Plant-pollintor networks worldwide are composed by the same specific building blocks

Abstract

Ecological processes leave distinct structural imprints on species interactions shaping the topology of mutualistic networks. Detecting those relationships is not trivial since they go beyond pair-wise interactions, but may get blurred when considering full network descriptors. However, recent work has shown the network meso-scale can capture this important information. The meso-scale describes network subgraphs representing patterns of interactions between a small number of species (i.e. motifs) and those constitute the building blocks of the whole network. Here, we have compiled 60 networks from 18 different studies and show that some motifs are consitently over-represented worldwide, suggesting that the building blocks of plant-pollintor networks are not random and are associated to . . . Second, we show that the position of pollinator guilds and plant reproductive strategies is not random with respect to the positions occupied within each motif. . . . Hence, we show that species ecology is shaping the building blocks that conform the web of life.

INTRODUCTION

The interaction between plants and pollinators can be studied at different scales, from species level interactions (micro-scale) to the full network structure (macro-scale). Research of the plant-pollinator network structure have proven common invariant structural properties across them including a degree distribution that decays as a power law (Jordano 1987), nestedness (Bascompte et al. 2003), or modularity in large networks (Olesen et al. 2007). In addition, species phenological overlap, morphological matching and species abundances have been shown to be determinant for the understanding of pairwise plant-pollinator interactions (Bartomeus et al. 2016; Stang, Klinkhamer, and Van Der Meijden 2006; Peralta et al. 2020). However, both species level information and the holistic view of the full network involves missing relevant information for the understanding of ecological processes (Cirtwill et al. 2018; Simmons, Cirtwill, et al. 2019).

Traditionally, plant-pollinator research has focused on direct interactions but overlooked indirect interactions (the mediated effect between two species by a third species), such as facilitative or competitive interactions between plants for pollinators (Moeller 2004; Sargent and Ackerly 2008). Despite the widespread nature of indirect interactions in ecological communities (Strauss 1991), plant-pollinator research often fails to finely capture those indirect interactions with the conventional analytical tools that condense the information either by species (e.g. interaction frequency) or in single topological indices (e.g. nestedness). Nonetheless, the emerging framework of network motifs in plant-pollinator research, the building blocks of a network that depict subsets of interactions (Milo et al. 2002), allows to consider both direct and indirect interactions (Simmons, Cirtwill, et al. 2019). The analysis of motifs (meso-scale) in plant-pollinator networks have revealed that the different ecological processes that govern species interactions (e.g., species abundances versus trait-matching) can lead to different patterns of indirect interactions (Simmons et al. 2020). Yet, the global patterns of indirect interactions in plant-pollinator networks (over- and under- represented motifs) are still unknown.

Motifs are abstract representations often decoupled from species ecology. Thus, linking the structural properties of the meso-scale with the species ecology can help the understanding of ecological processes. For instance, different motifs can have different ecological meanings (Simmons, Cirtwill, et al. 2019) and the position within a motif can determine the species functional role (Stouffer et al. 2012; Baker et al. 2015). However, it is unclear how the species ecology and life history traits determines the species functional role

within the network of interactions (Coux et al. 2016). For example, large pollinators can forage larger distances (Greenleaf et al. 2007), deposit greater pollen quantities (Földesi et al. 2021) and handle complex zygomorphic flowers in comparison with small pollinators that are restricted to lower floral complexity (Gong and Huang 2009). How this different pollinator behaviors translate into their interaction topology is unknown. Similarly, recent empirical findings indicate that the meso-scale is the best descriptor of plant reproductive success (Allen-Perkins et al. 2021), but little is known on how plants reproductive strategies shape their position within the network of interactions. Although some studies have evaluated plant reproductive strategies in plant-pollinator networks (Tur, Castro-Urgal, and Traveset 2013; Lázaro et al. 2020), they are often overlooked in a community context (Devaux, Lepers, and Porcher 2014) and rarely incorporated into plant-pollinator network studies. Hence, exploring how the main plant reproductive strategies integrate with the emergent motif framework can shed light on key aspects of ecosystem functioning.

Here, we used 60 plant-pollinator networks from 18 different studies and 14 countries, alongside functional groups of plants and floral visitors based on functional traits and taxonomic rank, respectively. To obtain plant functional groups, we used a comprehensive dataset that included floral, reproductive and vegetative traits compiled on a larger set of networks (Lanuza et al., unpublished). Floral visitor functional groups were divided by the main taxonomical groups that differed in life form and behaviour. Once we split the different plant-pollinator networks into their motif elements, we explored: (i) over and under-represented motifs; (ii) over and under-represented functional groups in the different motif positions; (iii) the probability of finding plant and floral visitor functional groups in the different motif positions; and, (iv) over- and under-represented functional group combinations within the different motifs.

METHODS

Plant-pollinator studies

We have compiled 60 plant-pollinator networks from 18 different studies (**Table S1**). All studies sampled plant-pollinator interactions in natural systems and were selected based on wide geographical coverage and presence of interaction frequency as a measure of interaction strength. In total, there were 503 plant species, 1,111 floral visitors species and 6248 pairwise interactions registered. For ease of data manipulation, plant and floral visitors species names were standardize with the help of the package *taxize* version 0.9.99 (Chamberlain et al. 2020).

