

Partitioning the contribution of bees with different traits and hoverflies to flower-visitor interaction networks

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ABSTRACT

Insect pollinators are key to maintaining biodiversity and providing important ecosystem services. Among them, bee species (i.e., Apidae) and hoverflies (i.e., Syrphidae) are two of the most important and well-studied taxa worldwide. Yet, their relative contribution to the structural and dynamic properties of plant-pollinator interaction networks remains poorly understood. This is an important gap in knowledge given that these phylogenetically and functionally different groups might play different roles within their communities and respond in contrasting ways to anthropogenic perturbations.

Here, we study the relative contribution of bee species (with different traits) and syrphids to maintain network properties (i.e., nestedness, network specialization (H2), and interaction diversity) and their influence on the temporal dynamics of these network metrics. To this end, we simulate species removals in community-wide flower-arthropod visitor interaction networks. These interactions were extensively sampled across four years in two different near-pristine temperate ecosystems in Japan.

We found that bee species contribute significantly more than syrphids or any random combination of species to network nestedness, low specialization, and interaction diversity across months and years. In addition, bees also played a particularly important role in maintaining the observed temporal dynamics over time. Conversely, although syrphids were an abundant and species-rich group, they did not contribute so prominently to network metrics or temporal dynamics, with the exception of network complementary specialization, to which they contributed positively. In addition, smaller bee species and those that were active for longer periods were particularly important for interaction diversity and the number of interactions, respectively, and to maintain observed network temporal dynamics.

Our results support that bee species, and especially the small ones, are cornerstone contributors to plant-visitor communities by shaping network properties and network temporal dynamics in natural ecosystems.

1. Introduction

Insects that visit flowers are critical for the functioning of many ecosystems, playing a vital role in the maintenance of biodiversity and the provision of pollination ecosystem services (Gallai et al., 2009; Klein et al., 2007; Porto et al., 2020). Yet, many pollinators are endangered due to human-induced global-change drivers (Goulson et al., 2015; Potts et al., 2010). Some of these anthropogenic impacts are known to affect different pollinator groups in contrasting ways. For instance, bees (i.e., Apidae) and hoverflies (i.e., Syrphidae), which are considered two of the most widespread and effective pollinator groups (Doyle et al., 2020;

Potts et al., 2010; Willmer et al., 2017), can respond differently to land-use changes (Jauker et al., 2009; Persson et al., 2020). Despite the key importance of bees and hoverflies and their likely different responses to some anthropogenic impacts, we still know little about their relative contribution to the structure and dynamics of plant-pollinator systems when the whole community of plants and flower visitors is considered. To gain insights into their different roles, traditional study frameworks such as focusing on species richness or abundance alone might not be sufficient. Instead, examining their importance in shaping the structure and temporal stability of plant-flower visitor interaction networks might prove more insightful (Mathiasson & Rehan, 2020; Poisot et al., 2015;

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Tylianakis et al., 2010; Valiente-Banuet et al., 2014) to understanding how these two groups differentially contribute to such communities.

Phylogenetically and functionally distant groups, such as bees and hoverflies, can play different roles in plant-pollinator interaction networks. Bees are characterized by having high per capita visitation rates and a high degree of trophic plasticity, being often able to change the plant species they use according to their environment (e.g., number of competing species or floral availability) (Klinkhamer, 2006; Waser et al., 1996; Williams et al., 2010; Winfree, 2010), and with that, the structure of plant-pollinator networks (Spiesman & Gratton, 2016). Therefore, bees might promote high interaction diversity, overall low specialization (H2), and low niche overlap. In addition, although many bees are generalist foragers, some others are more specialized, covering a wide spectrum in the generalist-specialist gradient (Klinkhamer, 2006). Since highly rewarding flowers are often visited by both generalists and specialists, bees could be a key group promoting the nested structure of these interaction networks, which is often associated with low competence and high community stability (Bastolla et al., 2009). On the other hand, syrphids are very active and overall generalist flower-visitors too, so they might increase the number of interactions (Klecka et al., 2018). Yet, they are putatively regarded as more selective than bees, and thus, they might contribute significantly to network specialization. In addition, different syrphid individuals and families seem to show some degree of complementary preference for different flowers (Klecka et al., 2018; Lucas et al., 2018a; Moquet et al., 2018). Therefore, their presence in the networks might reduce niche overlap. Although these considerations are crucial to better understanding the function of these two groups in their communities, they have been rarely explored. On top of this, the few studies comparing bees and hoverflies have focused on disturbed or highly anthropized ecosystems (Jauker et al., 2009; 2019; Persson et al., 2020). Therefore, we still know little about how these two groups contribute to shaping plant-flower visitor networks in near-pristine environments, in the context of the whole community of plants and flower visitors. Acquiring this knowledge can help us gain insights about their primary roles in their natural environments. In addition to their significance for structural network properties, the impact of various groups on the temporal dynamics of networks is a crucial aspect to consider too. Yet, this has been an aspect little explored to date.

