The friendship paradox in species-rich ecological networks: Implications for conservation and monitoring

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ABSTRACT

A great challenge in ecology and conservation biology is to deal with the inherent complexity of ecological systems. Because species are embedded in species-rich systems characterized by multiple interactions, it is often hard to identify which species are really important for ecological processes such as pollination. Here we show that species-rich networks describing plant-pollinator interactions share a property with networks depicting social relationships, the friendship paradox, which allows identifying highly-connected species without detailed information on the whole network of interactions. Numerical simulations support that the identified species are those more likely to affect community structure and ecological dynamics. A sampling protocol taking into account the friendship paradox property could be adapted to field studies, helping in the search for conservation surrogates or to monitor changes in the communities, such as functional extinction or the increase in ecological importance of invasive species. We hypothesize that the friendship paradox is likely to arise in networks describing other types of ecological interactions. Besides being useful for conservation and ecosystem management, the friendship paradox may have relevant implications in other areas of biology as well.

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1. Introduction

Understanding the role different species play in ecosystem functioning is a central issue in ecology and conservation biology (Loreau, 2001). Decades of development of the ecological theory and empirical studies have shown that species differ in their importance for ecological dynamics in ecosystems (Paine, 1966; Power et al., 1996). Species that interact strongly, directly or indirectly, with several other species in the community are often those that control ecological processes (Jordán, 2009; Jordán et al., 2006). In the absence of such species the system is expected to experience profound structural and functional changes (Jordán et al., 2006; Soulé et al., 2003). A classic example is the loss of apex predators, which produces cascading effects with far-reaching consequences for ecosystem structure and dynamics (Estes et al., 2011; Terborgh and Estes, 2010). For this reason knowledge on species interaction patterns within communities is key for our understanding of the dynamics of natural systems and for conservation and ecosystem management (Simberloff, 1998; Soulé et al., 2003).

Species are embedded within large networks of interactions with nonrandom structure (Bascompte and Jordano, 2007; Dunne, 2006). A number of metrics have been proposed to identify key species in ecological networks based on their interaction patterns (Fedor and Vasas,

2009; Jordán, 2009). However, obtaining a detailed description of who interacts with whom in a given locality is, by itself, a major challenge that entails intensive fieldwork (Burkle and Alarcón, 2011; Memmot, 2006; Tylianakis et al., 2010). Even though the relevance of networks in conservation has been increasingly recognized (Kaiser-Bunbury and Blüthgen, 2015) and the number of available well-resolved networks has been growing fast (e.g., Carvalheiro et al., 2014), the difficulty in obtaining detailed data on interaction patterns is still an obstacle for the use of networks in conservation planning (Tylianakis et al., 2010).

One key ecological process threatened by the biodiversity crisis is pollination. There is increasing evidence pointing out that both domesticated and wild populations of pollinators are dying off (Lever et al., 2014; Steffan-Dewenter et al., 2005). There is also evidence for parallel declines in the plants in response to the collapse of populations of pollinators, which might lead to ecological and economic negative impacts (Biesmeijer et al., 2006; Kearns et al., 1998; Potts et al., 2010). However, because plant-pollinator interactions often form large networks of interacting species (Bascompte and Jordano, 2007; Vázquez et al., 2009) identifying which species are truly important to system dynamics is challenging (Morales-Castilla et al., 2015).

Here, we address the problem of identifying ecologically important species within species-rich communities by combining data on plant-pollinator interactions and advances in the study of social networks (Christakis and Fowler, 2010). We first analyze species-rich plant-pollination networks to test if these networks share a similar feature with

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social networks, the so-called friendship paradox (FP). The friendship paradox posits that, on average, the friends of randomly selected people (nodes) have more social interactions (links) and are more central to the network than the initial, randomly selected, set of people who named them (Christakis and Fowler, 2010; Feld, 1990). By analogy we tested whether the interaction partners of species selected at random in plant-pollinator networks are more connected and centralized than the random set of species used to form the partners group (Fig. 1). The FP property has proven useful in early detection of contagious outbreaks because it allows the identification of central individuals, which are likely to be infected sooner, without information on the whole network of social ties (Christakis and Fowler, 2010; Vidondo et al., 2012). Similarly, the FP could help identifying species that are central in ecological networks, and thus important to community structure and dynamics, without detailed information on the interaction patterns of all species. Here we developed a sampling algorithm to test whether the friendship paradox applies to species-rich plant-pollinator networks. Then, we used differential equations to model community dynamics, and simulated extinctions to show that the species identified through the FP are ecologically important. Because a sampling scheme based on the FP property could be easily adapted to the field, helping in the identification of ecologically important species with minimal information, we argue that the FP can be useful for conservation and management.