Plant and floral visitors functional groups

First, plant species were grouped thorugh hierarchical clustering into the optimal number of functional groups that summarized the main plant reproductive strategies. We used the trait dataset collated in Lanuza et al., (unpublished) that comprised 1,506 plant species and contained the same 60 plant-pollinator networks used in this study plus some non-weighted and weighted metawebs (see **Table S1** Lanuza et al., unpublished). This dataset consisted on 8 floral, 4 reproductive and 3 vegetative traits excluding traits with high percentage of missing values (over 30%; **Table S2**). We opted to calculate the plant functional groups on this larger set of species because of the higher accuracy when delimiting functional groups with that many variables and species (Dolnicar et al. 2014). Previous to the clustering analysis, we calculated the distance between the different qualitative and scaled quantitative variables with Gower distance (Gower 1971). For this, we used the function *gowdis* with method *ward.D2* from the package *FD* version *1.0-12* (Laliberté et al. 2014). Finally, we conducted hierarchical clustering with the function *hclust* from the *R stats* package version *4.0.5* and calculated the optimal number of clusters with the function *kgs* from the package *maptree* version *1.4-7* (White and Gramacy 2009).

Second, floral visitors were grouped into functional groups based on taxonomic rank as done similarly in past plant-pollinator studies (Fenster et al. 2004; Ollerton et al. 2009). We opted to divide floral visitors on the taxonmoic rank level and not with functional traits because the main orders of floral visitors differed clearly in form and behaviour and had lower lower complexity of higher taxnomic ranks than plants (i.e., floral visitors had 6 orders versus plants that had 38). Thus, this allowed us to group floral visitors into functional groups that represented adequately the main life strategies: (i) Hymenoptera-Anthophila (bees),

(ii) Hymenoptera-non-Anthophila (other non-bee Hymenoptera), (iii) Syrphidae-Diptera, (iv) non-Syrphidae-Diptera, (v) Lepidoptera, (vi) Coleoptera, (vii). Further, other 3 functional groups (i.e., lizards, birds and other insects) were considered for analysis but excluded from results because of their low representation in the set of networks.

Overall motif patterns

Following previous work (Simmons, Cirtwill, et al. 2019; Simmons et al. 2020), we broke down the plant-pollinator networks into their constituent motifs. Prior to analyses, we turned the quantitative networks into qualitative (or binary) ones, where interactions are present or absent.

We calculated the frequency of all motifs up to five nodes (see **Figure 1**) for each empirical network, by using the *bmotif* package (Simmons, Sweering, et al. 2019). To control for variation in network size, motif frequencies were normalised as a proportion of the total number of motifs within each motif class (i.e., the number of nodes a motif contains). Like Simmons et al. (2020), we just used five-node motifs in our analyses for visualisation, interpretation and computational reasons. In addition, we also excluded two-node motifs (or links) from our analyses because their normalised frequencies would always equal one.

Figure 1. Adapted figure of Simmons et al., 2019 with all the possible motifs from two to five species in bipartite networks. There is a total of 17 possible motifs with 46 different positions denoted within each node.

To assess the significance of the observed frequencies, we created 1,000 simulated networks for each binary network using the *nullmodel* function and the *vaznull* model in the *bipartite* package (Dormann et al. 2009). Generated networks had the same number of plants and floral visitors, as well as the same connectance of their

corresponding empirical networks. After extracting the motif frequencies from the simulated networks, for each motif type and empirical network, we calculated the percentage of simulated networks whose frequencies were smaller than the ones observed, that is, we estimated the percentile of the observed motif frequencies. Motifs whose percentile is close to 0 or 100 are under- or over-represented in the empirical networks, respectively, and thus they cannot be predicted by connectance and the number of species alone. To summarize general patterns across networks, we used an intercept-only linear mixed model (LMM) per motif, where the response variable was the observed motif percentile per network. In these models, we used the study identifiers in **Table S1** as a random intercept. By doing so, we obtained estimates of the average motif frequency, in which we controlled the variation at the study level.

Over and under-represented functional groups on motif positions

We calculated which functional groups were over or under-represented in different motif positions by comparing position frequencies of empirical networks with those of their corresponding simulated counterparts. We extracted the position frequencies of all motifs from three to five nodes for each network and species by using the *bmotif* package (Simmons, Sweering, et al. 2019). To estimate the position frequencies of each functional group in a given network, we added the frequencies of those species that belong to the group, and then, we normalised the resulting frequencies by dividing the position measure for each group by the total number of times that a group appears in any position within the same motif size class. Then, we calculated the percentile of the observed position frequencies for each group and network, just like we did with motif frequencies. To outline the general patterns of position frequencies across networks and functional groups, we fit a LMM per motif position, where the response variable was the observed position percentile per network. We used the functional group identifier as an explanatory variable and the study identifiers as a random intercept. By adding the functional group estimates to the model intercept, we assessed the average motif frequency, after controlling the variation at the study level. Finally, we visualized with the help of the package ComplexHeatmap version 2.6.2 (Gu, Eils, and Schlesner 2016) over- and under- representation of plant and pollinator functional groups on the different motif positions.

To test the effect of singletones on the motif frequencies and motif functional groups' positions, we applied the previous analyses to the same set of networks (**Table S1**) but considering only interactions whose frequency was greater than one (64.98% of interactions; see **Figures S3 and S4**).

