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Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network

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Understanding the relative importance of multiple processes on structuring species interactions within communities is one of the major challenges in ecology. Here, we evaluated the relative importance of species abundance and forbidden links in structuring a hummingbird–plant interaction network from the Atlantic rainforest in Brazil. Our results show that models incorporating phenological overlapping and morphological matches were more accurate in predicting the observed interactions than models considering species abundance. This means that forbidden links, by imposing constraints on species interactions, play a greater role than species abundance in structuring the ecological network. We also show that using the frequency of interaction as a proxy for species abundance and network metrics to describe the detailed network structure might lead to biased conclusions regarding mechanisms generating network structure. Together, our findings suggest that species abundance can be a less important driver of species interactions in communities than previously thought.

1. Introduction

To understand the processes structuring the interactions in ecological communities remains one of the major challenges in ecology. Considering interacting species as complex networks has revealed some prevalent patterns for key interactions in communities, such as the skewed distribution of the number of interacting partners, nestedness and the asymmetry in the strength of the interactions [1]. These patterns have important implications for community dynamics [2] and may be driven by many different, but not mutually exclusive processes. Prevalent patterns in ecological networks can be generated by random interaction among species as well as by phenotypic mismatches influenced by the phylogeny (e.g. morphology, phenology and spatial distribution), which characterize the forbidden links [1,3–9].

The previous findings on the role of these numerous factors now lead to the intense debate on the relative importance of neutral- and niche-based processes to the structure of ecological networks [5,10]. In the context of ecological networks, neutral-based processes (often treated as neutrality, [9]) presume that species are ecologically equivalent. This means that individuals interact randomly in the community independently of their traits (specializations), thus more abundant species interact with more partners and with higher frequency than rarer species [8–12]. On the other hand, the concept of forbidden links assumes that niche-based processes constrain the interactions by means of matches and mismatches on the ecological traits of species [1,3–6,9,10,13].

Previous studies have found that species abundance has a major role in determining how interactions are structured in different ecological networks, including positive interactions such as plant–pollinators [9,14] and plant–plant facilitation [15], commensalistic interaction among epiphytes and phorophytes [16] or antagonisms between plant–herbivores and hosts–parasitoids [12,17]. These studies also showed that the observed interactions are better predicted by simulations when other factors are included together with the abundance, such as phenological

overlap [9,11,12], morphological matches among species [14] or the phylogenetic relationship, which ultimately influences the traits of the species [15]. In this sense, species traits affect the possibility of interactions by creating forbidden links in the community, although their importance seems to be secondary in comparison with species abundance.

Despite the increasing consensus on the major role of species abundance in structuring different ecological networks, possible limitations can be highlighted before achieving broader generalizations. Sampling insufficiency can pose misleading interpretations, making difficult to discriminate unobserved interactions owing to undersampling from truly forbidden links [13]. The lack of proper estimations of abundance can be another problem, because some studies have used the interaction frequency (extracted from the observed network) as a proxy for species abundance [8,9,18,19]. This procedure ignores the intrinsic dependence between the frequency of interactions and the 'abundance' generated. Ideally, independent measures of abundance should be collected directly in the field while the network data are collected [11]. Overcoming and investigating the effects of these limitations are then necessary steps towards broader generalizations.

Hummingbird interactions with their critical food resource, the flowers, are believed to be strongly influenced by the phenotype of both birds and plants, imposing constraints on the interactions within communities [20–24] (but see [25] for a different perspective). Nevertheless, studies applying a network approach to test the relative importance of abundance and forbidden links in structuring the interactions among hummingbirds and plants are still missing. With this in mind, we collected data on the interaction among hummingbirds and plants from the Atlantic rainforest in Southeast Brazil to ask: (i) what are the relative importance of species abundance, morphological match and phenological overlap in predicting the frequency of pairwise interactions among species in the network? (ii) Are the results obtained using independently collected estimates of abundances the same as using 'abundances' extracted from species interaction frequencies? (iii) Are abundance, morphology and phenology able to predict network aggregate statistics?

2. Material and methods

(a) Study area and data collection

We conducted fieldwork in the Santa Virgínia Field Station located in Serra do Mar State Park (23°17'–23°24' S and 45°03'–45°11' W) in the state of São Paulo, Brazil (see the electronic supplementary material, figure S1). The study site has 17 500 ha of Atlantic rainforest (montane ombrophilous dense forest—*sensu* [26]), slope between 24° and 37° and is situated from 850 to 1100 m a.s.l. The region has high precipitation with mean annual rainfall higher than 2000 mm, always higher than 60 mm per month. We collected data from September 2011 to August 2012, mostly along 12000 m of field trails and dirt roads in the forest borders. Sampling locations comprised primary forest (approx. 26%), secondary forest (approx. 54%) and forest borders, which included riversides and roadsides (approx. 20%).