Species with different functional traits have the potential to exhibit different behaviours, thereby exerting dissimilar impacts on network structure as well (Kendall et al., 2022). For example, in complex tropical systems, larger bee species display greater selectivity and specialization, while smaller species with shorter tongues tend to visit more open flowers, displaying a more generalized interaction pattern (Raiol et al., 2021). Furthermore, certain species show longer periods of activity throughout the year, while others have shorter active periods. Consequently, it is expected that species with different traits will contribute differentially to the structure and dynamics of plant-flower visitor networks. Although the influence of plant traits on species' roles in interaction networks has been recently explored (Lanuza et al., 2023; Lázaro et al., 2020), the relationship between bee traits and these networks remains uncertain.

In this study, we assessed the relative contribution of bees (also bees with different traits), and syrphids to network structural and temporal properties in a community-wide context. We use a well-documented set of community-wide insect-flower interaction networks in two semi-pristine forests across several months and four years (Inoue et al., 1990; Kato et al., 1990). We ran simulations in which we removed bees or syrphids from the community and calculated the effect on network metrics. Then, we compared the effect of each scenario against null scenarios (i.e., random removals) on network metrics across sampling dates. Certain groups may exert substantial influence on the networks' stability and dynamics consistently throughout the year, while others might have sporadic importance without assuming a pivotal role over time. Based on this simulation procedure, we examine four main

working hypotheses: i) Bees will be main contributors to network nestedness, low network specialization, and high interaction diversity; ii) Syrphids will contribute to higher specialization; iii) Bee species will contribute more than syrphids or any random group of species to the temporal dynamics in network properties across time due to their high relative weight on network structure and high species turnover, despite encompassing only 8–10 % of all flower-visiting species in the observed community; iv) the contribution of bees to network metrics and dynamics will be heterogeneous across species depending on their body size and the length of their activity period.

Improving our understanding of the role played by bees, syrphids, and bee species with particular traits in network metrics and dynamics, will provide in-depth knowledge about how plant-flower visitor networks work and about the implications of the loss of different types of species.

2. Materials and methods

2.1. Study sites

Data were acquired from two investigations led by Professor Makoto Kato, encompassing a comprehensive collection of flowering plants and their associated visitors in two remarkably biodiverse natural environments within the Kyoto prefecture, Japan. The data collection spanned from 1984 to 1987. The first study location was the Ashiu beech primary forest, while the second was the Kibune temperate deciduous forest (Fig. 1) (see Table S1 for a more detailed overview of each habitat type and the corresponding coordinates). Both Ashiu and Kibune sites were meticulously surveyed over a period of 30 and 47 days, respectively, during the years 1984 to 1987. These investigations mainly served to meticulously characterize the entirety of the flower-visiting community in these areas through several years (Fig. S1), but also provided an in-depth account of species phenology (Kato et al., 1990). These studies represent two of the most comprehensive temporal community-wide interaction networks to date, offering additional value due to their sampling location in Japan—an island boasting remarkable and distinct biodiversity within the Asian region.

2.2. Sampling methods

Sampling procedures were designed to characterize a comprehensive range of flower-visitor interactions, with detailed descriptions available in Kato et al., 1990, and Inoue et al., 1990, and synthesized herein. Specifically, sampling typically started between 9 and 10 am on fine days devoid of rain and wind during the flowering season, spanning from April to early November, over a span of four years, commencing in 1984. Two distinct routes were carefully chosen to conduct the samplings: the first route traced along the Kamidani stream and the Nodabata bog (Ashiu location), while the second route was conducted along the Asoga stream and the Kibune river (Kibune location).

During the census days, researchers walked the designated routes, surveying for the presence of all the flowering plants. The sampling methodology entailed quantitatively assessing the interactions between insect visitors and flowers. At each sampling location, arthropod visitors were methodically captured using nets for an approximate duration of 10 min, adhering to a meticulous protocol. During the initial 8 min of the sampling interval, exclusive attention was directed towards capturing flying insects approaching the flowers, thus ensuring minimal disturbance of the plants. In the subsequent two minutes, an exhaustive sweep of insects both on and within the flowers was carried out, allowing for the collection of a comprehensive array of arthropods. Diverse insect groups exhibited varying capture patterns during these distinct time intervals, with hymenopterans and dipterans predominantly captured during the initial 8 min, while coleopterans and hemipterans featured prominently in the subsequent sweeping phase. The resulting samples encompassed a diverse spectrum of flower visitors, including authentic