Over- and under-represented funtional group combinations of motifs

Finally, we studied which motif combinations of functional groups (up to five nodes) are over or under-represented in 95% of our empirical networks (57 out of 60 arrangements, due to computational limitations to identify all the nodes in the motifs of the three networks with the highest number of links). To do so, for each of the 53,250 possible motif combinations, we estimated the observed and the expected probability of finding those combination in empirical networks, respectively. Then, we determined whether the observed probabilities are likely to come from the expected probabilities or not. To calculate the observed probability (p_i^O) of functional groups within a motif (i; e.g., motif 3, bee + bee + functional group 2), we divided the number of times that i appears in our set of empirical networks (n_i^O) by the sum of the number of times that each possible combination appeared: $p_i^O = n_i^O / \sum_{k=1}^{53,250} n_k^O$. To estimate the expected probability of a given motif combination i, p_i^E, firstly, we calculated the probability of finding a given functional group x in the position α of i, $p_i(x, \alpha)$. Then, by assuming the independency of $p_i(x, \alpha)$, we computed the expected probability of the combination i as the product of the probability of its pairs (x, α), that is, $p_i^E = \prod_{(x,\alpha) \in i} p_i(x, \alpha)$. To obtain $p_i(x, \alpha)$, we proceeded as follows. First, we calculated the number of times that the functional group x appears in the position α in each empirical network η, denoted as $n_i^\eta(x, \alpha)$. Then, by controlling the variation at the network level, we assessed the average value of the absolute frequency of functional group x appears in the position α, $n_i(x, \alpha) = E[n_i^\eta(x, \alpha)]$, and estimated $p_i(x, \alpha)$ as $p_i(x, \alpha) = n_i(x, \alpha) / \sum_k n_i(k, \alpha)$. To obtain $n_i(x, \alpha)$, we fitted a LMM per motif position, where the response variable was the number of times that a given position was observed per network, the explanatory variable was functional group identifier, and the random intercept was given by network identifiers nested within the study identifiers. We used the 'lmer' package (Bates et al. 2015) to fit the LMMs models in our analyses.

Once we obtained p_i^O and p_i^E, we used simulation to determine whether the former is likely to come from the latter or not, since the large number of possible motif combinations and the small probabilities for some

of them advise against using an exact test of goodness-of-fit or a Chi-square one. Specifically, we created 1,000 random samples with repetition of possible motif combinations, where each sample contained 10 million elements and, for each combination, the probability of being selected was equal to its expected probability. From those random samples, we extracted the mean and the standard deviation of the expected probability of i, denoted as $E\left[p_i^E\right]$ and $\sigma\left[p_i^E\right]$, respectively, and calculated the z-scores of p_i^O as $z_i^O = \left(p_i^O - E\left[p_i^E\right]\right)/\sigma\left[p_i^E\right]$, for those motif combinations with $p_i^O > 0$. According to the usual interpretation of z-scores, combinations with $z_i^O > 1.96$ are over-represented, whereas those with $z_i^O < -1.96$ are under-represented, at the 95% confidence level. Notice that we focused on combinations with $p_i^O > 10^{-7}$ because, beyond the interest that can arouse the combinations that appear at most once, we do not have enough numerical resolution to accurately detect whether or not those combinations are under-represented (due to the limited size of our random samples).

RESULTS

Plant and floral visitor functional groups

The hierarchical cluster analysis divided the dataset into five different clusters with different and overlapping characteristics (**Figure S3** and **Figure S4**). Cluster 1 referred to as 'selfing herbs' consisted on herbs with hermaphroditic flowers with high levels of autonomous selfing. Cluster 2 or 'small outcrossing perennials' had small perennial species with a mixed of life forms (i.e., trees shrubs and herbs) with outcrossing hermaphroditic flowers. Cluster 3 referred to as 'self-incompatible perennials with large flowers' comprised perennial species with a mixed of life forms and large self-incompatible hermaphroditic flowers with high number of ovules. Cluster 4 or 'tall plants with small unisexual flowers' had the tallest species, highest proportion of shrub and tree life forms, dioecious and monoecious breeding systems with small flowers but the highest numbers of flowers and inflorescences per plant. Finally, cluster 5 or 'short-lived outcrossers with long zygomorphic flowers' consisted on small perennial and short-lived herbs with long self-compatible zygomorphic flowers that were unable to self-pollinate.

In total, there were 1126 species of floral visitor with 6325 interactions recorded with plants. We divided them into 6 main different taxonomical groups: bees with 2256 interactions with plants, non-syrphid Diptera with 1768 interactions, syrphids with 845 interactions, Lepidoptera with 437 interactions, Coleoptera with 432 interactions and non-bee Hymenoptera with 362 interactions.