2. Materials and methods

To test whether the friendship paradox applies to ecological networks and to evaluate the potential usefulness of the friendship paradox we focused on six quantitative, species-rich (>50 species), plant–pollinator networks (Table A1). We restricted our analyses to a subset of available plant-pollinator networks for three reasons. First, we only used species-rich networks because the challenge of identifying species that are important to ecological dynamics increases with species richness. Second, because interaction strength plays a fundamental role in ecological dynamics (Vázquez et al., 2015) and in the friendship paradox property (see below), we constrain the analyses to weighted networks in which links depict the frequency of interactions, used as a proxy for the strength of interactions among plants and their pollinators (Fig. 1). Third, this dataset encompasses networks assembled using data collected using a variety of sampling methods at different timescales (see Appendix A). By choosing a heterogeneous dataset we expected to avoid obtaining results that are a consequence of choosing networks

built using a particular type of data or representing a particular timeframe. To test the robustness of the friendship paradox in species-rich pollination networks we used a second dataset of highly resolved quantitative networks sequentially sampled (Kaiser-Bunbury et al., 2014, Kaiser-Bunbury et al., 2009; see Appendix A). These networks allowed us to test whether the FP is consistent over time while considering sampling time windows that ensure all species co-occurred and could potentially interact. From this second dataset we only used those networks with more than ten plants and ten pollinator species, totaling 32 analyzed networks.

2.1. The friendship paradox

If the friendship paradox (FP) applied for the analyzed pollination networks, the interaction partners of a given random subset of species should have, on average, more interactions and should be more centralized than the species within the random group (Christakis and Fowler, 2010). Thus, we designed a sampling algorithm, which simulates the process of identifying the friends of randomly selected people in social networks. In social science studies (Christakis and Fowler, 2010), randomly selected individuals were asked to name their closest friends, i.e., those with which they interact more frequently, to identify the partner group. Similarly, in a field study where plants are selected for focal observations of pollinators, those pollinators that interact more frequently with the observed plants are more likely to be the most relevant for the plants (Vázquez et al., 2015). Along the same lines, in a field study focused on sampling pollinators and then identifying the pollen in their bodies, the most visited plants are expected to be the most important for the pollinators (Vázquez et al., 2015). The FP sampling algorithm builds upon this assumption and searches for the interaction partners of randomly selected species based on interaction weights.

The FP sampling algorithm starts by randomly sampling n species of a given assemblage (plants or pollinators). Then the algorithm searches for the three interaction partners of these randomly selected species with which they interact more strongly. This step emulates the process of people nominating their three closest friends in the FP studies with social networks (Christakis and Fowler, 2010). To form a new group of size n, hereafter the partners group, the algorithm chooses the n species appearing more frequently among the selected partners (Fig. 1b; the algorithm is available as an R function available as online Supplementary code). Ties are handled by randomly sampling species with the same number of indications until the group reaches n species. Thus, the FP sampling algorithm generates two groups of n species, the initial
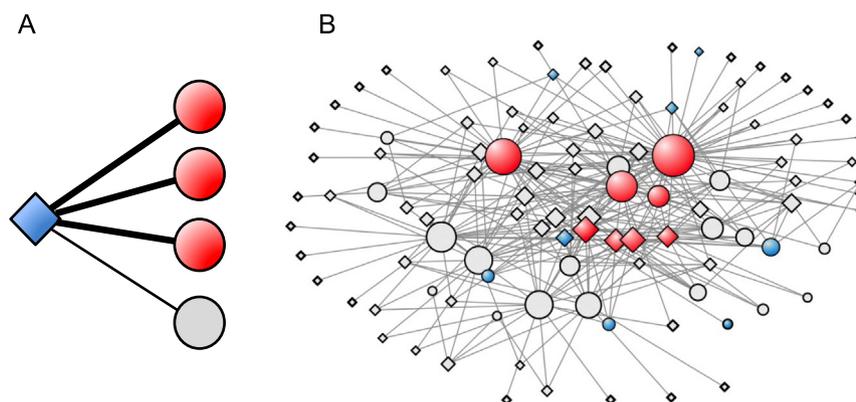
Fig. 1. Identifying species within the partner group based on the friendship paradox (FP) property. (a) Diagram showing the formation of the partners group using the FP algorithm. In an algorithm run it finds for each randomly selected species (blue) three species among those species with which it interacts more frequently (red), as indicated by edge width. The process is repeated for n randomly selected species. A subset of n partners, those "nominated" by more species in the initial random group, is grouped to form the partners group. This process is repeated for plants (circles) and pollinators (diamonds). (b) Random (blue nodes) and partner group (red nodes) within a plant-pollinator network after one algorithm run with $n = 4$. The size of nodes is proportional to the number of interactions. Memmott (1999) network was used as an example. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