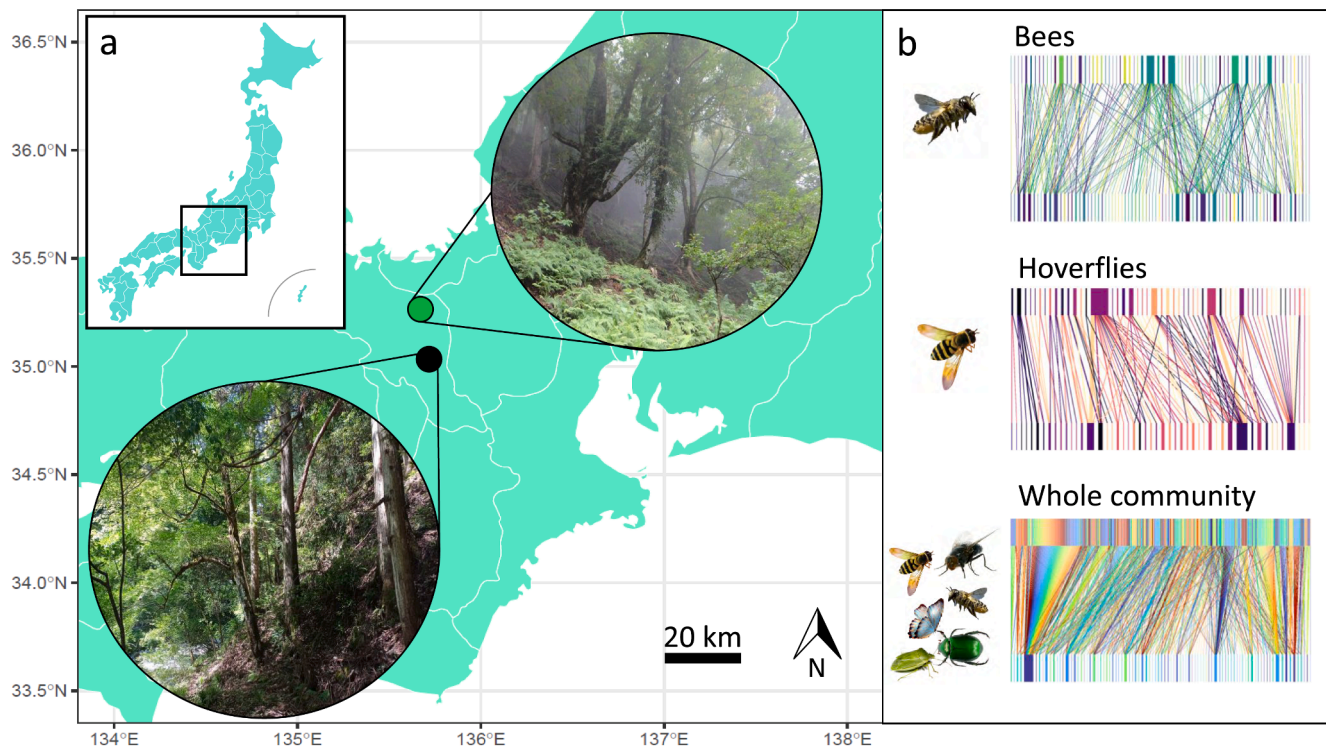


Fig. 1. a) map of Japan showing the two sampling locations and the ecosystems sampled (Ashiu beech forest (green symbol) and Kibune deciduous forest (black)). b) Interaction networks including the interactions in Ashiu between plant species and: only bees, only hoverflies, and the whole flower-visiting community. Photo of Ashiu Forest kindly provided by Dr. Kazuya Takeda.

consumers of nectar and pollen, ambush predators, feeders of flower petals and plant leaves, and insects present within the floral environment. It is important to highlight that these categories collectively represent the entirety of the arthropod flower-visitors community, thereby enabling a comprehensive understanding of the intricate dynamics at play.

Sampling intervals were subject to variation. Typically, during the period spanning from 1984 to 1986, the sampling intervals were typically biweekly, while in 1987, they were reduced to a weekly cadence. Each sampling session had a duration of up to six hours, contingent upon the abundance of flowering plants encountered during the survey. Specific sampling dates for each year were registered with each sample (further details regarding these dates can be found in Table S2). To facilitate subsequent analyses and taxonomic classifications, every arthropod specimen collected during the sampling campaign was labelled and affixed with complete census data encompassing the date, locality, and specific flower (i.e., plant species) associated with the specimen. Identification of these specimens was conducted at the species level by esteemed specialists acknowledged in the original studies (Inoue et al., 1990; Kato et al., 1990). In cases where specific identification was unattainable, higher taxa codes were employed to categorize the specimens by morphospecies level. Currently, these specimens are kept at the Kyoto University Museum, ensuring their availability for future studies.

These flower-visitor data were used to build community-wide quantitative bipartite interaction networks.

2.3. Interaction networks

For each site and sampling date consisting of about six hours of active sampling, we built an interaction network, from which we calculated network metrics. We focused on three metrics deemed important for robustness and pollination efficiency in pollination systems (Kaiser-Bunbury & Blüthgen, 2015; Martínez-Núñez et al., 2019), but also

calculated three extra ones to gain a deeper understanding of the processes at play.

First, we calculated NODF (nestedness metric based on overlap and decreasing fill) (Almeida-Neto et al., 2008). The NODF is a measure of the nestedness of a network, and it is a metric that normalizes for matrix size, allowing matrices of varying sizes to be compared. Nestedness is a sign of complex mutualistic networks (Almeida-Neto et al., 2008), and is frequently associated with system stability and resilience to perturbations (Burgos et al., 2007; Schwarz et al., 2020). Second, we calculated the H2 index, which represents the amount of “complementary specialization” or selectivity in a bipartite network. This index shows the level of specialization or partitioning throughout the whole network and quantifies how much the observed interactions differ from what would be predicted given the marginal totals of the species. H2, which is derived from Shannon entropy, increases as the observed interaction frequencies deviate from the predicted frequencies. It serves as a network-level index for comparisons between various interaction webs. Its lowest and maximum values are often used to normalize the measure between 0 and 1 for extreme specialization vs extreme generalization, respectively. Third, we measured the Shannon diversity of interactions (i.e., the variety and evenness of different types of interactions within a network). This measure is positively linked to species diversity, ecosystem complexity, ecosystem health, and depends secondarily on the degree of specialization or generality of the interacting species. Fourth, we measured the niche overlap of the flower visitors by calculating the similarity of their interaction patterns. This informs us about the extent to which different species interact with the same set of partners, providing insights into the degree of possible resource competition in a community.