Overall motif patterns

Most motifs were under- and over-represented (close to the 1st and 99th percentile, respectively) in the comparison between empirical and simulated networks (**Figure 2**). Further, the exclusion of singletones did not change these results (**Figure S1**). Motifs 3, 5, 9, 10 and 14 were under-represented in empirical networks, that is, all under the 25th percentile and the closest motifs to the 1st percentile. Remarkably, four out of five of these motifs belonged to the largest path length classification (i.e., core-peripheral). In addition, motifs 2, 6, 7, 16 and 17 were over-represented, all over the 75th percentile and thus the closest to the 99th percentile. In contrast to the under-represented motifs, over-represented motifs belonged to the two shortest path length groups (i.e., complete and fan). The remaining motifs (i.e., 4, 8, 11, 12, 13, and 15) were between the 25th and 75th percentile but closest to over-representation.
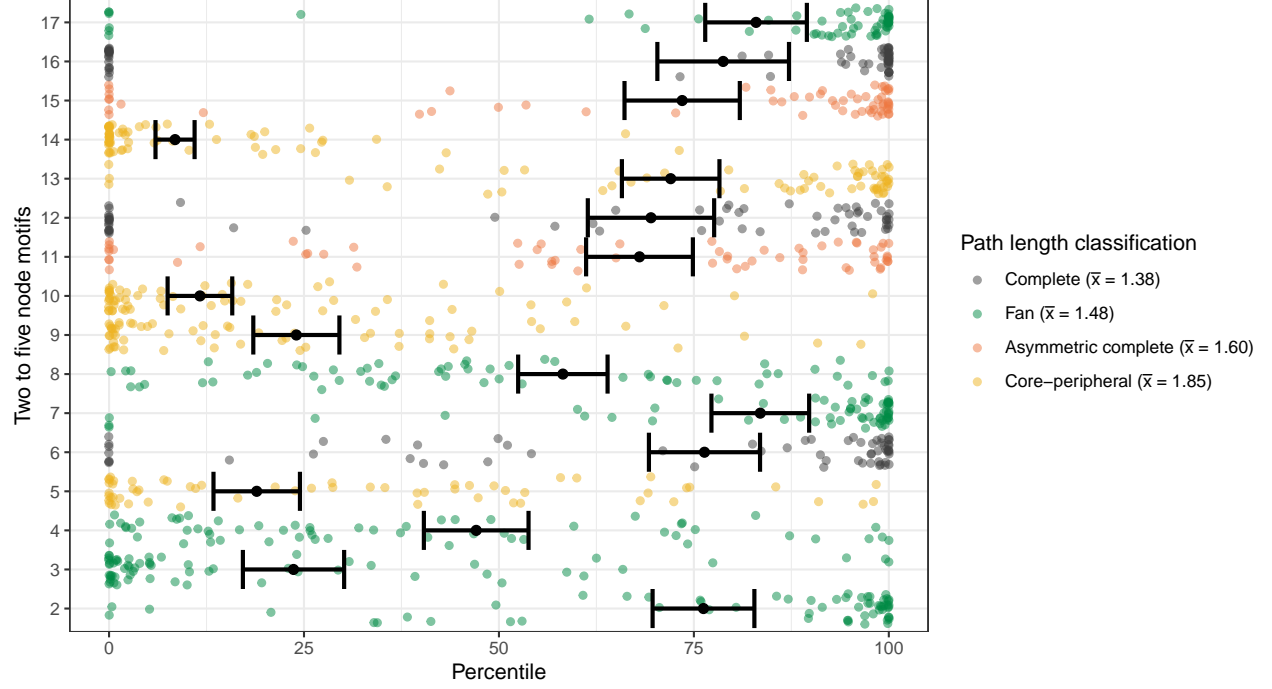
Figure 2. Comparison of the motif frequencies between empirical and simulated networks. Average percentages of motifs close to 0 and 100 indicate under- and over- representation in empirical networks. The different motifs are coloured by the mean motif path length as done in Simmons et al. (2020).