random group and the partners group. To test if the friendship paradox occurs in plant-pollinator networks we analyzed the topological roles of species assigned to each group.

The algorithm discussed above emulates the sampling process used in social studies (Christakis and Fowler, 2010). However pollination networks are formed by two different assemblages, the plants and the pollinators. Thus, each group (partner and random groups) includes species of one of these non-overlapping sets and the comparisons between the properties of the partner and random group are comparisons across assemblages. To make sure the friendship paradox allows finding important species within a given assemblage we can also define random groups within the same assemblage of the partner group. To do that, the algorithm chooses *n* species at random from each assemblage while ensuring the same species was not assigned to the random and partner groups at the same time. We thus tested if the friendship paradox allows identifying central species across and within assemblages in plant-pollinator networks. Both approaches equally supported the occurrence of the friendship paradox in the plant-pollinator networks analyzed (see Results).

2.2. Testing the FP property

The FP posits that, on average, the friends (partners) of randomly selected people establish more social interactions and are more central to the network than the initial randomly selected people who named them (Christakis and Fowler, 2010; Feld, 1990). Similarly, if the FP applies to plant-pollinator networks we should expect that species within the partners group would have, on average, more interactions and would be more centralized than species within the random group. To test whether the FP takes place in plant-pollinator webs we ran the FP sampling algorithm 100 times (for groups of size $n = 2, 4$, and 8) for both plants and pollinators, for each of the studied networks.

To test the FP property we calculated the average degree (k), which is the number of species each species interacts with, and average centrality of species within the partners group and the random group obtained for each run of the FP algorithm. There are multiple indexes of centrality available in the network literature (e.g., see the review by da Costa et al., 2007), but most of these indexes are often strongly correlated in mutualistic networks (e.g., Sazima et al., 2010). Therefore, we used one centrality measure that reveals a particular aspect of the role of a node in the network topology: the betweenness centrality, B_i, defined as the ratio between the number of shortest paths among all pairs of species that pass through species i and the total number of shortest paths (da Costa et al., 2007). We calculate B from the one-mode projections, built for plants and pollinators, from the two-mode networks (Newman, 2001; Opsahl, 2009; Padrón et al., 2011). In a one-mode projection two pollinators (or two plants) are connected if they share at least one plant (or pollinator) partner. Here we used weighted projections as proposed by Newman (2001), which correct weights in the projection for the number of shared interactions.

We performed all tests using weighted and un-weighted versions of k and B, which are available in the R package *tnet* (Opsahl, 2009; Opsahl et al., 2010). The weighted degree incorporates both the information on the number of interactions (k) and their summed weights (s) in a single metric so that a species with high k^w is connected strongly to many other species:

$$k_i^w = s_i^\alpha k_i^{1-\alpha} \tag{1}$$

The α parameter is a tuning parameter that determines the influence of interaction weights on k^w. The weighted betweenness centrality (B^w) can be defined as:

$$B_i^w = \sum_j \sum_{l \rhd j} \frac{g(i)_{j,l}^w}{g_{j,l}^w}, \tag{2}$$

where g_{jl}^w is the number of weighted shortest paths linking nodes j and l, and $g(i)_{jl}^w$ is the number of weighted shortest paths linking nodes j and l passing through node i. The length of the weighted shortest path is defined as $d_{jl}^w = \min(\frac{1}{w_{jh}^\alpha} + \ldots + \frac{1}{w_{hl}^\alpha})$. Here α controls how weights affect the distances between nodes (Opsahl et al., 2010). We used $\alpha = 0.5$ in all analyses, which results in estimates that take both the number of interactions and their strength into account in an equivalent way.