Lastly, we also calculated the connectance and number of total interactions to understand the implications of the different scenarios in these two measures. Connectance shows the proportion of all the links that actually occur, where a value of 0 indicates no interactions and a value of 1 indicates that all plant species interact with all pollinator

species. Some of the network metrics were correlated (Fig. S2), and then, we focused on the three that we considered more informative and conceptually interesting: NODF, network specialization, and interaction diversity. However, we show results concerning connectance, niche overlap and the number of interactions too, in [Supplementary Material](#).

2.4. Species traits

We collected information about two important bee traits: body length (in mm) and length of the activity period (in months). Size is a key trait that can affect the ecology of bees. For instance, it has been related to their dispersal capacity, foraging range, or pollen-carrying capacity ([Greenleaf et al., 2007](#); [Kendall et al., 2022](#)). On the other hand, the number of months when species are active can be associated with their capacity to tolerate a wider range of climatic and environmental conditions and can also indicate the capacity to use diverse resources ([Herrera et al., 2023a](#)). These two traits might be related to the role or contribution of bee species in their communities, as revealed by interaction networks. To obtain a representative and non-biased measure of species' mean trait values, and ensure independence between explanatory and response variables ([Moretti et al., 2017](#); [Violle et al., 2007](#)) (i.e., avoiding circularity issues), we obtained traits from literature specialized in bee fauna from Japan ([Tadauchi, 2014](#)) instead of measuring voucher species. For bee morphospecies (20 % of species), we used the median value of the congeneric species found in Japan. Species traits were not significantly correlated ([Table S3](#)), however, there was a significant positive correlation between bee size and the number of interactions in which that species was involved, bee size and frequency of occurrence, and bee activity ([Potts et al., 2010](#)) and number of interactions or frequency of occurrence (only significant in Kibune forest) ([Table S3](#)).

2.5. Statistical analyses

All the analyses were run in R version 4.2.2 ([R Core team, 2022](#)).

First, to examine the contribution of bees and hoverflies to network metrics (hypotheses i and ii), we first simulated two scenarios with their respective null models. The first scenario consisted of randomly removing 90 % (but see sensitivity analysis) of the bee species observed in a location (considering all the samples collected in Ashiu or Kibune forests) and calculating the network metrics for each sampling date independently. Then, we removed an equivalent number of species of any group randomly and repeated the calculation. This process was iterated 100 times for the bees and the null model. In the second scenario we did the same but focusing on hoverfly species (i.e., Syrphidae). We removed species instead of links to evaluate the contribution of species while accounting for differences in the number and diversity of interactions in which they are typically involved (e.g., removing only links might lead to the conclusions that different species contribute similarly, while this would only be true under the assumption that they engage in the same number of interactions). We calculated the six metrics (i.e., NODF, H2, Shannon diversity of interactions, niche overlap, connectance and number of interactions) of the network in each sampling date. To statistically examine the differences in metrics among the two scenarios and the two corresponding null models, we constructed linear mixed effect models (LMMs) using the lme4 package ([Bates et al., 2015](#)). We used the network metrics as the response variables, scenario as the fixed explanatory variable of interest and date as a random factor to block comparisons within each sampling date only. Separate models were fitted for each response variable (i.e., network metric) and location (i.e., Ashiu and Kibune), since random factors with two levels only are highly discouraged. Therefore, a model was fit using samples of 100 iterations times the number of sampling dates (28 for Ashiu forest or 47 for Kibune forest) and the number of scenarios (including null models) (4). Pairwise post-hoc Tukey tests were run to check for significant differences between different scenarios while controlling for sampling

date.

Second, we examined the contribution of each group to the temporal dynamics of network metrics (hypothesis iii) by comparing dynamics of the original community and each of the four scenarios. We ran Pearson correlation tests between the metric values of the original community and the median value of the 100 iterations for each scenario or null model to not inflate correlation coefficients. This approach reveals the extent to which each scenario or null model deviates from the original community in terms of temporal dynamics across days, months and years, showing the contribution of each group to network metrics in a temporal framework.

Third, to study whether bees with different ecological traits contribute differently to network metrics and dynamics (hypothesis iv), we simulated four new scenarios. In the first scenario of bigger bee removal, 50 % of bee species (in each site – Ashiu and Kibune) were removed following a probabilistic approach where the chances of being removed scaled exponentially with body size ($\text{Prob} = \text{size}^3$). The same was done for small bee removal ($\text{Prob} = 1 - \text{prob}(\text{size}^3)$). Then, we had a scenario where bigger bee species were much more likely to be removed, and another one where smaller bee species were much more likely to be removed (note that we did not classify species into groups *a priori*). Later, we repeated the process using the length of the activity period as a criterion.