(b) Flowering phenology and abundance of hummingbird-pollinated plants

Every month, we counted all hummingbird-pollinated plants flowering within 2.5 m of each side of the study trails. Plants in

the canopy were considered only when their flowers were visible from the ground. For mass-flowering species with hundreds of flowers per individual (e.g. *Erythrina speciosa*), we estimated the mean number of flowers per inflorescence, and then multiplied this by the number of inflorescences per individual. The total number of flowers produced was considered as the abundance of each plant species after verifying a strong and linear correlation between the total number of flowers produced and the number of individuals for each plant species in our data (see the electronic supplementary material, figure S2).

(c) Phenology and abundance of hummingbirds

We defined hummingbird phenology as the presence of each species during each month of sampling, and abundance as the frequency of species occurrence in the 60 days spent in the field during the study period (approx. 5 days per month). In order to check whether the frequency of occurrence could be used as an adequate measure of abundance, we compared it with the abundance estimated through 'line transect count' [27] in 10 fixed transects (100 m each) distributed in primary (approx. 47%) and secondary forest (approx. 32%), as well riversides (approx. 21%) along our study trails. Every month, we walked each transect for 10 min in the early morning, always keeping the same sampling sequence during the study period. To avoid counting the same hummingbird individual more than once, transects were at least 100 m apart from each other, which ensured some spatial independence. We counted birds up to 3 h after the sunrise and only during days without rain. The positive and linear relationship between these two estimates (see the electronic supplementary material, figure S3) suggests that frequency of occurrence adequately describes species abundance.

(d) Flower and bill morphology

We considered the corolla length as the primary constraint determining the ability of a hummingbird to access the nectar in the flower, and measured the effective corolla length [21] for all plant species. For each species, we measured between three and 20 flowers, collected from different individuals.

Hummingbirds' bill lengths were measured from voucher specimens in the zoological museums of the University of São Paulo and the University of Campinas. As hummingbirds can project their tongues to drink nectar [28], bill measurements that ignore tongue extension can underestimate the bird's capacity to access nectar. Because precise measurements of tongue length were unavailable for different hummingbird species, we added one-third to the bill length for each species. We consider this correction adequate, because it preserves the proportion by which birds with longer bills also have longer tongues [28].

(e) Plant–hummingbird interactions

The hummingbird–plant network was constructed from observations of legitimate visits (when hummingbirds contacted the flower reproductive structures). For each flowering species, we conducted focal plant observations for 12 to 31 h, using binoculars or video-cameras. Our observations totalled 881 h, during which we quantified the interactions between pairs of hummingbird and plant species. Observations were conducted in at least two individuals for each plant species, and the use of video-cameras was restricted to plant species that produced few flowers per individual in order to prevent any underestimation of the interactions. Finally, we evaluated the sufficiency of our sampling using individual-based rarefaction analysis [29], applied to links in the network rather than in individual organisms [30].

(f) Determinants of the network: constructing interaction probability matrices

To evaluate the contribution of distinct determinants to the plant–pollinator network structure, we followed the conceptual framework developed by Vázquez *et al.* [9]. To assess whether frequency of interactions can be predicted by species abundance, morphology and phenology, the observed interaction matrix was compared with interaction probability matrices. These probability matrices were constructed from data on abundance, morphology and phenology of species, or a combination of them. In the following, we present a brief description of the analyses, detailing some modifications in relation to Vázquez *et al.* [9].

Observed matrix (O): we constructed a quantitative plant–pollinator matrix with rows corresponding to plant species (*i*) and columns to pollinators (*j*). Each cell entry represents the number of interactions recorded between a hummingbird and plant species (*o_{ij}*).

Probability matrix based on abundance (A): the abundance of each plant species was multiplied by the abundance of each hummingbird species to generate a matrix representing the product of all plant and pollinator abundances. The cell values in this matrix were normalized by dividing each cell by the matrix sum such that its elements totalled to one, resulting in a probability matrix **A**. This matrix can be considered a ‘neutral model’ or ‘null model based on abundances’ [31], because by ignoring phenotypic traits relevant for the interaction among species (e.g. phenology and morphology, which reflect species specializations), this matrix considers species to interact randomly, irrespective of their ecological differences. One important remark is that abundance is an emerging property at population level that can be regulated by neutral processes, but also by species phenotypes and consequently niches [32]. In this sense, the use of abundance does not mean an evaluation of the role of purely neutral-based processes in structuring the communities and must be taken as a ‘neutral statistical model’ generator of patterns, but which does not specify exactly the mechanism behind it [31].

