Reports

Reports

The indirect paths to cascading effects of extinctions in mutualistic networks

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Abstract. Biodiversity loss is a hallmark of our times, but predicting its consequences is challenging. Ecological interactions form complex networks with multiple direct and indirect paths through which the impacts of an extinction may propagate. Here we show that accounting for these multiple paths connecting species is necessary to predict how extinctions affect the integrity of ecological networks. Using an approach initially developed for the study of information flow, we estimate indirect effects in plant–pollinator networks and find that even those species with several direct interactions may have much of their influence over others through long indirect paths. Next, we perform extinction simulations in those networks and show that although traditional connectivity metrics fail in the prediction of coextinction patterns, accounting for indirect interaction paths allows predicting species' vulnerability to the cascading effects of an extinction event. Embracing the structural complexity of ecological systems contributes towards a more predictive ecology, which is of paramount importance amid the current biodiversity crisis.

Key words: biodiversity loss; coextinction; complex networks; extinction cascades; indirect effects; perturbation; pollination.

INTRODUCTION

Predicting the consequences of biodiversity loss is one of the main challenges in ecology. Whenever a species starts declining towards extinction its closest interaction partners may follow (Colwell et al. 2012). For instance, extinctions of butterflies in Singapore are associated with the decline and local extinctions of their host plants (Koh 2004), and parallel declines in the diversity of bees and bee-pollinated flowering plants were documented in the Netherlands and in the UK (Biesmeijer et al. 2006). However, species that do not interact directly can be indirectly linked through shared interactions (Carvalheiro et al. 2014, Bergamo et al. 2017), such that a local extinction may trigger cascading effects that impact multiple species (Brodie et al. 2014, Montoya 2015).

Network analysis offers a vast toolkit to investigate how interactions are organized (Delmas et al. 2019) and to examine how the structure of interaction networks shapes ecological dynamics (Tylianakis et al. 2010). Previous work simulating extinctions has shown that the architecture of ecological networks has considerable influence on the formation and effects of extinction cascades on the rest of the community (Solé and Montoya

Reports

2001, Dunne et al. 2002). Mutualistic networks such as those comprised by plant–pollinator interactions are particularly robust to species extinctions because they often involve many redundant partners and form a nested structure where specialists interact with generalists (Memmott et al. 2004). However, the loss of species with many interactions can result in the collapse of the network (Memmott et al. 2004, Berg et al. 2015, Vidal et al. 2019), especially if the network is densely connected, which provides multiple paths for cascading effects to spread (Campbell et al. 2012, Vieira and Almeida-Neto 2015).

Most metrics used to characterize network structure describe the arrangement of direct interactions or focus on the shortest paths connecting species pairs (Simmons et al. 2019). Nevertheless, the numerous paths of different lengths connecting species provide multiple alternative routes for indirect effects (Borrett et al. 2007, Guimarães et al. 2018), which can have profound consequences for the emergent dynamics of ecological communities (Wootton 1994, Montoya et al. 2009). Experimental and theoretical work has shown that indirect effects can comprise a large part of the changes in population densities and species composition of ecological communities following perturbations (Yodzis 1988, Menge 1995, Novak et al. 2016). As a consequence, focusing on the shortest paths while ignoring the multiple paths connecting species restricts our ability to predict how the community will respond to a changing environment (Montoya et al. 2009).

Here we combined an approach derived from the study of information flow in complex systems (Guimarães et al. 2017), stochastic extinction models (Vieira and Almeida-Neto 2015), and empirical plant–pollinator networks to test whether the analysis of indirect paths in networks allows predicting extinction dynamics in ecological systems. We focus on plant–pollinator interactions, which are critical for natural systems and for economies, but are threatened worldwide by habitat loss, invasive species, and improper agricultural practices (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2016). Moreover, plant–pollinator interactions exhibit large variation in the degree to which they are dependent on their specific partners, generating a diverse array of possible responses to extinction (Traveset et al. 2017). Being able to predict how local extinction events impact plant–pollinator assemblages is therefore critical for the management of pollination services. We show that accounting for indirect paths allows predicting how the network responds to species loss and to estimate species-specific vulnerability to the cascading effects of extinctions.