Then network metrics were calculated for each scenario and each sampling date. The linear mixed models were constructed again with a network metric as response variable, scenario (network metric under the four simulated scenarios and original network) as explanatory variable, and date as random intercept factor. The sample size of the analyses is the number of dates (28 for Ashiu forest or 47 for Kibune forest) multiplied by 401 (the number of the scenarios (4) x 100 iterations plus one for the original matrix). Pairwise post-hoc Tukey tests were run to check for significant differences between different scenarios and the original network. Here, also Pearson correlation tests were run to examine the contribution of each bee trait group to observed temporal patterns in network values across dates.

All the models presented here met the assumptions of normality and independence in the residuals.

Correlations were run using the *cor.test* function in *stats*, base R. Also, the *bipartite* package ([Dormann et al., 2009](#)) was used to calculate network metrics, *tydiverse* ([Wickham et al., 2019](#)) was used for data management, and *ggplot2* ([Wickham, 2016](#)) to create plots.

2.6. Sensitivity analysis

A sensitivity analysis was conducted to assess the consequences of eliminating a lesser fraction of bee and syrphid species from each site, specifically 75 % and 50 %, respectively. The observed patterns were very similar to the results presented here, but their magnitude was reduced along with the percentage of species removed. The objective of this analysis was to comprehend the distinct roles of species rather than to investigate realistic scenarios of species extinctions. Therefore, the results pertaining to the simulation of 90 % species removal are presented in the main text. Additionally, the decision to simulate the removal of 90 % of bee and syrphid species (instead of removing all of them) was made for analytical purposes. This choice aimed to avoid losing networks that were composed by bee species to a large extent (i.e., if we remove all the bees, then some networks become too simple, and are not robust to network analyses) and to introduce some variability in the measurements across iterations, enabling comparisons with the null model, which entails the removal of a distinct set of species in each iteration.

3. Results

In total, 682 species of flower visitor were recorded in Ashiu Forest and 855 in Kibune Forest. These species were involved in a total of 6815

interactions (Table S4). Bees constituted only the 8–10 % of species visiting flowers, but they were involved in 31–37 % of the interactions (in Ashiu and Kibune forests, respectively) (Table S5). Hoverflies accounted for 6–8 % of the species visiting flowers, and were involved in 9–16 % of the interactions.

Most part of the variability in network metrics was found across dates, and not across iterations within the same scenario (Table S6). Compared to the random removal of species, the simulated removal of bee species reduced on average (across all the dates) the nestedness (NODF) by a 30 % in Ashiu and a 19 % in Kibune, the Shannon diversity of interactions (SH) by 10 % in Ashiu and 8 % in Kibune, and increased network specialization (H2) by 58 % in Ashiu and 17 % in Kibune (Fig. 2) (percentages calculated using the random scenario as reference). Also, the number of interactions was reduced more than expected by random deletions, connectance increased, and niche overlap did not show a substantial change (Fig. S3). The simulated removal of syrphids had a lower impact on network structure. Their effect on nestedness and interaction diversity was relatively low and site-dependent (Fig. 2). However, their removal decreased network specialization by a 45 % (in Ashiu) and a 17 % (in Kibune) more than expected by random removals (Fig. 2). Their impact on niche overlap (4 % in Ashiu and 3 % in Kibune) or connectance was also low (Fig. S3). Simulations where only 50 % or 75 % of bee or hoverfly species were removed rendered qualitatively similar results, with weaker effects (Figs. S4 and S5).

Smaller bee species contributed more than bigger species to interaction diversity (Fig. 3), yet, their tendency to increase nestedness and to reduce network specialization was site-dependent (Fig. 3). In addition, bee species that were active for longer were the ones involved in a higher number of interactions (Fig. S6).

The removal of bees and syrphids had different impacts on observed network dynamics (Fig. 4). The diversity of interactions (SH) did not vary substantially. On the other hand, the removal of bee species had a relatively high impact on the dynamics of nestedness and network specialization, while the removal of syrphid species affected the dynamics of network specialization only (Fig. 4). Smaller bees and bees

that were active for longer were the ones with a higher contribution to observed nestedness dynamics over time (Fig. 4). The role of bee traits on the observed temporal dynamics of diversity of interactions, niche overlap or number of interactions was negligible (Fig. 4). However, temporal dynamics of network specialization was more subject to removal of functional groups, with the impact of species with different traits being not consistent across the sites (Fig. 4).

4. Discussion

The increased rates of species loss caused by anthropogenic activities threaten the structure of plant communities, flower visitor communities, and their interactions in many environments (Dirzo et al., 2014; Harvey et al., 2017; Tylianakis & Morris, 2017). Estimating the impact of different scenarios of species deletions in almost pristine ecosystems can provide an important understanding of the functioning of these communities and the role played by different taxa or functional groups. Here, we show that some pollinator taxa and types of species are more important than others when it comes to shaping the topological and dynamic properties of plant-flower visitor interaction networks.