Motif functional groups position

Although motifs positions determined over- and under- representation independently of the identity of functional groups for most cases (rows in **Figure 3**), we found differences in the average percentile within floral visitors and pollinators functional groups (columns in **Figure 3**). Remarkably, the same patterns were observed but with lower average percentiles when singletones were exluded (**Figure S2**). Thus,
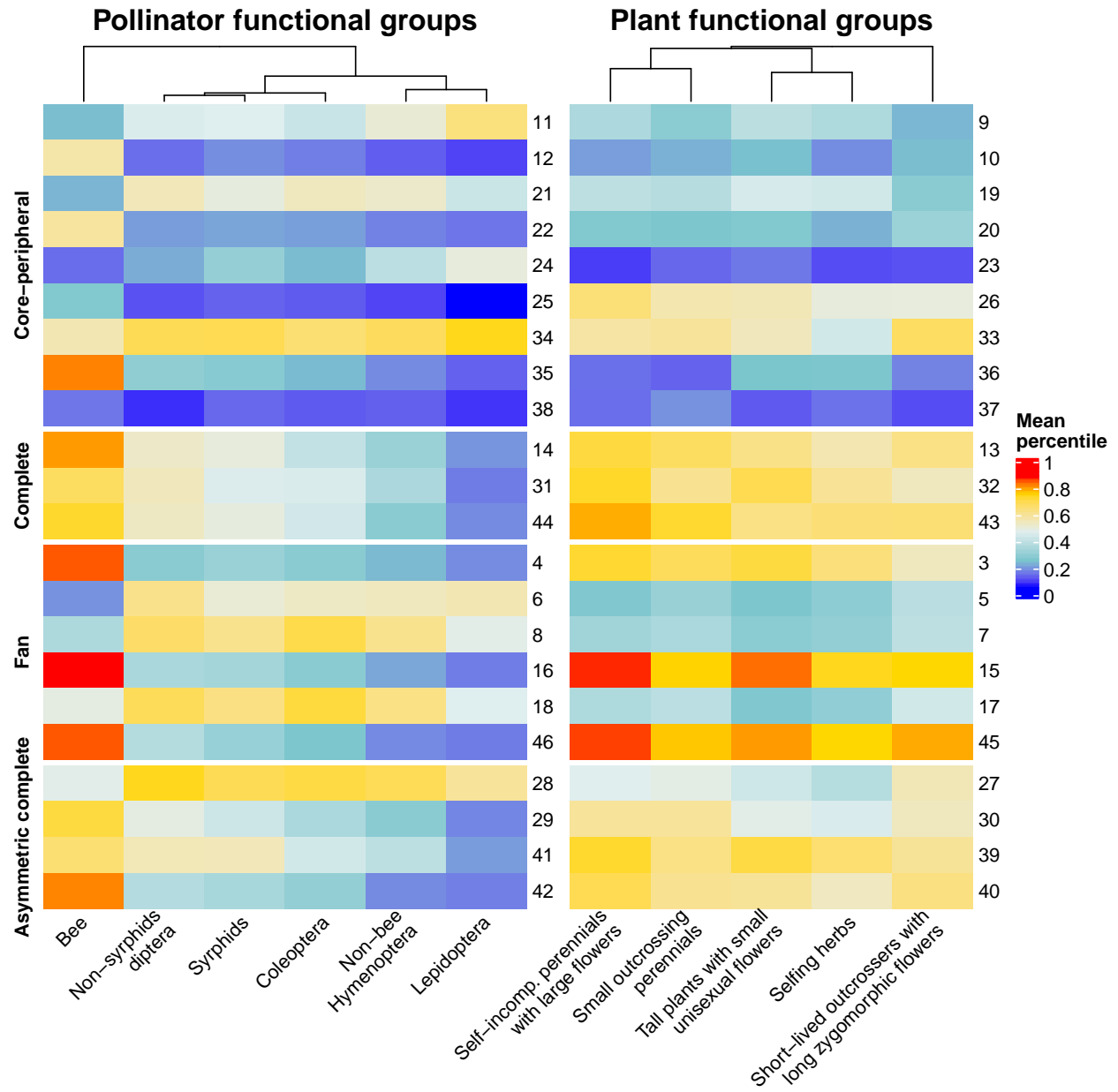
Figure 3. Heatmap indicating under- and over- representation of pollinator and plant functional groups in the different motif positions. The different motif positions are dividied by the average path length clasification by @simmons2020.
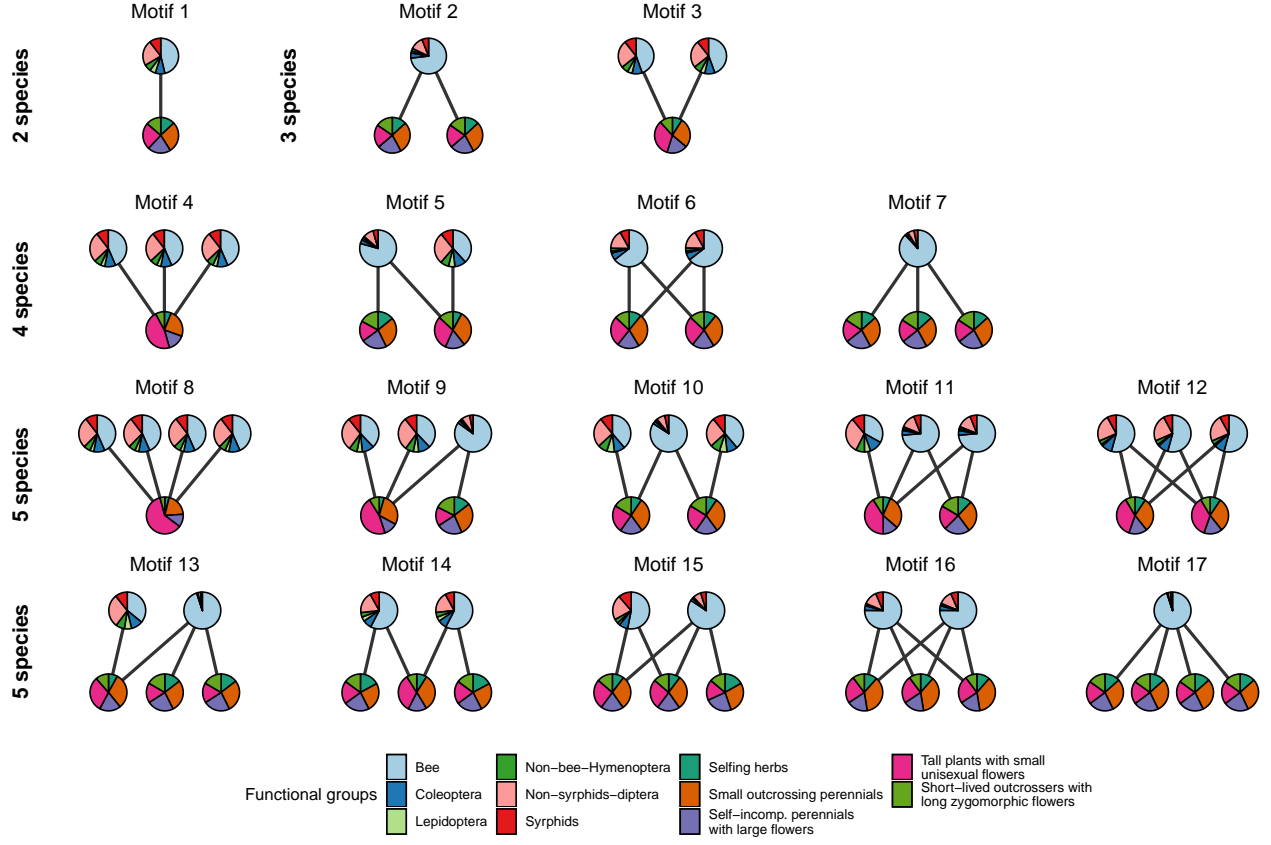
Figure 4. Graphical representation of the probability of finding a given functional group x in the position α of motif i, $p_i(x, \alpha)$, for all the possible motifs from two to five species in bipartite networks. The slices in the nodes for a given functional group x are proportional to the corresponding value of $p_i(x, \alpha)$.