To allow comparisons across the different assemblages we divided k and B values by the maximum value for each assemblage, obtaining relative values for k and B for each species. Species with relative B close to one are those that are part of the shortest paths connecting most of the other species (da Costa et al., 2007).

To test if the average relative degree (k) and average relative betweenness centrality (B) were larger in the partners group generated by the FP algorithm than in the random group, we performed paired *t*-tests, for k and B and each plant-pollinator network separately. Pairs consist of the average values of k or B for species in the random and partners group for each algorithm run (100 simulations per network). We performed all tests across (plants vs. pollinators) and within assemblages (plants vs. plants; pollinators vs. pollinators; see above) and for group sizes $n = 2, 4$, and 8. For the supplementary analyses using the second set of 32 networks we performed analyses only using group size $n = 4$ for the sake of simplicity. We also tested the effectiveness of the FP sampling algorithm by computing the frequency with which the most connected species were assigned to the partners group. To do that we ranked species according to degree and registered how often the top ranked (highest degree) plants or pollinators in a network were assigned to the partners group.

2.3. The importance of species identified by the FP algorithm

To test if the species identified by the FP sampling are indeed important species in the analyzed networks, we combined dynamical models and extinction simulations. Using coupled differential equations that describe how species abundances vary over time (Okuyama and Holland, 2008; Thébault and Fontaine, 2010) we simulated community dynamics (100 simulations) for each network until the system reached equilibrium (see Appendix A for a detailed description of the model). Then, we performed trials simulating the extinctions of plants or pollinators within the partners and random groups ($n = 4$ species in each group) and reran the model starting from the equilibrium. We removed all four species in a given group simultaneously in each trial. For each of the 100 simulations per network we used a different combination of species in the random and partners group obtained from the 100 runs of the FP algorithm. In this set of analyses the random group can be thought as a control group, providing a benchmark for the expected effect of the extinction of four randomly selected species in the network. We only compare the effects of extinctions of species within the same assemblage because it makes more biological sense to compare the ecological consequences of losing species that are part of the same assemblage (i.e., pollinators vs. pollinators and plants vs. plants) than to compare the consequences of losing plants versus the consequences of losing pollinators.

Because in mutualistic systems species are dependent on their interaction partners to some degree, the extinction of a highly interactive species may result in secondary extinctions (Kaiser-Bunbury et al., 2010; Memmott et al., 2004). Thus, for each simulation under each extinction scenario we registered the number of secondary extinctions. The loss of species that are topologically important should also reconfigure the network altering its structural properties. To detect changes in topology we used two topological descriptors as proxies: nestedness and modularity. Regardless of the different potential underlying mechanisms that generate nestedness or modularity (Vázquez et al., 2009), these two descriptors offer a way of characterizing how species interaction patterns overlap in a network (Bascompte and Jordano, 2007).

Moreover, macroscopic network properties such as nestedness tend to be robust to minor changes in the network (e.g., Petanidou et al., 2008). Therefore, we should only expect large changes in nestedness and modularity after a removal simulation if topologically important species have been lost. We evaluated the changes in network topology after species removal by calculating nestedness (N) and modularity (M) for all the networks that resulted from the extinction simulations (see Appendix A for additional details). We measured the relative change in nestedness and modularity as:

$$N^* = (N'-N)/N \qquad (3)$$

$$M^* = (M'-M)/M \qquad (4)$$

where N and M are nestedness and modularity values in the original network and N' and M' are nestedness and modularity after extinctions simulations.