METHODS

Plant–pollinator networks

We investigated indirect effects of extinctions in mutualistic networks depicting interactions between flowering plants and pollinating animals. We performed all analyses using a set of 88 quantitative plant–pollinator networks that vary in species richness and structure, and that have been constructed from empirical observations in different ecosystems. All used data is available at the Web of Life repository (www.web-of-life.es) or in Data S1. In the main text and figures we focus on a manageable set of 10 networks (Appendix S1: Table S1) to allow visualization. The results for the main analyses with the additional 78 networks are reported in Data S2. To analyze the effects of network structure on the predictability of extinction cascades, we generated an additional set of 300 simulated weighted networks with nonrandom realistic structure (see Appendix S1 and Fig. S1 for further information).

The total effects matrix: computing direct and indirect effects

A quantitative plant–pollinator network can be represented as a square adjacency matrix $\mathbf{A}$, where link weights, $a_{ij} \geq 1$, represent the observed frequency of interactions between species i and j. The dependence of species i on species j, d_{ij}, is computed from the adjacency matrix $\mathbf{A}$ as the proportion of all observations for i that involve j:

$$d_{ij} = \frac{a_{ij}}{\sum_k a_{ik}}. \tag{1}$$

Because (1) most plant species have a nonzero probability of persisting in the absence of pollinators by selfing or vegetative reproduction, and (2) most animal species have a nonzero probability of persisting in the absence of flowering plants by feeding on other resources (Traveset et al. 2017), the dependencies should not sum to one. To reproduce that we rescale dependencies so that

$$\mathbf{Q} = \mathbf{RD} \tag{2}$$

in which $\mathbf{D}$ is the matrix describing the pairwise dependencies of species and $\mathbf{R}$ is a diagonal matrix containing species' R_{ii} values, which account for the relative contribution of plant–pollinator interactions for the reproduction of a plant or the diet of a pollinator (Traveset et al. 2017). Because each row of $\mathbf{D}$ sums to 1 and $0 < R_{ii} < 1$, the condition $\sum_{j=1}^{N_p + N_a} q_{ij} < 1$ holds for any species i among all N_p plant and N_a animal species in the network.

Pairwise dependences (Eq. 1) represent the direct effects species may have on each other through paths of length $l = 1$. To compute total effects a species may have on others we have to account for the indirect effects, which develop through paths longer than 1. If we consider q_{ij}^2 an element of the matrix product $\mathbf{Q}^2 = \mathbf{QQ}$, $q_{ij}^2 > 0$ if there is any path of length $l = 2$ connecting the species i and j. We can extend this definition so that $\mathbf{Q}^l$ describes how species are connected through paths of

length l. The sum of the multiple paths of lengths 0 to ∞ converges to a matrix

$$\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1}, \qquad (3)$$

where $\mathbf{I}$ is the identity matrix. Matrix $\mathbf{T}$ thus describes the total influence species exert upon each other through paths of all lengths (Guimarães et al. 2017), such that each element of $\mathbf{T}$, t_{ij}, represents the potential a species on column j has to affect a species on row i, whether they interact directly or not. The average contribution of a species to spreading the effects of perturbations can be computed as the mean value for each column of $\mathbf{T}$, herein referred as T^{out}. T^{out} will be greater for species that have a larger influence on other species by channeling effects through multiple paths of different lengths. For the analyses we rescale the range of T^{out} to be between 0 and 1. From matrix $\mathbf{T}$ we also computed the proportional contribution of indirect paths to total effects for the entire network: $U = \sum_i^N \sum_j^N t_{ij} \times (1 - b_{ij}) / \sum_i^N \sum_j^N t_{ij}$; or for a given species i: $u_i = \sum_j^N t_{ij} \times (1 - b_{ij}) / \sum_j^N t_{ij}$, where b_{ij} are the entries of $\mathbf{B}$, a binary version $\mathbf{A}$ in which $b_{ij} = 1$ if $a_{ij} > 0$.

Simmons et al. (2019) have recently shown that examining how indirect interactions are structured by analyzing network motifs improves the characterization of species' roles. Instead of examining the structure of indirect links, here we compute $\mathbf{T}$ to assess how direct and indirect paths contribute to network dynamics. The approach we use here relates to the framework used to investigate how species abundances in a community near a steady state respond to press perturbations (Yodzis 1988, Montoya et al. 2009, Novak et al. 2011, Novak et al. 2016). However, we compute the total effect matrix directly from the interaction network without considering a specific underlying dynamic model. Matrix $\mathbf{T}$ is thus an approximation of how direct and indirect effects propagate through the network according to topology and interaction weights.