Figure 5.

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SUPPLEMENTARY MATERIAL

TABLES

Table S1. List of studies ordered by author with the year of publication, number of contributed networks and digital object identifier

First author	Year	Number of networks	Country	DOI
Arroyo-Correa	2019	3	New Zealand	https://doi.org/10.1111/1365-2745.13332
Bartomeus	2008	6	Spain	https://doi.org/10.1007/s00442-007-0946-1
Bartomeus	2015	16	Spain	https://github.com/ibartomeus/
Bundgaard	2003	1	Denmark	Unpublished, Master thesis
Burkle	2013	1	United States	https://doi.org/10.1126/science.
Dicks	2002	2	England	https://doi.org/10.1046/j.0021-8790.2001.00572.x
Dupont	2003	3	Denmark	https://doi.org/10.1111/j.1365-2656.2008.01501.x
Elberling	1999	1	Sweden	https://doi.org/10.1111/j.1600-0587.1999.tb00507.x
Fang	2008	1	China	https://doi.org/10.1111/1749-4877.12190
Inouye	1988	1	United States	https://doi.org/10.1111/j.1442-9993.1988.tb00968.x
Kaiser-Bunbury	2017	8	Seychelles	https://doi.org/10.1038/nature2
Kaiser-Bunbury	2011	6	Seychelles	https://doi.org/10.1111/j.1365-2745.2010.01732.x
Kaiser-Bunbury	2010	2	Mauritius	https://doi.org/10.1016/j.ppees.
Lundgren	2005	1	Denmark (Greenland)	https://doi.org/10.1657/1523-0430(2005)037[0514:TDAHCW]:
Olesen	2002	2	Mauritius and Portugal (Azores)	https://doi.org/10.1046/j.1472-4642.2002.00148.x
Peralta	2006	4	Argentina	https://doi.org/10.1111/ele.135
Small	1976	1	Japan	/13960/t4km08d21
Souza	2017	1	Brazil	https://doi.org/10.1111/1365-2745.12978

Table S2. Traits used to delimit the different plant functional groups divided in quantitative and categorical traits.

Quantitative traits		Categorical traits	
Type	**Traits**	**Type**	**Traits**
Vegetative	Plant height (m)	Vegetative	**Lifepan**
Floral	Flower width (mm)	Vegetative	**Life form**
Floral	Flower length (mm)	Floral	**Flower shape**
Floral	Inflorescence width (mm)	Floral	**Flower symmetry**
Floral	Style length (mm)	Reproductive	**Autonomous selfing**
Floral	Ovules per flower	Reproductive	**Compatibility system**
Floral	Flowers per plant	Reproductive	**Breeding system**
Reproductive	Autonomous selfing (fruit set)		