Probability matrix based on phenological overlap (F): cell entry in phenological overlap matrix was expressed by the number of months in which a plant and a pollinator co-occurred. This matrix was also normalized to produce the probability matrix based on phenological overlap (**F**).

Probability matrix based on morphological match (M): in this matrix, interaction between a given plant and hummingbird was allowed when the length of the hummingbird bill + tongue (hereafter ‘bill’ for simplification) was equal to or longer than the flower corolla length. For interactions considered as possible based on this morphological match, we assigned 1, and 0 otherwise. This matrix was normalized in the same manner as other matrices. It is important to note that three plant species had longer corollas than the longest bill (electronic supplementary material, figure S4). In spite of the apparent bill–corolla mismatch, these interactions were considered possible in the matrix. In these three cases, the nectar accumulates in the base of the narrow corolla, allowing the hummingbird with the longest bill to access the nectar.

From the matrices **A**, **F** and **M**, we also constructed probability matrices with all the possible combinations: **AF**, **AM**, **FM**, **AFM**, in order to investigate the combined effect of multiple models. These combined matrices were calculated by Hadamard (or elementwise) product and then also normalized. In this sense, each of the original matrices (**A**, **F** and **M**) had equal importance in structuring the interactions in the combined matrices. Additionally, as a benchmark matrix for comparison with other probability matrices, we constructed a null matrix (**NULL**) in which all plant and hummingbird species have the same probability of interaction.

(g) Comparing the ability of probability matrices to predict observed interactions

To evaluate whether abundance, phenological overlap and morphological match can predict detailed structure of the observed interaction matrix, we used a likelihood approach. If a probability matrix can predict the observed interactions, then cells with higher probability in our models (probability matrices **A**, **F**, **M**, **AF**, **AM**, **FM**, **AFM**, **NULL**) would also have a higher number of interactions in the observed matrix (**O**). We used the Akaike information criteria (AIC) to evaluate the prediction ability of each model and Δ AIC to compare them. Δ AIC is the value obtained by subtracting the AIC of the best-fitting model from the AIC of each model. As in Vázquez *et al.* [9], we assumed that the probability of interaction between a given plant and pollinator followed a multinomial distribution. The likelihood was calculated using the function *dmultinom* in the *stats* package in R [33].

The number of parameters used to weight different models’ complexities was defined as the number of species of each probability matrix included in the given model. In this sense, the models **A**, **F** and **M**, with nine pollinators and 47 plants, had 56 parameters (species), and by the same calculation, models **AF**, **AM** and **FM** had 112 (56 for each matrix) parameters. The most complex model **AFM** had 168 parameters from three matrices. The simplest model ‘**NULL**’ was assigned with one parameter, because it was not properly based on a matrix. Using the number of species as a parameter is more conservative than using the number of matrices, as done in Vázquez *et al.* [9], and our decision was intended to avoid under-penalization of the most complex models. For the purpose of comparison, we also repeated the analyses using the number of matrices as parameters, but the results remained consistent (see the electronic supplementary material, figure S5).

(h) Is model selection biased by abundance measures?

In order to answer this question, we repeated the abovementioned analysis considering the observed frequency of interaction as a proxy for species abundance, as often assumed in previous studies [8,9,19]. The frequency of interaction of each hummingbird (**h**) was multiplied by the frequency of interaction of each plant species (**p**) producing a matrix **hp**. This matrix was normalized, resulting in the probability matrix based on frequency of interaction (**hp**). To verify whether model selection can be biased by **h** or **p** independently, we constructed hybrid models based on the frequency of interaction (**h** and **p**) and independent measures of abundances (**H** and **P**), mentioned before and used to construct the probability matrix **A**. These combinations resulted in two more models: **Hp**, which combines the abundance for hummingbirds and frequency of interaction for plants, and **hP**, which combines frequency of interaction for hummingbirds and abundance for plants. Note that we did not use an **HP** model because it would be equal to **A**. These models were also compared with the observed matrix (**O**) using a likelihood approach, as in the previous analysis.