Extinction simulations

To simulate extinctions we used the stochastic extinction model proposed by Vieira and Almeida-Neto (2015). Simulations start with removing a single target species (plant or pollinator) from the network. The extinction of this target species z can result in the extinction of another species i with probability $P_{iz} = R_{ii}d_{iz}$, where d_{iz} is the dependence of i on z. Extinction effects can thus cascade through the network, and the simulation stops when there are no further coextinctions. Because each coextinction event changes the matrix of pairwise dependences, $\mathbf{D}$, the probabilities of further coextinctions change iteratively as the effects of the extinction cascade through the network. After each simulation we recorded (1) the cascade size, which is the number of species that went extinct in a given simulation relative to the total number of species, and (2) the

species-specific frequency of extinctions, which is the proportion of simulations in which a given species went extinct. The frequency of extinction is a proxy for the probability that a species will go extinct following the primary extinction.

In a recent work Traveset et al. (2017) estimated plant reproductive dependence on pollination in two communities as the fraction of the seed set that could be attributed to interactions with pollinators, obtaining mean R values of 0.59 and 0.71. However, estimates of R are scarce and we know little about its distribution for plants and pollinators in most real systems. Thus, we explored how R affected the ability to predict extinction patterns by performing the same analyses assuming high (0.8), intermediary (0.5), and low (0.2) values of R. We also performed analyses assigning varying R values for each species, drawn from a uniform distribution with ranges (0, 1), allowing species to vary along the full range of R, and (0, 0.5) to test the effect of an R distribution bounded to lower values. Among the many reasons why a species may be less dependent on a mutualism is that it may be able to switch to alternative resources (pollinator) or reproductive strategies (plant) in the absence of partners (Traveset et al. 2017). Thus, by simulating species loss under different distributions of R we indirectly account for behavioral responses such as partner switching or rewiring (Kaiser-Bunbury et al. 2010).

Statistical analyses

To test whether considering indirect effects and multiple path lengths improves our ability to predict the effects of species loss, we simulated the extinction of each single species in each empirical network and tested whether the T^{out} value of the removed species predicted the size of the resulting extinction cascade. We used linear models with mean cascade size (from 100 extinction simulations) as a response variable and T^{out} as a predictor. Because T^{out} measures the potential of a species to route propagating effects through a network, it depends on how connected a species is to the other species and on the strength of those ties. To understand better how T^{out} of a species is related to its connectivity, we examined the correlation between T^{out} and different species' connectivity descriptors (Appendix S1): species degree (k), weighted degree (k^w), closeness centrality (C^c), and species strength (S). We also tested the performance of these descriptors as predictors of mean cascade size using linear models and compared model fit using the Akaike information criterion (AIC).

Because the elements t_{ij} in matrix $\mathbf{T}$ represent the potential for species j to affect species i through both direct and indirect effects, we hypothesized that we would be able to estimate coextinction probability of each species from $\mathbf{T}$. We thus used generalized linear models with a logit link function to test whether the probability of extinction of each species i following the extinction of the initial target z, P_{iz}, could be predicted from t_{iz}. In the baseline analyses,

Reports

the target species was always the species with the highest T^{out}. We performed additional analyses where we removed the second or third species with the highest T^{out}. We restricted these analyses to targets with high T^{out}, because removing species with low T^{out} results in fewer coextinctions or none at all. We also tested the relationship between extinction probability and the different species' connectivity descriptors (k, k^w, S, C^c), including the distance between i and z in terms of the shortest paths connecting them (l_{iz}).

To examine the effect of network organization on coextinction predictability, we performed extinction simulations using simulated networks and examined whether network-level properties such as connectance, modularity, nestedness, and average shortest path length (Appendix S1), affected the association between P_{iz} and t_{iz} measured by Spearman's ρ. We performed all analyses using R (R Development Core Team 2019). To characterize network structure we used functions from the R package "bipartite" (Dormann et al. 2008). The codes to reproduce analyses are provided as supporting information (Data S1).

RESULTS

We derived for each network the matrix of total effects **T**, wherein a cell t_{ij} represents the sum of the direct and indirect effects a species j exerts upon species i (Fig. 1A, B). The contribution of indirect paths to interaction effects increases, and that of direct paths decreases, with the dependence of species on their mutualistic interactions, R (Fig. 2A). Even though direct effects are often individually stronger, there are many more indirect paths than direct ones in any network (Fig. 2B). The contribution of indirect paths to the influence of a species over others can be highly variable in a network (Fig. 2C), but even species with several direct partners (high degree) may have a large share of their influence through indirect paths (Fig. 2D).