FIGURES
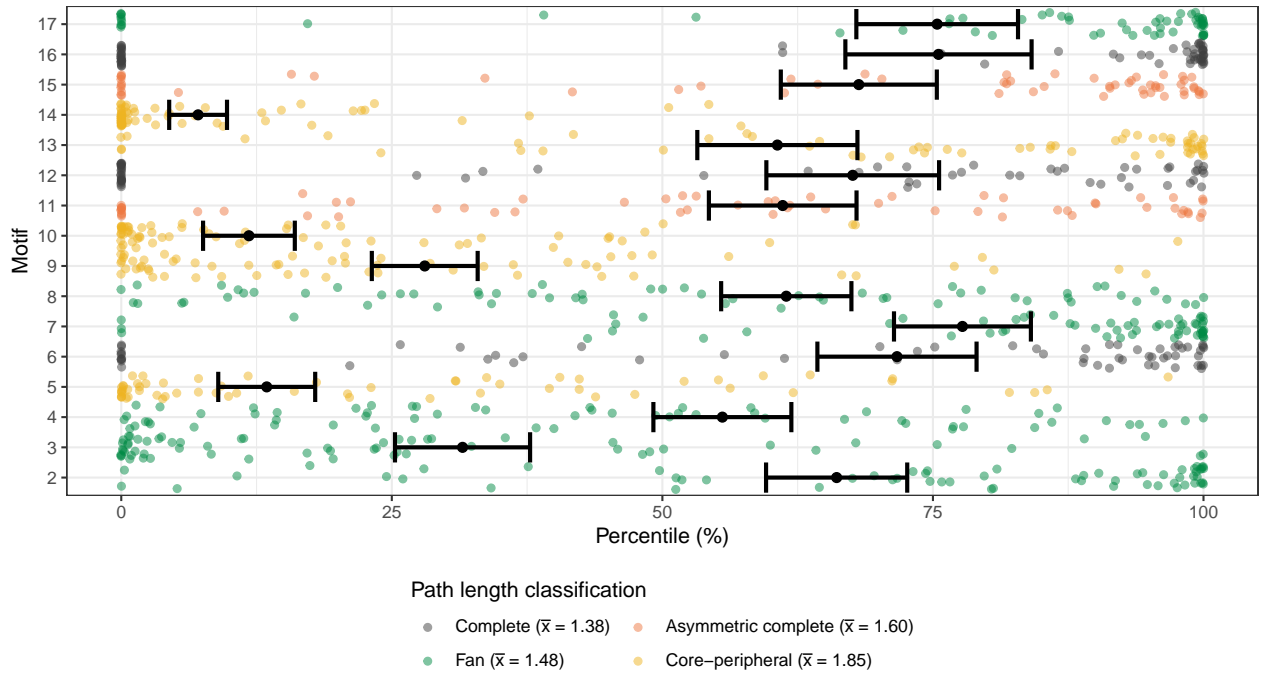
Figure S1. Comparison of the motif frequencies between empirical and simulated networks excluding singletones. Average percentages of motifs close to 0 and 100 indicate under- and over- representation in empirical networks, after removing non-robust links, that is, interactions whose frequency was equal to one. The different motifs are coloured by the mean path length as done in Simmons et al. (2020).
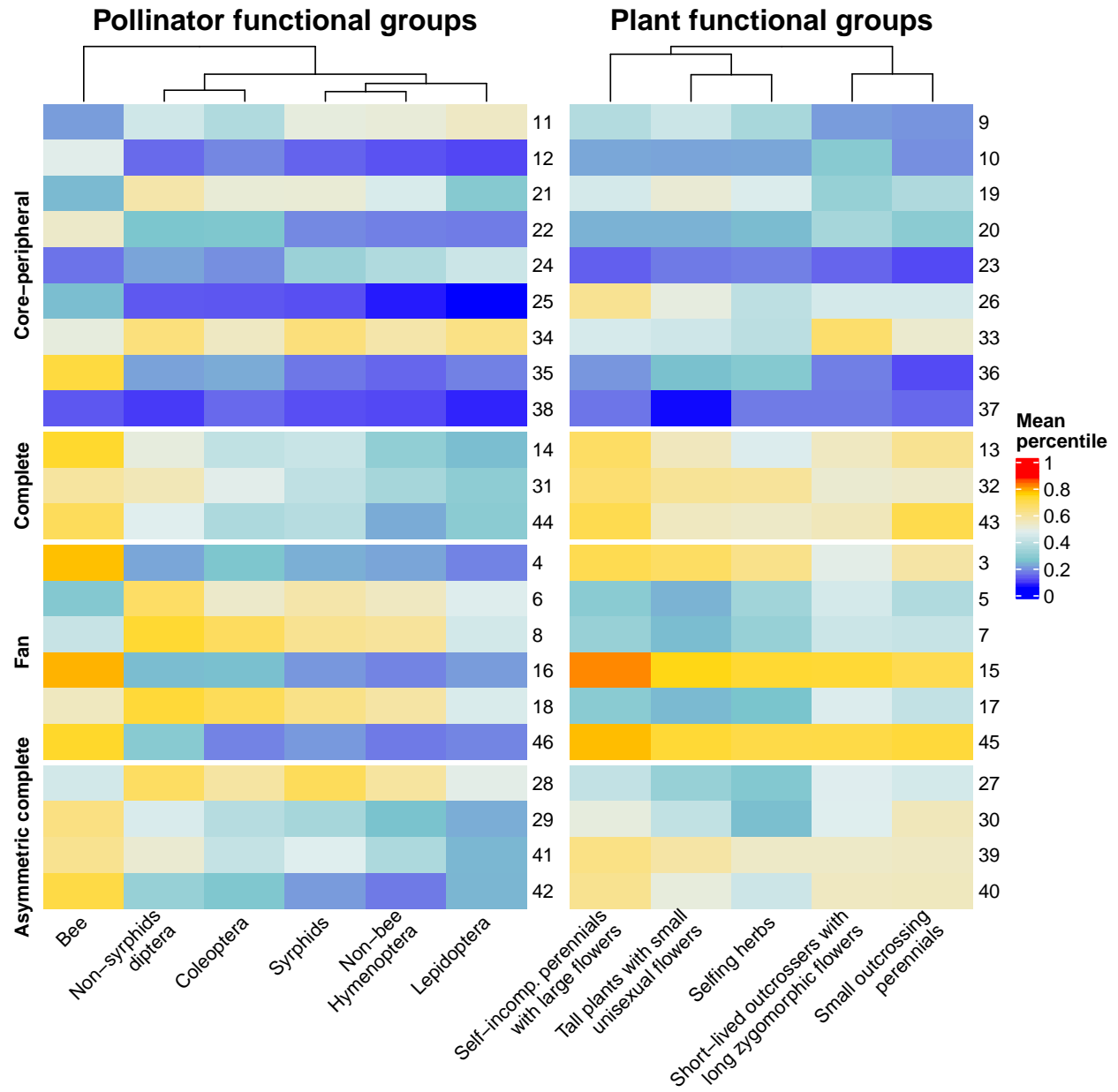
Figure S2. Heatmap indicating under- and over- representation of pollinator and plant functional groups in the different motif positions excluding singletones, after removing non-robust links, that is, interactions whose frequency was equal to one. The different motif positions are dividied by the average path length clasification by @simmons2020.
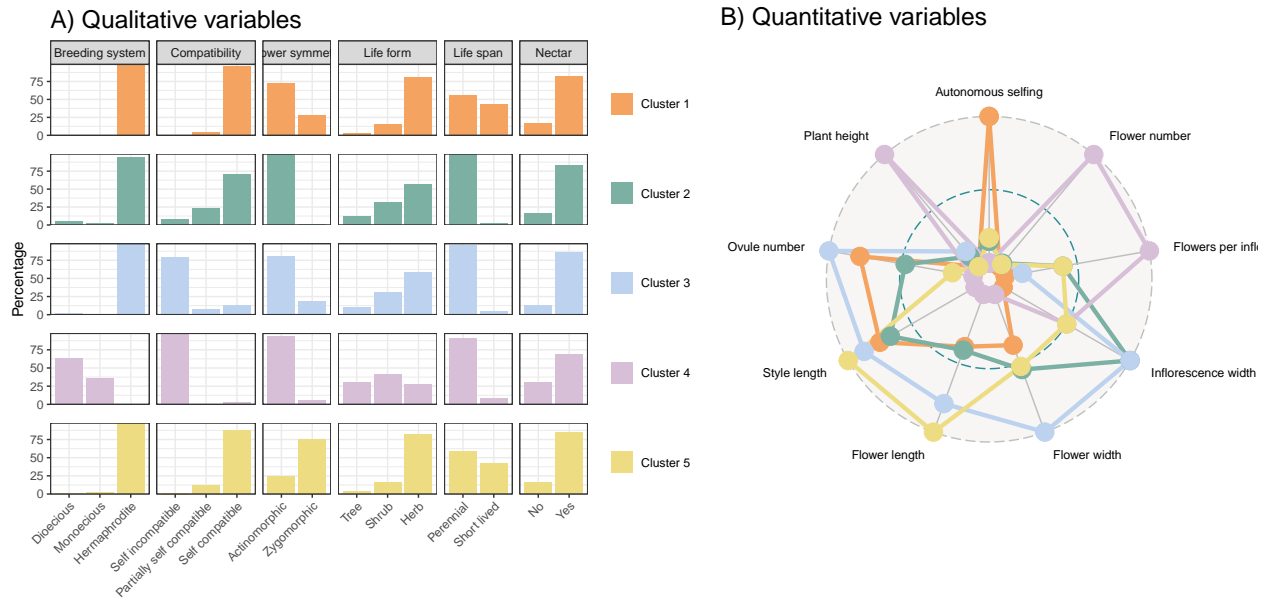
Plant functional group composition