(i) Analysis of network aggregate statistics

We tested how well each of the above-mentioned models predicts five frequently used network aggregate statistics (hereafter metrics): nestedness, connectance, interaction evenness, specialization and interaction asymmetry (the last was calculated separately for pollinators and plants). Nestedness was calculated with WNODF (weighted nestedness metric based on overlap and decreasing fill) [34] implemented as function *weighted NODF* in the R package *bipartite* [33,35]. Specialization was calculated as the H2 index (*H2* function in *bipartite*), which measures network-level specialization in quantitative networks [36]. Other network metrics were calculated as in Vázquez *et al.* [9]. Using *mgen* (in *bipartite* package), 1000 randomized networks were created according to eight

probability matrices (**A**, **F**, **M**, **AF**, **AM**, **FM**, **AFM**, **NULL**). The randomization algorithm generated matrices of the same size as the observed one and distributed the interactions (1231 in our case) in the cells according to the probability of each interaction. A constraint was determined such that each species in randomized matrices received at least one interaction. The observed metrics values (calculated from matrix **O**) were compared with values from randomized networks and considered as predicted by probabilistic matrices when we found overlap (95% confidence interval, calculated with function *confint* in *bipartite*).

3. Results

(a) The plant–hummingbird network

We recorded 47 species of plants pollinated by nine hummingbirds in the study site (figure 1). Bromeliaceae (20 species) and Gesneriaceae (seven species) were the most common plant families. Flowering period was short for most plants, with only nine species (19%) flowering for more than three months, and just *Fuchsia regia* flowering all year around (see the electronic supplementary material, figure S6). In general, flower abundance was low and relatively similar for all plants; 82% of plants produced fewer than 150 flowers in total, and only four species produced more than 1000 flowers (see the electronic supplementary material, figure S7). Flowers' corollas were generally tubular, with length varying from 0.3 cm in *Spirotheca rivieri* to 5.1 cm in *Mannetia chrysoderma* (see the electronic supplementary material, figure S4).

From the nine hummingbird species recorded, *Phaethornis eurynome*, *Thalurania glaucopis* and *Clytolaema rubricauda* were the most abundant (see the electronic supplementary material, figure S8) and recorded in the study area all year round (see the electronic supplementary material, figure S9). Other species were rare, with occasional records. The bill length (+ tongue) varied from 1.6 cm in *Lophornis chalybeus* to 4.5 cm in *P. eurynome* (see the electronic supplementary material, figure S4).

We recorded 1231 hummingbird visits with 86 distinct pairwise interactions (figure 1). Rarefaction analysis indicated that our sampling recorded most of the interactions (see the electronic supplementary material, figure S10). The network was not nested (WNODF = 22.18, null model interval was between 16.30 and 25.88), with low connectance (0.20), intermediate value of specialization ($H2 = 0.51$), high interaction evenness (0.83) and mean interaction asymmetry lower for plants (−0.17) than for hummingbirds (−0.68; figure 2).

(b) Determinants of the network and their ability to predict network metrics

The model combining morphological match and phenological overlap (**FM**—expressing the forbidden links) was the best predictor of the interaction frequency between plants and hummingbirds, with all models including abundance (**A**) performing poorly (figure 2). This result, however, changed when we used the frequency of interaction as a proxy for abundance (figure 3). Among three models using the frequencies of interaction, two fitted better to the observed network than **FM** and both included **p** (frequency of interaction as a measure of abundance for plants). The model including **h** (frequency of interaction as a measure of abundance for hummingbirds) together with an independent measure of abundance for plants exhibited a fit to the observed data that

was similar to **A** (which used an independent measure of abundance for both hummingbirds and plants).

In general, abundance, phenology and morphology were unable to predict nestedness, connectance, specialization, evenness nor interaction asymmetry (figure 4). Exceptions were interaction asymmetry for the pollinators, which could be predicted by the complete model, including all matrices (**A**, **F** and **M**) and nestedness predicted by the 'NULL' model with equal probabilities for all interactions (figure 4). Although not accurate for predicting most of the metrics, models including abundance generated the closest results to the observed ones for connectance, evenness and asymmetries of interaction.

4. Discussion

(a) Determinants of network structure

Contrary to the growing consensus that species abundances is a critical factor determining the interaction network structure [9–11,15,16], our study shows that morphological match and phenological overlap are more important than abundance for predicting plant–hummingbird interactions. The modest importance of abundance in our study can be attributed to several factors, including the low variation in relative abundances—at least among the three most abundant hummingbird species and many plants. This characteristic of the network gives the model based on abundance similar probabilities for most pairwise interactions. At the same time, morphological and phenological traits varied considerably among species, thus forbidden links generated distinct probabilities for the pairwise interactions even among species with similar abundances. We believe that both of these factors contributed to the modest importance of abundances.

Abundance clearly did not positively correlate with visitation for some plant species, such as the abundant but scarcely visited *Psychotria eriocarpa*, which has very small flowers producing small amounts of nectar, or the less abundant, but highly visited *Quesnelia* sp. with copious nectar production. In this sense, flower abundance seems to be insufficient to predict the frequency with which a plant will be visited without considering species phenotype and details of their natural history, such as nectar production or floral display, which affect pollinator activity [37].