3. Results

We first tested if pollination networks were characterized by the friendship paradox (FP) property. Both the average relative degree (k) and the average relative betweenness centrality (B) of animal species within the partner group were greater than those recorded for the random group of plant species used to identify partners (Fig. 2a). Accordingly, plant species in the partner group often show higher relative degree and centrality than animal species in the random group (Fig. 2b). This pattern was consistent across all networks analyzed for
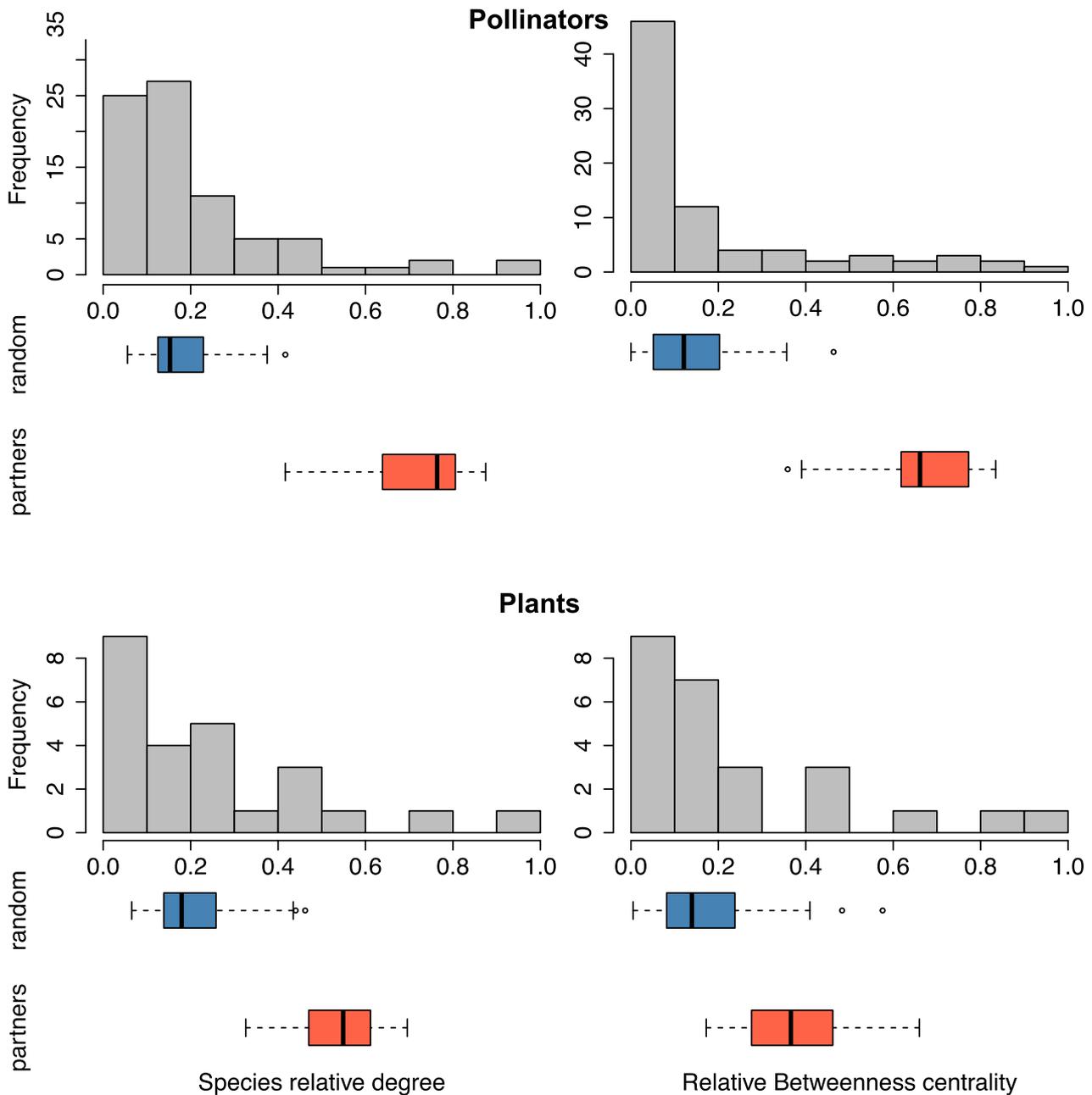
Fig. 2. Distributions of the un-weighted relative degree (k) and relative betweenness centrality (B) of all pollinators and plants (histograms) and species within partner and random groups (boxplots) for Memmott (1999) plant-pollinator network. The boxplots summarize the distribution of the mean values of k and B for each group (size $n = 4$) identified in 100 runs of the FP algorithm. Similar figures for the other analyzed networks are available as Supplementary material (Figs. A1–A5).

groups containing two, four and eight species ($p < 0.05$ in all paired *t*-tests; Tables A3 and A4 and Figs. A1–A5). We then tested if the FP sampling led to the identification of central and highly connected species within each assemblage (plants or animals). Plant and animal species assigned to the partner group had, on average, higher number of interactions and higher centrality than randomly sampled plant and animal species, respectively (Tables A5 and A6). In the vast majority of the simulations the partner groups of size $n = 4$ included at least one of the four most connected plants (94–100% of the simulations) or pollinators (80–100% of the simulations; Fig. A6). The results were similar using the weighted degree (Fig. A7). The FP property was also present in 123 of the 128 comparisons (within and across assemblages) for the 32 networks in the supplementary dataset (see Table A7). The exceptions were networks where all plants had virtually the same number of interactions, i.e., networks in which there was little variation in degree.