Figure S3. Plant functional group composition separated in qualitative and quantitative variables. Panel A) shows the percentage of the different categories within trait represented with different colours for each functional group. Plot B) shows the radar plot of the different quantitative variables standardize on the same scale also coloured with the same patterns of colours as qualitative variables per cluster.
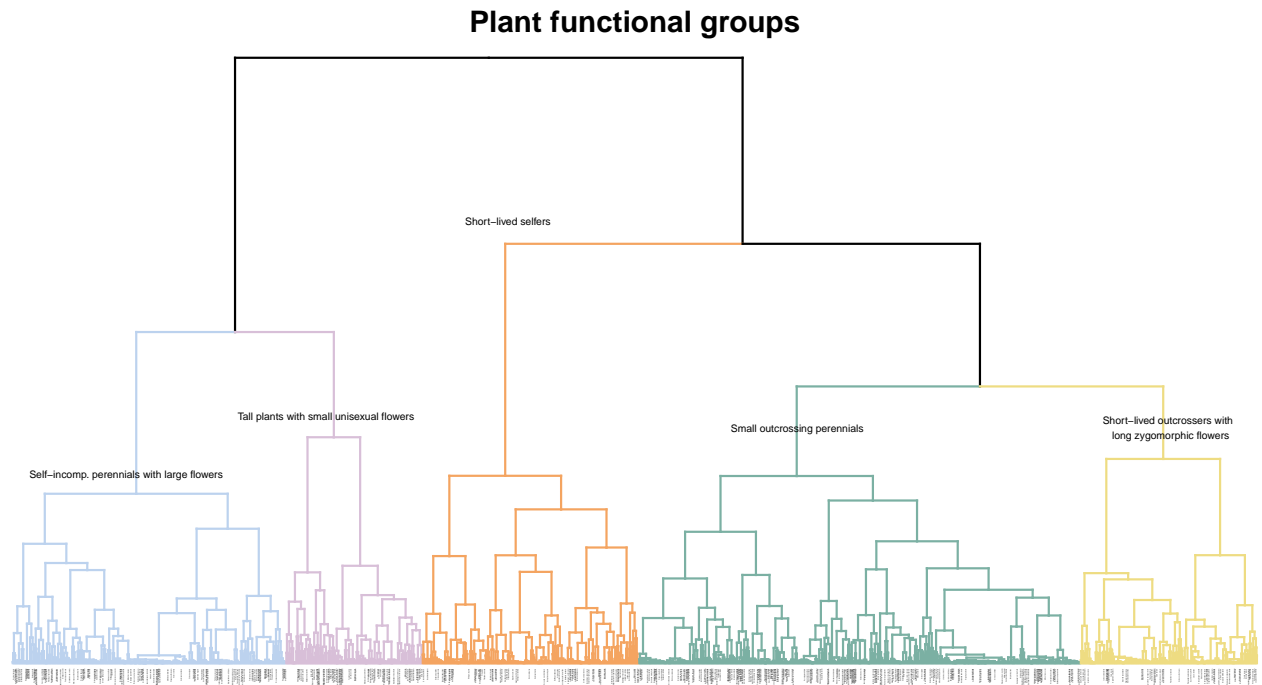

Figure S4. Hierarchical clustering dendrogram with the branches coloured by the optimal number of clusters (5). The labels of the subgroup of species (N = 524) used in this study are coloured in black in order to show the evenness of the distribution of the species across clusters. The rest of species labels are omitted for visualization purposes (N = 982).