The striking evidence that phenological overlapping and morphological match are important for network structure can be illustrated by other examples. Most of the plants had short flowering times and most hummingbirds occurred occasionally. This implies that many species that could potentially interact because they present a morphological match, do not overlap in time. This might be the case for the short-billed *Leucochloris albicollis*, which does not interact with the short corolla flowers of *Quesnelia* sp. even though this hummingbird regularly visits other plants with similar flowers. On the other hand, some species with phenological overlap did not interact owing to morphological mismatch. This was the case for many long corolla plants such as *Vriesea* spp. and *Nidularium* spp., species whose flowering overlapped with the presence of short-billed hummingbirds such as *Clytolaema rubricauda* and *Thalurania glaucopis*. Our finding is in accordance with previous studies showing the role of morphology and phenology in organizing plant–hummingbird communities [20–24], pointing to the importance of ecological and evolutionary processes in generating the forbidden links.

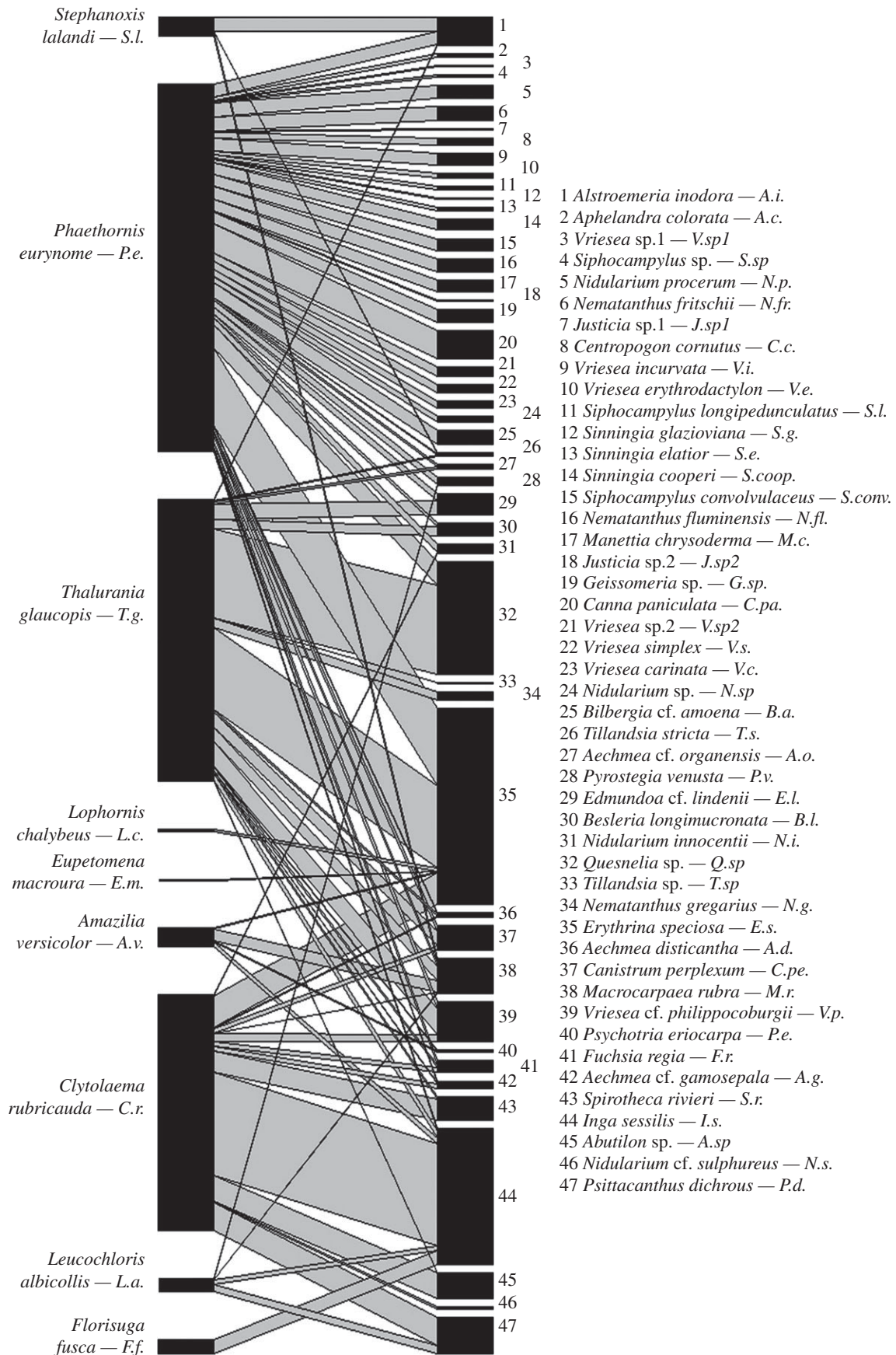


Figure 1. Hummingbird–plant mutualistic network in the Atlantic rainforest of the Santa Virgínia Field Station, Serra do Mar State Park, SE Brazil. Hummingbirds (right) and plants (left). Grey lines represent species interaction and line thickness indicates frequency of interaction.