Simulating the loss of each single species in each empirical network, we found that the average influence of the removed species z, measured by T_z^{out}, often predicted more than 90% of the variation in the size of the resulting extinction cascades (Fig. 3; Appendix S1: Table S2). The extent of cascading effects increases with increasing R, but T_z^{out} was a good predictor of cascade size regardless of the assumed R values (Appendix S1: Table S2). Although T^{out} correlates with traditional connectivity metrics, such as species degree and species strength ($r > 0.8$, $P < 0.001$ for all networks; Appendix S1: Table S3), T_z^{out} outperforms these other metrics in predicting the mean size of extinction cascades for most networks (Fig. 3; Appendix S1: Table S2).
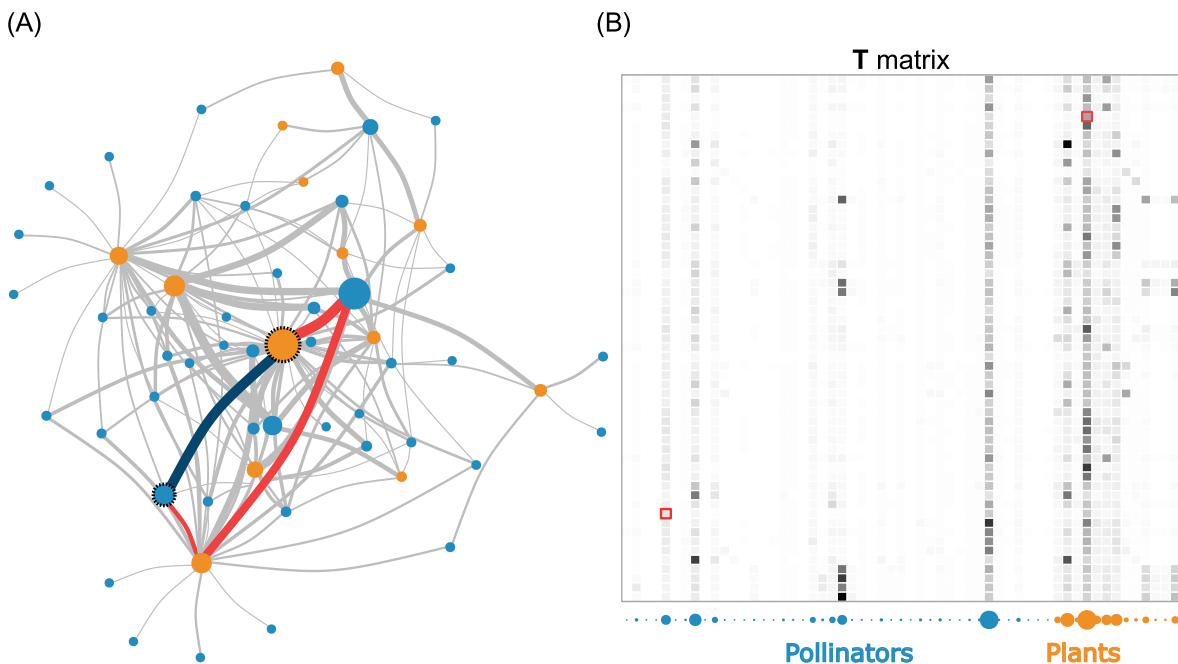
(A)

(B)