The results of this study supported our first hypothesis, since bees proved to be key contributors to network nestedness, interaction diversity, and generalization within natural ecosystems. Most bee species are generalists and are known to engage in a wide range of interactions with plants. This suggests that the foraging behaviour of bees contributes significantly to the nested structure that characterizes the topology of plant-pollinator networks worldwide (Bascompte et al., 2003). Bees not only participated in a higher number of interactions per capita than any random set of flower-visitor species, but also, behaved as trophic generalists, even in semi-pristine ecosystems. This explains, simultaneously, their observed high contribution to interaction diversity and low network specialization too. These three properties promoted by bees are also characteristics associated with the stability and resilience of plant-flower visitor communities to ecosystem perturbations (Burgos et al., 2007; Moreira et al., 2015; Soares et al., 2017). Bees are not the

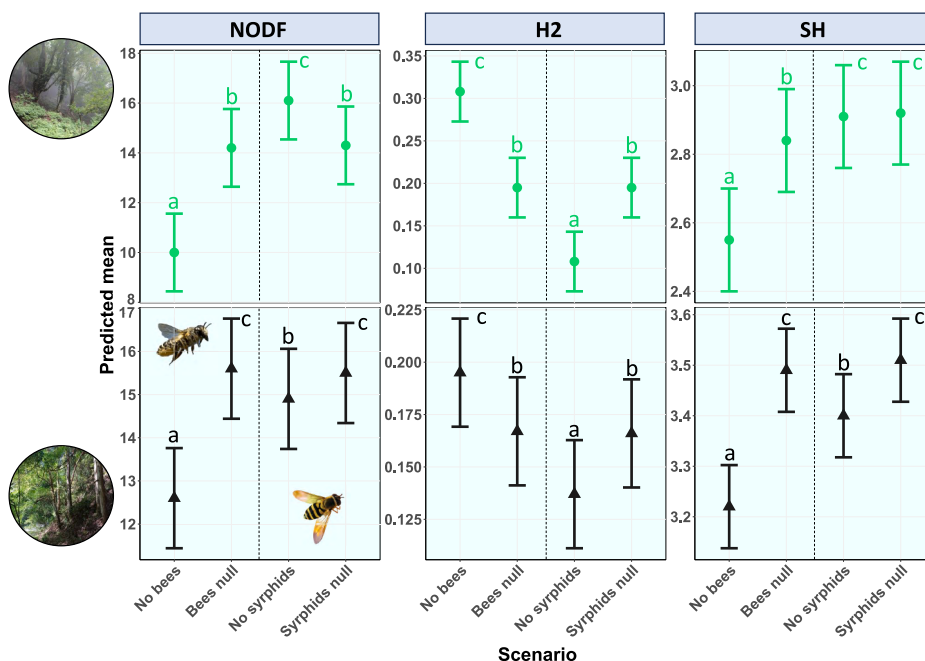


Fig. 2. Contribution of bee and syrphid species to interaction network metrics. Network metrics after removing 90 % of the bee species and syrphid species ("No bees" and "No syrphids", respectively) compared to the random removal of the same number of species (null models). Means and standard errors show the predicted mean and model uncertainty (SE) across all the iterations and dates (the whole-time range). Letters show the significance of a Tukey post-hoc pairwise test based on pairwise comparisons (comparing different scenarios for the same date). NODF = Nestedness. H2 = Network specialization. SH = Shannon interaction diversity. In green, Ashiu beech forest, and in black, Kibune deciduous forest. Note that means and SE represent the average mean across all sampling dates (i.e., SE also represents variation across time, not only across iterations), but letters correspond to pairwise comparisons (controlling for date).