If a large proportion of unobserved interactions in the networks with robust sampling is in fact forbidden [13], then sampling insufficiency might underestimate the importance of forbidden links in structuring the networks. Although undersampling potentially influences the structure and

metrics of interaction networks [1,7,9,12], studies have only recently started to evaluate this limitation [30,38–40]. Non-detection of interactions owing to sampling insufficiency is probably a widespread problem in plant–pollinator networks [39], and estimating the sampling sufficiency as done

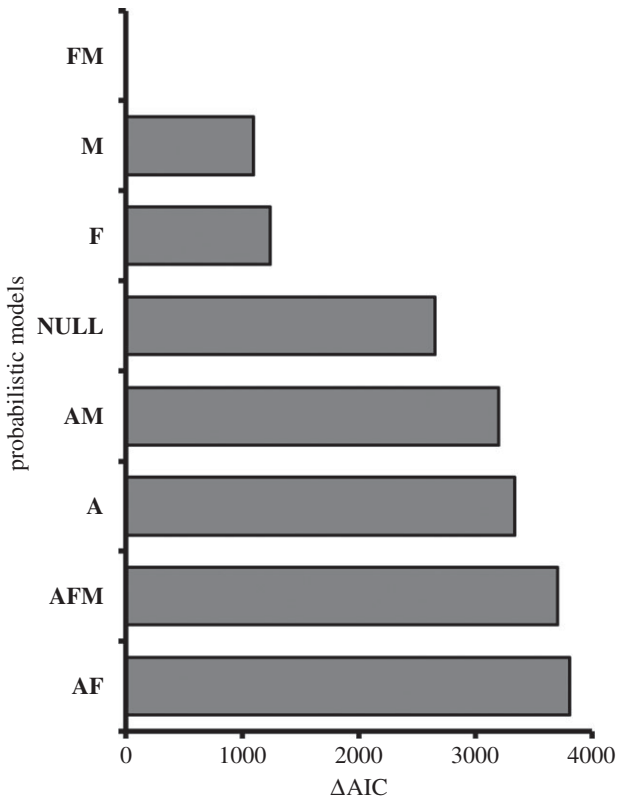


Figure 2. Δ AIC values of the probabilistic models (probabilistic matrices) resulting from species abundance (A), phenology (F) and morphology (M) and all possible combinations among them in relation to the best model (FM); NULL is the model in which all pairwise interactions have the same probability. Shorter bars indicate better fit of a given model in relation to the FM model, which presented the best fit to the observed network.

here and in other studies [13,40] seems to be a necessary procedure in future studies.

(b) Can frequency of interactions be used as a proxy for species abundance?

We provide evidence that frequency of interaction is a poor proxy for abundance, which might drastically change the interpretation of the relative importance of factors structuring the networks. Abundance was not able to predict the observed network better than forbidden links, but when frequency of interaction was used as proxy for abundance, models including it performed better than forbidden links. The contrast between our findings and some of the previous studies that reported higher importance of abundance over forbidden links [8,9,18,19] might be due to this difference. This bias might be especially severe when there is no correlation between species' abundances and their frequency of interactions, as we observed for the plants (see the electronic supplementary material, figure S11). When there is a correlation, as for hummingbirds (see the electronic supplementary material, figure S12), the bias seems to be minor. However, if there are no data for abundance, this correlation cannot be checked. In this rationale, using the frequency of interaction as a proxy for species abundance is not recommended, because it uses the data to predict itself [11], and might generate misinterpretations by overestimating the importance of the abundance at the expense of forbidden links in structuring the ecological networks.

