percentage change in the values of each metric with and without *A. mellifera*. However, this is not an adequate measure to assess the impact of *A. mellifera* on network organization mainly because when removing any species and their interactions from a network, the metric values will change. In other words, with this approach, it is difficult to accurately estimate whether the impact is only due to removing *A. mellifera* itself or any other species that go with it (i.e., changes in network size). To control this possible bias, we calculated the weighted impact of *A. mellifera* on the values of network metrics (i.e., specialization, niche overlap, and robustness).

For each of the networks ($A_{[r,c]}$, r = floral visitors and c = plant species), we extinguished one floral visitor node (r_i) at a time. Removing a specific floral visitor implies removing all of its interactions and plant nodes that exclusively interacted with the removed floral visitor node. Thus, for each network we have as many estimates of the metric values as there are floral visitors in the network. Each network had a specific metric estimate, M_{Am}, representing the extinction of *A. mellifera*, while all other M_i estimates represent the extinction of other floral visitors. For each network, we averaged the metric estimates when floral visitors other than *A. mellifera* were removed ($\overline{M}$). Then, the weighted impact of the removal of *A. mellifera* from the networks was calculated as $(M_{Am} - \overline{M})/(M_{Am} + M_{Am})$. A schematic representation of the calculation is presented in Figure S4. Positive values of the weighted impact indicate higher metric values when *A. mellifera* is excluded. In contrast, negative values of the weighted impact indicate that the average response when floral visitors other than the honeybee were removed was higher.

3. Data analysis

To test whether the standardized impact of *A. mellifera* on specialization, niche overlap, and robustness could be affected by the interactive role of *A. mellifera* in the pollination networks, we used generalized additive mixed models (GAMM) with gaussian error distributions and identity link functions. In these models, we used the positive scores of PC1, describing the interactive role of *A. mellifera* as the smoothed explicative variable and network metrics and the weight impacts of *A. mellifera* as response variables. GAM models are sensitive to the number of splines (k), and even a relatively low number of splines (4+) can lead to overfitted models with response oscillations with no biological meaning. Therefore, we fixed the number of splines to three (k = 3) with the low rank isotropic smoother (*bs = tp*), which is sufficient to predict nonlinear responses including those with marked asymptotic behavior [78]. Because some networks were sampled within the same site, we used the network's original location as a random factor to control for this hierarchical nature of our study and to incorporate dependency among measurements within sites. All models were built in R [66] using the *gamm* function in the *mgcv* package [79].

To verify that GAMM models represented a good fit to the data, we visually explored the residual behavior in two ways. First, we plot the theoretical quantiles of a normal distribution against the residuals' quantiles. If normally distributed, the plot will depict a straight-linear pattern in the middle sector with slight to marked departures at the tails, a common pattern even when data are truly randomly extracted from a theoretical normal distribution. Also, we plotted the predicted values against the residuals to assess the variability of the error (departure from the theoretical expectation, zero) all through the model predictions. Here, we can conclude that the assumption of homoscedasticity is met when there is an equally variable normal-random departure from zero all through the predicted values.

4. Results

Across all 109 networks, *A. mellifera* interacted with 380 different plant species. Within individual networks, *A. mellifera*'s degree ranged from 1–38 plant species with an average degree of 6.23 ± 5.72 (mean ± standard deviation) plant species at each site.