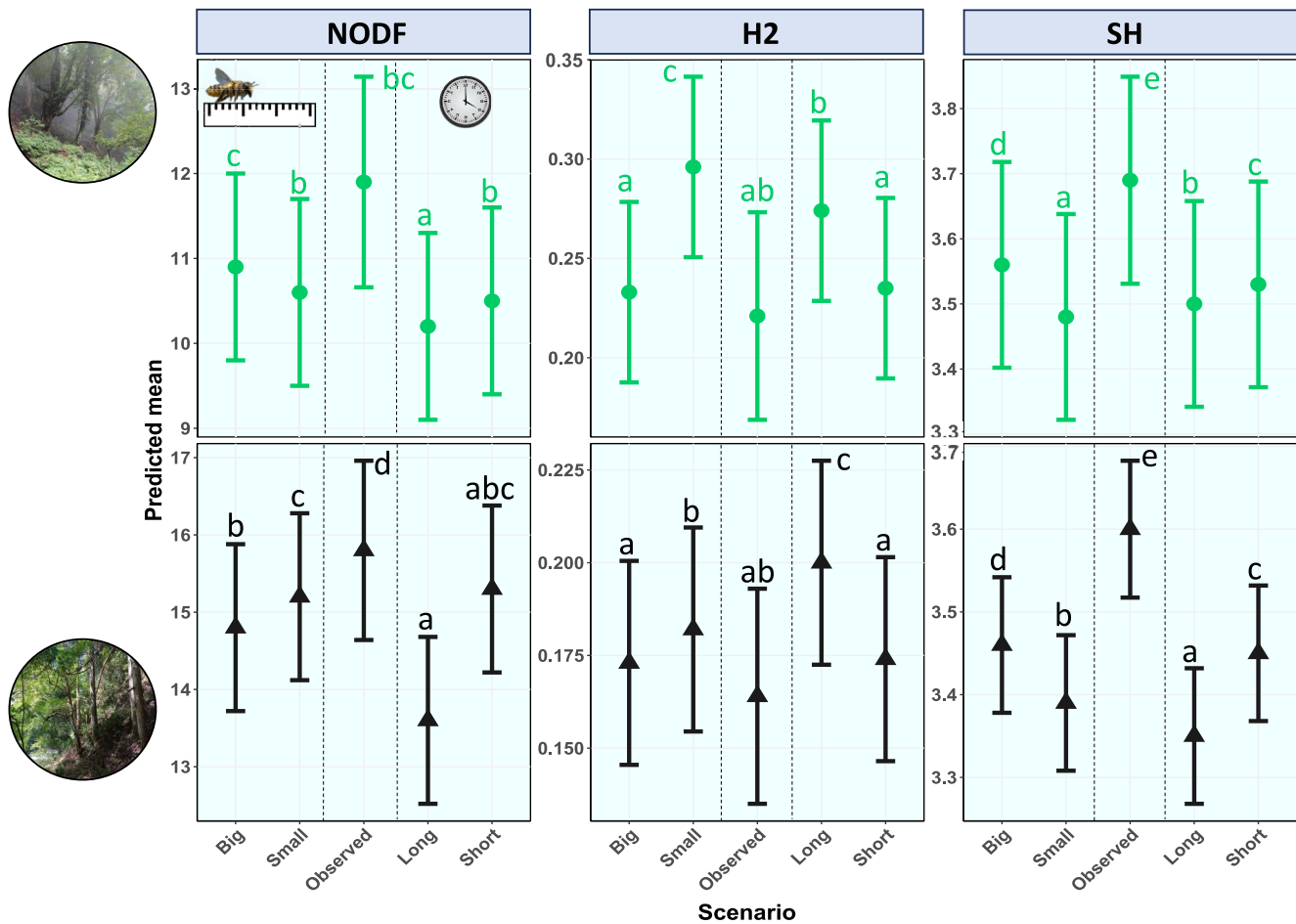


Fig. 3. Effect of the simulated removal of bee species with specific traits on interaction network metrics, compared to the observed values (no removal). Means and standard errors show the predicted mean and model uncertainty (SE) across all the iterations and dates (the whole-time range). Letters show the significance of a Tukey post-hoc pairwise test based on pairwise comparisons (comparing scenarios for the same date). Scenarios = Big (in absence of bigger species), small (in absence of smaller bees), observed (observed value with the complete community), long (in absence of species active for more months), short (in absence of species active for fewer months). NODF = Nestedness. H2 = Network specialization. SH = Shannon interaction diversity. In green, Ashiu beech forest, and in black, Kibune deciduous forest. Note that means and SE represent the average mean across all sampling dates (i.e., SE also represents variation across time, not only across iterations), but letters correspond to pairwise comparisons (controlling for date).

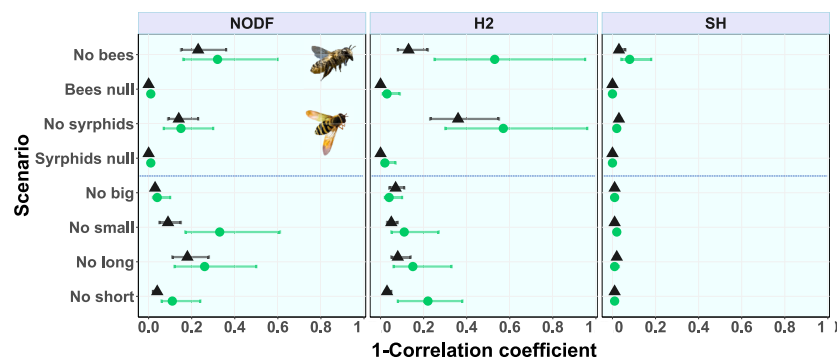


Fig. 4. Contribution of bees (with different traits) and syrphids to network metric dynamics. The plots show inverse of the correlation ($1 - \text{Pearson correlation coefficient}$) with 95 % CI between the median network metrics of 100 iterations under different scenarios and the values for the original community across sampling dates ($n = 28$ in Ashiu forest and $n = 47$ in Kibune forest). Scenarios: No bees (90 % of bees removed), Bees null (same number of species as in the previous scenario removed randomly), No syrphids (90 % of syrphids removed), Syrphids null (same number of species as in the previous scenario removed randomly), No big (50 % of bigger bee species removed with a higher probability), No small (50 % of smaller bee species removed with a higher probability), No long (50 % of the bees with longer activity periods across seasons removed with higher probability), and No short (50 % of the bees with shorter activity periods across seasons removed with higher probability). NODF = Nestedness. H2 = Network specialization. SH = Shannon interaction diversity. In green, Ashiu beech forest location, and in black Kibune deciduous forest location. Higher values indicate a stronger deviation from (lower correlation with) observed values, showing a stronger contribution to network dynamics of the species in a particular scenario.

only pollinator group that displays generalized trophic behaviour. For instance, plant-pollinator networks that consider only hoverflies also show an overall high degree of generality and robustness (Lucas et al., 2018a; Schweiger et al., 2007). However, although we found that hoverflies contribute more than a random set of species to stabilizing properties, such as interaction diversity, bees' contribution was higher. This goes in line with another study conducted in grasslands across more anthropized landscapes (Jauker et al., 2019), which suggests that the high relative weight of bees in network properties might be a widespread pattern. In addition, wild bees have proved to be highly valuable not only for network structure but also for pollination in pollinator importance networks (Ballantyne et al., 2017).