Once we showed the FP applies to this set of plant-pollinator networks, allowing the detection of central and highly connected species, we sought to test whether the species identified by the FP algorithm are indeed ecologically important species within the pollination networks they are part of. As predicted, we found more secondary extinctions (up to 50% of the species; Fig. 3) after removing species in the partner group than when compared to the removal of species in the random group. Likewise, the removal of species assigned to the partners group resulted in more pronounced changes in network topology, reducing nestedness (up to 40% reduction; Fig. 3) and increasing modularity (up to 50% increase; Fig. 3; Tables A8–A10). These results were consistent for five of the six analyzed networks.

Because all species-rich pollination networks used here have far more pollinators than plants, the number of secondary extinctions and the effect on network topology were greater when we simulated extinctions of plants (Fig. 3). For instance, in these networks, four pollinator species (which is the size of the groups represented in Fig. 3) often represent <5% of the total of pollinators. However, even the removal of this small set of highly connected and central pollinators identified by the FP algorithm (Fig. 3) is more likely to have greater impacts on ecological dynamics than the loss of randomly selected pollinator species.

4. Discussion

The studied species-rich pollination networks share a fundamental topological property with social networks: the friendship paradox, in which randomly selected nodes show, on average, less interactions and are less centralized in the network than nodes that interact with them. One of the reasons the FP property arises in social and plant-pollinator networks is because the distribution of links among nodes in these networks is often uneven so that a few nodes possess many links, whereas most nodes possess only a few links (Christakis and Fowler, 2010). In addition to that, plant-pollinator networks tend to be nested, with several asymmetric interactions where species with a few connections interact with highly connected species (Bascompte et al., 2003). Finally, interaction strength also tends to be asymmetric, with certain species being highly dependent on species that interact with multiple partners (Bascompte et al., 2006). The FP will not hold for a given network if interactions are randomly distributed among species, if most species have similar number of interactions, if the network is highly modular (although it may occur within modules) or if dependences are symmetric. The emergence of the FP property is thus linked to multiple topological properties. In fact a single network-level metric such as nestedness is not enough to predict the magnitude of the differences between the groups identified through the FP (even though all analyzed networks are significantly nested; see Figs. A8 and A9). Because uneven connectivity distributions and asymmetry in interaction patterns are common to several types of networks (Newman, 2008), including other types of ecological networks such as other mutualistic networks (Bascompte and Jordano, 2007) and food webs (Dunne, 2006), we hypothesize that the FP is likely to occur in other ecological
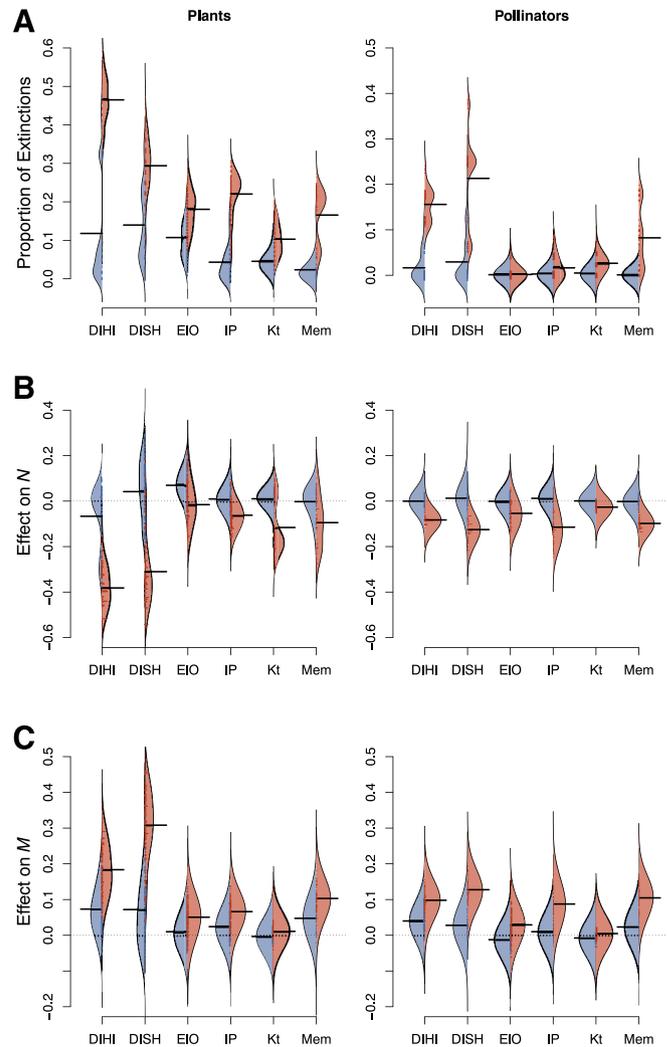
Fig. 3. The effects of extinction simulations of plants and pollinators in the partner (red) and random (blue) groups (group size $n = 4$). (a) Proportion of secondary extinctions after species removal; (b and c) Relative change in nestedness and modularity after species removal. Split violin plots show how measured variables resulting from the removal of species in the partner and random groups are distributed considering 100 replicates. Horizontal bars depict the mean values. Each pair represents a different plant-pollinator network (Table A1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