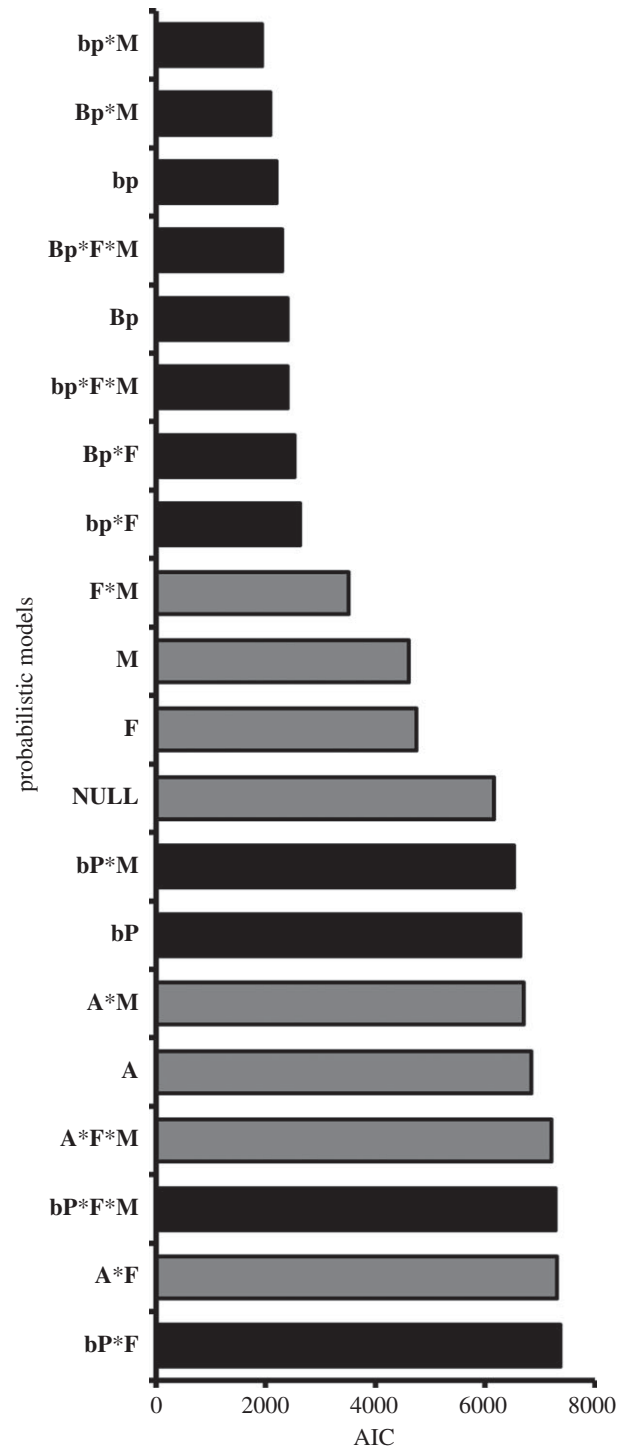


Figure 3. Δ AIC values of the probabilistic matrices generated from species abundance (A), phenology (F) and morphology (M) and all possible combinations. Data were re-analysed considering the frequencies of interaction as an abundance measure, which was represented by **b** for hummingbirds and **p** for plants; **B** and **P** represent the 'real' abundance measures. Analyses were carried out including both abundance measures in combination with **F** and **M**. NULL is the model in which all pairwise interactions have the same probability. Shorter bars indicate better fit of a given model in relation to the observed network. Grey bars show AIC values calculated using the real abundance measure. Note that when abundance models are constructed using frequencies of interaction (black bars), most of the better models (shorter bars) include this 'abundance', whereas models constructed using the independent measures of abundance had worse fit (longer grey bars).

(c) Prediction of network-aggregated statistics

Although forbidden links better predicted the interaction frequency between plants and hummingbirds, they were unable to reproduce values of network metrics similar to those from