When evaluating the weighted impact of *A. mellifera* on pollination networks, we observed a negative impact of the interactive role of *A. mellifera* (PC1 scores) on the values of the plant's niche overlap (*NO*), indicating that pollination networks without *A. mellifera* had less niche overlap (GAMM: F = 49.06; $p < 0.001$; $R^2_{(adj)}$ = 0.441). Our findings showed that pollination networks without *A. mellifera* had less niche overlap and decreased sharply as the interactive role of *A. mellifera* increased in the networks (Figure 2A). For specialization, we found a positive impact of the interactive role of *A. mellifera* (PC1 scores) on the values of network specialization (H_2'), indicating that pollination networks without *A. mellifera* were more specialized (GAMM: F = 31.68; $p < 0.001$; $R^2_{(adj)}$ = 0.341) (Figure 2B). Finally, we found a positive impact of the interactive role of *A. mellifera* (PC1 scores) on the values of network robustness (*R*), indicating that pollination networks without *A. mellifera* were more robust to species extinction (GAMM: F = 12.52; $p < 0.001$; $R^2_{(adj)}$ = 0.156) (Figure 2C). The three GAMM models were a good fit to the data. Residuals followed the pattern expected from a theoretical normal distribution, and there was no marked bias in models' predictions (homoscedasticity). Support plots are shown in Figure S5.
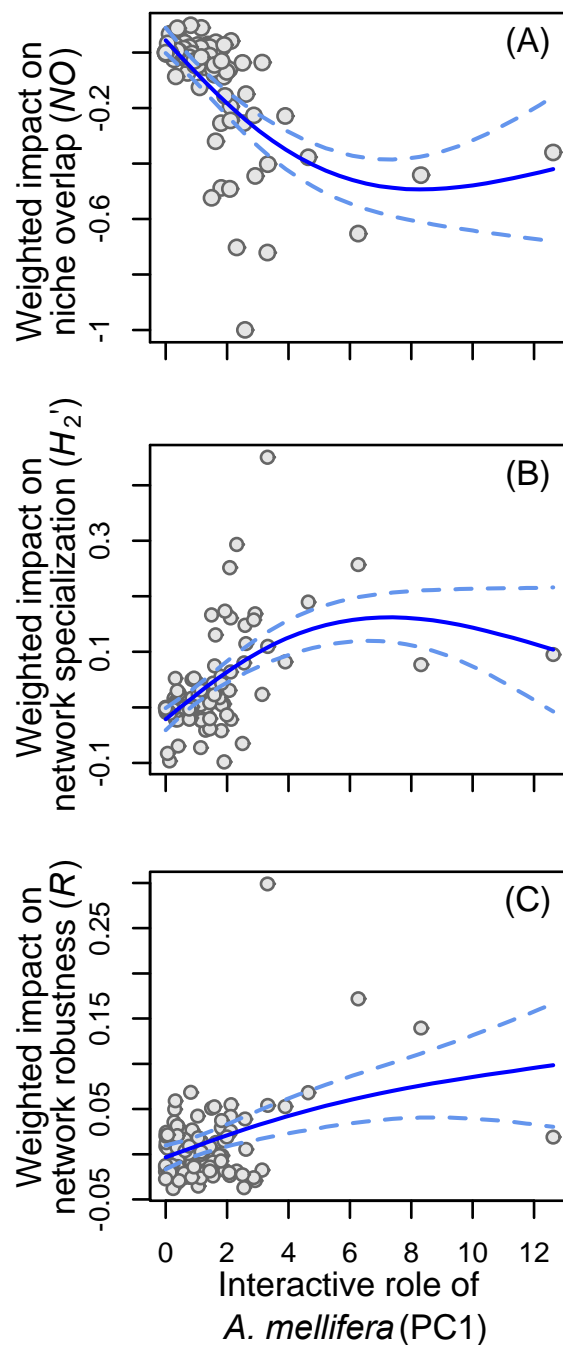
Figure 2. Standardized impacts of the interactive role (PC1) of the honeybee *Apis mellifera* after its exclusion from the pollination networks by using random species removal simulations on (**A**) plants' niche overlap (GAMM: F = 49.06; $p < 0.001$; $R^2_{(adj)}$ = 0.441), (**B**) specialization (GAMM: F = 31.68; $p < 0.001$; $R^2_{(adj)}$ = 0.341), and (**C**) robustness to species extinction (GAMM: F = 12.52; $p < 0.001$; $R^2_{(adj)}$ = 0.156). Negative impacts indicate that pollination networks without *A. mellifera* had lower values of the metrics, while positive impacts indicate that pollination networks without *A. mellifera* had higher values of the metrics (see text for details). The dotted lines represent 95% confidence limits.

5. Discussion

Using an extensive and geographically broadly distributed dataset, we showed that the impact of *A. mellifera* on the niche overlap, specialization, and robustness of pollination networks is correlated with the interactive role *A. mellifera* in these networks. These findings show that *A. mellifera*'s effects on pollination networks were not homogeneous across space,

suggesting that the impact of *A. mellifera* on pollination networks could influence both ecological and evolutionary factors acting at local scales. Our results also indicate that the impact of *A. mellifera* on the organization of pollination networks differs between sites (i.e., some sites tend to be more vulnerable to *A. mellifera* than others).

Previous efforts e.g., [33] compared network estimates with and without *A. mellifera* overseen that fact that any *in-silico* extinction will affect the metric values. Here, we used a new framework in which the effect of in-silico extinction of *A. mellifera* was weighted against the average effect of the extinction of the other floral visitors. It is important to highlight that our framework could be applied to any study involving in-silico extinction of species within interaction networks Here, we showed that when the honeybee is removed from the networks, plant species tend to have less niche overlap (i.e., share fewer interactions via their pollinators) and the networks tend to become more specialized. Specifically, the more *A. mellifera* is directly and indirectly connected with other species within the networks (i.e., higher centrality), the more it could affect plant niche overlap and the specialization of the interactions between all species, meaning that *A. mellifera* tends to increase the homogenization of interactions within pollination networks. In fact, a study performed by Giannini et al. [7] showed that the number of interactions of *A. mellifera* within pollination networks is directly related to a higher niche overlap. Our findings also agree with a recent study by Corcos et al. [35], which showed that an increase in the abundance of *A. mellifera* leads to greater specialization of other pollinators on plants, that possibly change their floral hosts possibly to avoid competition with *A. mellifera.* (i.e., pollinator niche rewiring [54,80]). Moreover, *A. mellifera* would lead to greater exploitative or interference competition per resource, not only between pollinators and their preferred floral hosts, but also between plants by their effective pollinators. This is because *A. mellifera* could monopolize the resource and move pollen loads among different species (which does not favor effective pollination), impairing the reproductive success of plant species that are highly visited by honeybees [34], disrupt the seasonal dynamics [81], and alter plant genetic structure [82]. Furthermore, the homogenization of interactions by generalist species could disrupt native coevolutionary systems [33,83], mainly because these generalist species promote trait-matching and convergence through direct and indirect interactions [32]. Therefore, this threat is of particular concern in regions where the honeybee has been introduced [33,84] and where it plays a higher interactive role in plant-floral visitor networks [37].