networks as well. If so, the FP property adds to the potential general properties displayed by complex networks so disparate as human social interaction networks and networks of mutualisms among plants and animals (Albert and Barabási, 2002; Bascompte, 2007).

The structure of ecological networks can shape how the consequences of population decline or local extinctions spread through ecological communities (Memmot, 2006; Memmott et al., 2004; Solé and Montoya, 2001). In networks depicting mutualisms, such as plant-pollinator interactions, structural properties like nestedness, interaction asymmetries, and heterogeneity in the number of interactions among species improve the robustness of these networks when facing species loss (Fortuna et al., 2006; Memmot, 2006; Memmott et al., 2004; Saavedra et al., 2011). Nevertheless, the nonstop extinction of key mutualistic partners, such as some pollinating insects (Biesmeijer et al., 2006) and seed-dispersing vertebrates (Vidal et al., 2014) eventually erode the diversity in species-rich ecosystems, with long-lasting consequences to the ecological services provided by mutualisms (Potts et al., 2010). With the emergence of network ecology there has been increased interest in identifying potential network properties to be used

as indicators of human induced changes in ecological systems, as well as determining the most efficient ways of applying network tools to management and conservation planning (Kaiser-Bunbury and Blüthgen, 2015; Tylianakis et al., 2010). However, obtaining good quality data on the network structure of a given locality of conservation concern is laborious, imposing challenges to the use of networks with conservation purposes (McCann, 2007; Tylianakis et al., 2010). We propose that the FP property can contribute to conservation biology by allowing the identification of ecologically important species while circumventing a major hurdle in monitoring species-rich systems: obtaining detailed information on the patterns of interactions of species in a local community.

The FP property may be useful for conservation in at least three different ways. First, species identified by a sampling scheme based on the FP can be used as conservation surrogates (Caro and O'Doherty, 1999). The use of keystone species as targets for conservation has been recommended (Simberloff, 1998). However, keystone species may be context-dependent and the detection of keystone species in a particular community can be difficult, often demanding experimental manipulation (Power et al., 1996). Species identified by the FP sampling may not always be keystone species in the strict sense (Power et al., 1996), but tend to be highly interactive species (Soulé et al., 2003), i.e., species not only topologically important, but important for system dynamics. The FP thus offers a shortcut for identifying species that are central players in a network. Protecting such species by keeping viable populations is expected to aid in maintaining ecosystem functions and should indirectly benefit other species (Jordán et al., 2006; Simberloff, 1998), including endangered species, which might not be central players in the network, but are still of conservation concern for the maintenance of biodiversity.

Second, the FP may be useful for monitoring local communities. Because the species identified via FP sampling tend to be important for structure and dynamics, monitoring their populations may help to early detect drastic changes in ecological assemblages. Declines in the population densities of species falling within the partner group could be interpreted as a red flag indicating the potential for marked effects on community structure or state transitions (Scheffer et al., 2012). Monitoring changes in the composition of the partner group over time may also help to monitor how the structure of interaction network is changing. Network properties suggested as indicators for conservation, such as interaction diversity and network-level and species-level specialization (Kaiser-Bunbury and Blüthgen, 2015) are related to evenness in interaction patterns and thus affect the FP property. Recent work on the consequences of restoration suggest that pollination networks in restored sites show greater redundancy in interaction patterns and greater generalization (Kaiser-Bunbury et al., 2017). Topological changes in this direction should result in more variable groups identified by repeated sampling via the FP. Therefore the consistency of the partner group over time may signal whether the network is changing and in which direction. In this sense successive sampling via FP may allow using the changes in the network structure for monitoring ecological systems (Gray et al., 2014), even in the absence of data on the network itself.