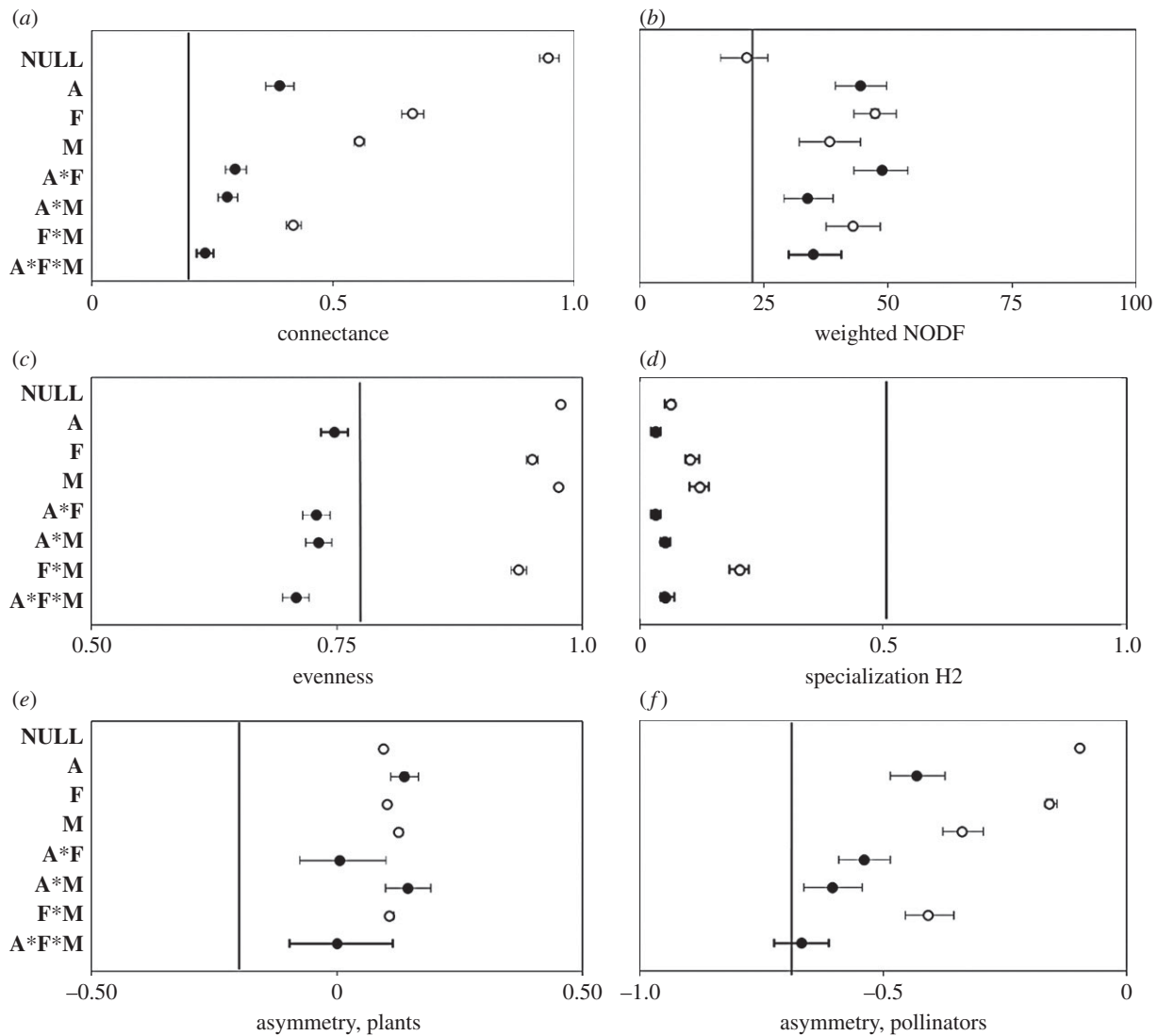


Figure 4. Values of aggregate network statistics (circles, mean; bar, 95% confidence) produced by 1000 randomizations of the eight probabilistic matrices in relation to the observed values (vertical lines inside the boxes). Black filled circles are models that include the abundance. The eight probabilistic matrices were constructed based on species abundance (**A**), phenology (**F**), morphology (**M**) or combinations of them. **NULL** is the model in which all pairwise interactions have the same probability. Probabilistic models predict a given aggregated network statistic when there is overlap in the observed and expected values.

the observed matrix. Instead, models including abundance often showed the closest values to observed metrics. This result contradicts the mechanisms influencing interaction frequencies and the metrics of network structure, which represent distinct attributes of the network. The frequency of pairwise interactions represents the structure of the network because it describes each interaction individually, and ultimately this is used for the calculation of the metrics. In this sense, it seems that although networks metrics are useful for investigating patterns on specific network attributes [7,41], they might be losing some of the data complexity in the process of synthesizing a single number. Thus, we suggest that network metrics should be chosen carefully when the point is to investigate different mechanisms generating the network structure as a whole.

In summary, to the best of our knowledge, this study reports, for the first time, that forbidden links are of higher importance than species abundance in structuring an ecological network. More studies will be required to reveal whether our result is an exception or not. It would be necessary for this purpose to investigate different kinds of plant–pollinator systems and interactions (other than mutualisms) in distinct ecosystems. We also provided evidence that using the

frequency of interaction as a proxy for abundance (when there is no correlation) might overestimate the relative importance of abundance in structuring ecological networks, and this procedure should be avoided. In addition, even the best predictor models of network structures failed in reproducing the observed values of network metrics. This might suggest that, although useful in capturing some specific properties, network metrics could be failing in synthesizing the complexity of the whole network. In sum, our findings suggest that species abundance is not always the most important driver of species interactions in communities.

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