Our second hypothesis was also supported by the results since the loss of syrphid species decreased network complementary specialization. This aligns with other studies that have also highlighted the potential for specialization patterns in certain syrphids (Klecka et al., 2018; Lucas et al., 2018a; Lucas et al., 2018b). The loss of syrphid species had a significant impact on reducing the number of interactions, however, this reduction was not substantial, indicating that hoverflies, although very active, play a secondary role in these interaction networks compared to bees. Also, their effect on nestedness and diversity of interactions was weak and context-dependent (i.e., depending on the type of forest studied), indicating a limited impact on network topology. This does not necessarily mean that syrphids are not important pollinators. Their key role in the pollination of some plants has been highlighted on numerous occasions (Doyle et al., 2020; Klecka et al., 2018). Moreover, their foraging behaviour could be complementary to that of bees because they have very different life-history traits. Furthermore, this group encompasses important species involved not only in plant pollination, but also in antagonistic interactions as predators. Therefore, syrphids are appreciated for their dual role as pollinators and pest controllers in many (agroeco-) systems (Dunn et al., 2020). Our results imply that syrphid species have a relatively low weight in the structure of the networks when taking into account the whole community of floral visitors. Similar conclusions were distilled from other studies, where hoverflies showed a relatively low weight on network metrics (Jauker et al., 2019), compared to bees. This relatively low importance on network structure was also evidenced by hoverfly's low influence on network temporal dynamics compared to bees, which supported our third hypothesis.

The high temporal and spatial turnover of wild bee species in (semi-) natural ecosystems is a key characteristic of these communities (Martínez-Núñez et al., 2022). This high temporal turnover, together with the presence of bee species during the whole flower season, but concentrated in spring, explains why the removal of bee species has a high impact on the temporal dynamics of these networks. Interestingly, however, bee removal did not affect the dynamics of all network properties. Nestedness and network specialization underwent relatively strong deviations from the original dynamics, while the dynamics of interaction diversity stayed similar over time. This result suggests that bee seasonality shapes the temporal dynamics of the nested structure and vulnerability of these interaction networks in an asymmetric (i.e., highly variable) manner throughout the months and years, while their contribution to the diversity of interactions appears to remain more stable. Therefore, focusing on interaction diversity alone might not suffice to understand underlying changes in community structure. These results find support in other studies that have shown how species' phenology determine species' interactions and shape network properties such as modularity (Morente-López et al., 2018).

Larger bee species are becoming less frequent and species size tends to decrease over time, probably due to temperature stress (Herrera et al., 2023b) and other perturbations, such as intensive agricultural management. At the same time, bee size is a key functional trait, that shapes the foraging behaviour and dispersal capacity of bees (Greenleaf et al., 2007; Kendall et al., 2022). For instance, smaller species tend to have short tongues, being able to forage on a variety of generalist open

flowers, which allow them to adapt their foraging niche more easily and be less vulnerable to environmental perturbations. Bee size was linked to specialization in tropical plant-pollinator networks (Raiol et al., 2021). The fact that small species contributed the most to the nestedness, interaction diversity, and temporal dynamics observed suggests that the architecture of these flower-visitor networks is basically very resilient to some of the currently prevailing threats (Martínez-Núñez et al., 2020).

Similarly, species that were active for more months were important contributors to interaction diversity, nestedness, and the temporal dynamics of these metrics. This observation suggests a potential link between species activity duration and measures of interaction diversity. This link is not surprising because bee species with extended activity periods have the opportunity to interact with a changing community of diverse plant species across the season. Yet, interestingly, we found that these bee species maintain this generalist trait even in brief snapshots, such as in single-day observation record interaction networks.

5. Conclusion

This study sheds light on the roles of different groups (i.e., bees and hoverflies) and bee species with contrasting traits (big vs. small and short vs. long activity periods) in plant-flower visitor networks. This knowledge is key to improving our understanding of these systems and also to helping anticipate how global-change drivers or species extinctions can affect the structure of these interaction networks (e.g., Mathiasson & Rehan, 2020). Therefore, changes that disrupt bee communities such as the introduction of bee diseases and parasites, or pesticide use might decrease the resilience of these networks by decreasing their degree of nestedness, decreasing interaction diversity, and altering temporal dynamics. On the other hand, the loss of syrphid species might decrease network complementary specialization, posing a threat to specific plant species. Future works should delve into the resilience mechanisms of these communities, since their high plasticity and rewiring capacities might buffer some of the expected impacts but are relatively little explored.

Author contributions

CMN and SS developed the main ideas of the study. SS provided the dataset. CMN analysed the data and wrote the first draft of the manuscript. Both authors contributed significantly to the final version of the study.

CRediT authorship contribution statement

Carlos Martínez-Núñez: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Shoko Sakai:** Writing – review & editing, Supervision, Resources, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data used in this paper are already publicly available.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112041>.

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