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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.

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; Memmott, 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

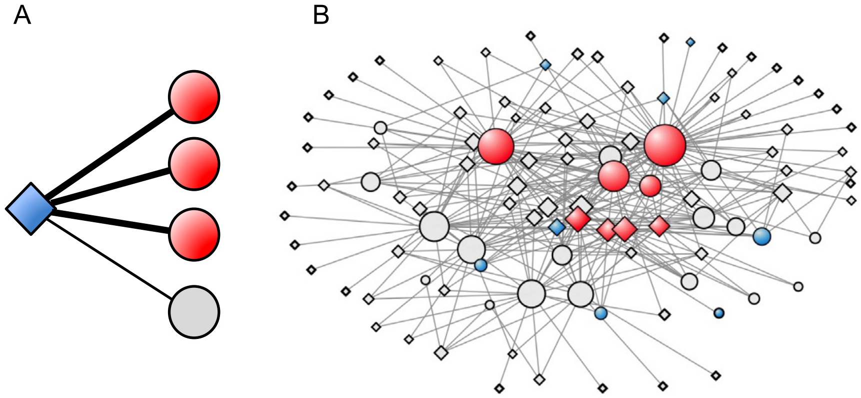

Fig. 1. Identifying species within the partner group based on the friendship paradox (FP) property. (a) Diagram showing the formation of the partners group using the FP algorithm. In an algorithm run it finds for each randomly selected species (blue) three species among those species with which it interacts 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.)