We also found that when *A. mellifera* is removed from pollination networks, these networks tend to become more robust to species extinction. These results partially contrast with those of Santos et al. [33] where the authors showed that although *A. mellifera* did not affect network robustness, this bee species changes the structure of six native pollination networks in the Brazilian Caatinga (i.e., decreased nestedness and increased modularity caused by the removal of this bee species). Also, in partial contrast to our results, Corcos et al. [35] showed that network robustness increased with increasing honeybee abundance in the Italian Alps. However, note that like niche overlap and specialization, we show that the magnitude of the impact of *A. mellifera* on network robustness to species extinction is proportional to its interactive role within pollination networks and not just to its presence and abundance as studied by Santos et al. [33] and Corcos et al. [35]. It is imperative to highlight that all these studies have been focused on small spatial scales. Therefore, our study is the first assessment of the interactive role of *A. mellifera*, covering much of the global extent of the species' current distribution. Overall, by using a simulation approach, we found that a higher interactive role of *A. mellifera* could affect not only how plants and pollinators interact within pollination networks, but also the fragility of those interactions to possible species extinction events.

We suggest that the significant impact of *A. mellifera* on the niche overlap, specialization, and robustness of pollination networks shown in this study occurs precisely in disturbed sites and where it is exotic, which could strongly impact the stability of these pollination systems. This is because as we recently showed in Cruz et al. [37], *A. mellifera* has a higher interactive role at sites where it is exotic compared to sites where the species is

native. Moreover, some studies have shown that *A. mellifera* tends to be more abundant in disturbed habitats [37,85] and is likely to favor invasion by exotic plant species [86]. Therefore, efforts related to the conservation and restoration of the ecosystems need to reestablish community function and mitigate the homogenization of interactions generated by *A. mellifera* [57,87] since this species could have a greater interacting role in more disturbed environments.

Mainly due to the domestication, management, and commercialization of *A. mellifera* as a pollinator and honey producer in different regions of the planet, the number of honeybee workers and the foraging of this species on plants has increased in recent decades (i.e., greater interactive role in networks' pollination) around the world. Recent studies have shown that resource overlap between wild pollinators and *A. mellifera* increase with increasing trait similarities [88]. Further, the short-term deployment of honeybee colonies could negatively affect the foraging of other bee species within pollination networks (mainly bumble bees and carpenter bees) [36]. In this sense, Valido et al. [34] also assessed the effects of pre- and post-establishment stages of hives of *A. mellifera*. These authors showed that this honeybee disrupts the hierarchical structural organization of pollination networks (i.e., loss of interactions by generalist species and impairs pollination services by wild pollinators) and reduces plant reproductive success. This increase in the interactive role of *A. mellifera* could have a strong effect on the organization and structure of biotic interactions between pollinators and plants at the local level, especially on those pollinators that share floral hosts with *A. mellifera*. On the other hand, it is important to mention that this species can be an effective pollinator of wild plants and crops, especially at those sites where native bees have already been extirpated by other factors (e.g., habitat loss and fragmentation) [89].

We emphasize that all patterns reported here are based on *in-silico* extinctions, a first step that need to be supplemented by field experimentation. Future studies should assess what determines a greater or lesser interactive role and abundance of the honeybees within local pollination networks since this species disrupts and influences the organization of pollination networks [7,33–36]. Also, there is a need of field experimental research to address changes in abundances of floral visitors, temporal variations, frequency of flowers visitation, rewiring and reweighting of interactions in interactive networks when *A. mellifera* is locally excluded. Because *A. mellifera* is managed worldwide to provide pollination services in may crops, further research must consider not only the impacts of *A. mellifera* on interactive networks of wild floral resources but there is an urgent need to explicitly incorporate cultivated floral resources.

In conclusion, we showed that the higher the interactive role of the honeybee *A. mellifera* within pollination networks, the higher its impact on plants' niche overlap, specialization, and robustness in such networks. Specifically, in sites where the honeybee was a higher generalist floral visitor, the niche overlap of the plants increased while the specialization and robustness of the interaction networks decreased.

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