Third, the FP property may help keeping track of how the role of a particular species in the community changes over time, including how invasive species integrate into a community. As a species succeeds in invading and becoming dominant in a community, its interactions are expected to increase in frequency (Kaiser-Bunbury and Blüthgen, 2015). Therefore, the likelihood that this species shows up in the partners group should increase over time. Conversely, the interactions of a species going through functional extinction should become less and less frequent over time (Valiente-Banuet et al., 2015) and sampling such species through the FP approach would become harder. Repeated sampling in a given locality would reveal how the composition of the partner group is changing and may signal how the role of a species in the network topology is shifting, even if the overall network topology is unknown.

Here we test the FP sampling algorithm using networks with known structure. However, no detailed information of network topology would be needed to use an analogous sampling strategy in the field. As long as a species list is available for a given location, a random sample of species is drawn from the list and fieldwork is carried out to identify a subset of species that heavily interact with the randomly selected set. Those interaction partners that were "nominated" more often form the partners group. Our findings suggest that this sampled set of species and interactions can be relatively small as all results presented here are based on groups with two, four or eight species, which represent very small subsets in the species-rich assemblages used here.

The fact that the most interactive species are often, but not always included in the partner group shows that sampling based on the FP is not flawless: Our analyses show that the method often succeeds in finding highly interactive species important for network structure and dynamics, but because the FP sampling scheme is based on random sampling, the partner group may include some species that are not highly connected or centralized. One way of increasing success in identifying central species is to perform replicated sampling and check which species are consistently identified. Although this increases sampling effort, a sampling scheme based on the FP is simple and easy to implement and it might still be considerably less laborious than acquiring data for constructing the network. Future work focusing on iterative sampling techniques may also help increasing the success rate of the FP sampling.

Another important caveat is that the meaningfulness of the identified species will depend on how interaction sampling is performed. Interaction patterns of a species are often related to its local abundance, since abundant species often participate in many interactions and are expected to be central to network topology (Vázquez et al., 2009). However, interaction sampling based on interaction frequency alone may underestimate the roles of rare species for the network structure and dynamics (Kaiser-Bunbury and Blüthgen, 2015; King et al., 2013). Rare species are often of conservation concern and may be important for ecological functions despite their abundance (Kaiser-Bunbury and Blüthgen, 2015). Adjusting how ecological interactions are sampled may allow identifying relevant species in an ecologically meaningful way that is appropriate for the specific goals of a conservation program. If, for instance, only legitimate visits where pollen is transferred are considered (King et al., 2013; Vázquez et al., 2015), then there is a greater chance that species identified through the FP are indeed important for system functioning. Moreover, combining sampling methods with information on abundance (when available) would allow discerning between species that are topologically important solely because of abundance and those that are important despite low abundance, aiding in the definition of conservation priorities. Finally, available information on natural history should always be used to evaluate whether species sampled via FP could indeed be key drivers of ecosystem processes.

We are aware that more information may be needed before the implementation of the method presented here for conservation purposes. Moreover, we are, by no means, suggesting such approach could replace a thorough study to accurately describe species interactions. The knowledge acquired in such studies is invaluable (e.g., Aizen et al., 2012; Chacoff et al., 2012; Olesen et al., 2008). Moreover, combining good quality network data with robust topological descriptors can help monitoring ecological systems and setting conservation goals (Gray et al., 2014; Kaiser-Bunbury and Blüthgen, 2015; Tylianakis et al., 2010). However, a sampling approach that takes advantage on the FP could be useful as an initial step in conservation programs, especially in areas where information about interaction patterns is limited. The FP may have relevant applications in other areas of biology beyond biodiversity conservation. Species that establish more interactions and are more central to the network are likely to be the drivers of evolutionary dynamics in multispecific systems (Guimarães et al., 2011). The possibility of quick identification of such species with little information

may contribute to a better understanding on the processes shaping ecological and evolutionary dynamics.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.02.026.

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