FIG. 1. Characterizing direct and indirect effects in mutualistic networks. (A) Example weighted plant–pollinator network (Memmott 1999). Nodes depict plant (orange) and pollinator (blue) species and lines the interactions between them. The direct path, with length $l = 1$, between the highlighted species pair is signaled in dark blue and one of the multiple indirect paths, with length $l = 3$, is signaled in red. (B) The corresponding matrix of total effects, **T**. Darker colors in the matrix indicate the species in the column have a larger influence over species in the corresponding row. The matrix cells highlighted in red represent the mutual effects for the species pair signaled in the network. Circles in A and B are scaled according to T_j^{out}, the mean value of the columns in **T**, which represents the average influence species j exert upon others through direct and indirect paths.
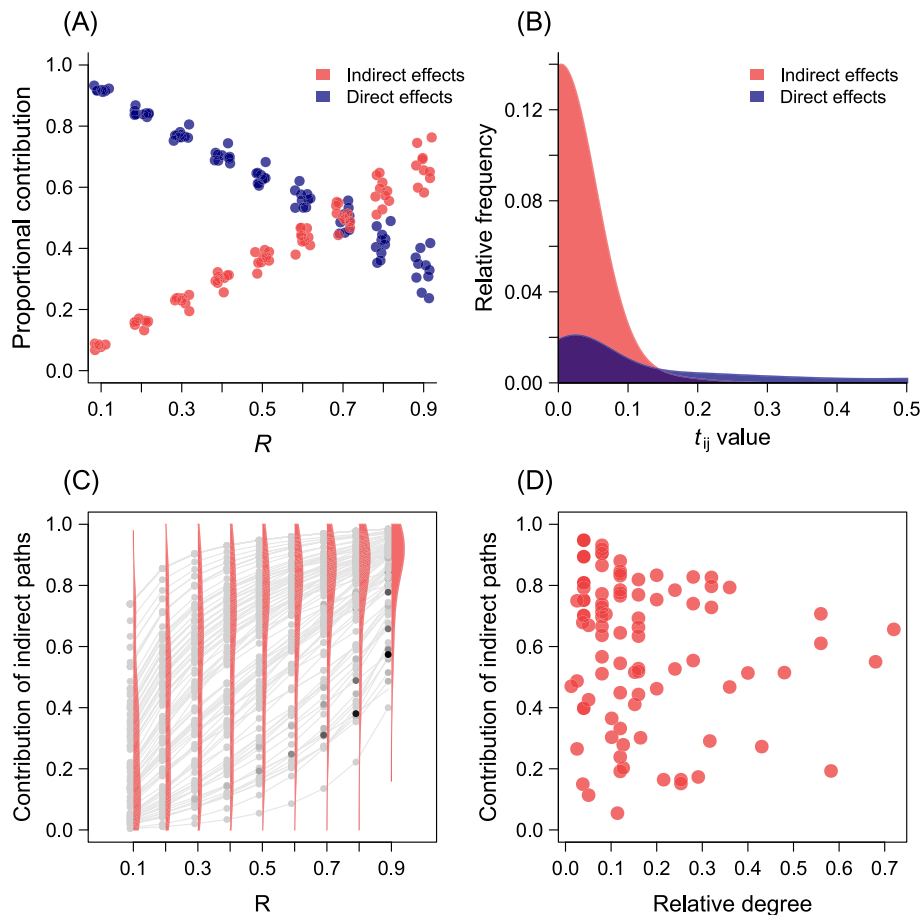
Fɪɢ. 2. Proportional contribution of indirect paths to interaction effects. (A) Contribution of indirect paths in each network as a function of R, the dependence of species on their mutualistic interactions. (B) Distribution of indirect and direct effect sizes for an example network assuming $R = 0.5$ for all species. (C) Contribution of indirect paths to the influence of each species within a single network. Darker points represent species with larger total influence (T^{out}). (D) Contribution of indirect paths as a function of species' relative degree in an example network (Memmott 1999).

The vulnerability of each species to the cascading effects of a primary extinction was not predicted by any traditional connectivity metric (k, k^w, S, C^e), or by the length of the shortest path between the species i and the initial target z (Appendix S1: Fig. S2). However, more than 80% of the variation in coextinction probability was often predicted by t_{iz} (Fig. 4; Appendix S1: Table S4). These results were consistent for the whole set of analyzed networks (Data S2). **T** values predict the probability of coextinction for species that interact directly or only indirectly with the target species (Appendix S1: Fig. S3). Coextinction probability was associated with t_{iz} even when assuming low R (Appendix S1: Table S4) or when we simulated different levels of sampling error in the network (Appendix S1: Fig. S4). The relationship between t_{iz} and coextinction probability was only weak for networks with very short mean path lengths (Fig. 4C, D) and low modularity (Appendix S1: Fig. S5), suggesting that the **T** matrix approach only fails in predicting species' vulnerability for densely connected networks.

Discussion

Our results point to three main reasons why accounting for the multiple paths that form ecological networks is key to predicting how the community and its individual species respond to diversity loss. First, we show that the relative importance of indirect effects grows, becoming greater than that of direct effects, as the functional dependence of species on their interactions increases. Even when indirect effects are quantitatively restricted by low functional dependence, indirect paths are qualitatively important because they provide alternative routes over which perturbations can travel. Second, examining both direct and indirect paths allows detecting the most influential and the most vulnerable species in interaction networks. Although ecological specialists are vulnerable to sequential species loss (Memmott et al. 2004, Brodie et al. 2014), connectivity metrics that measure ecological specialization based on direct links, such as degree and species strength, failed in predicting species' responses to the loss of specific targets. Only when accounting for
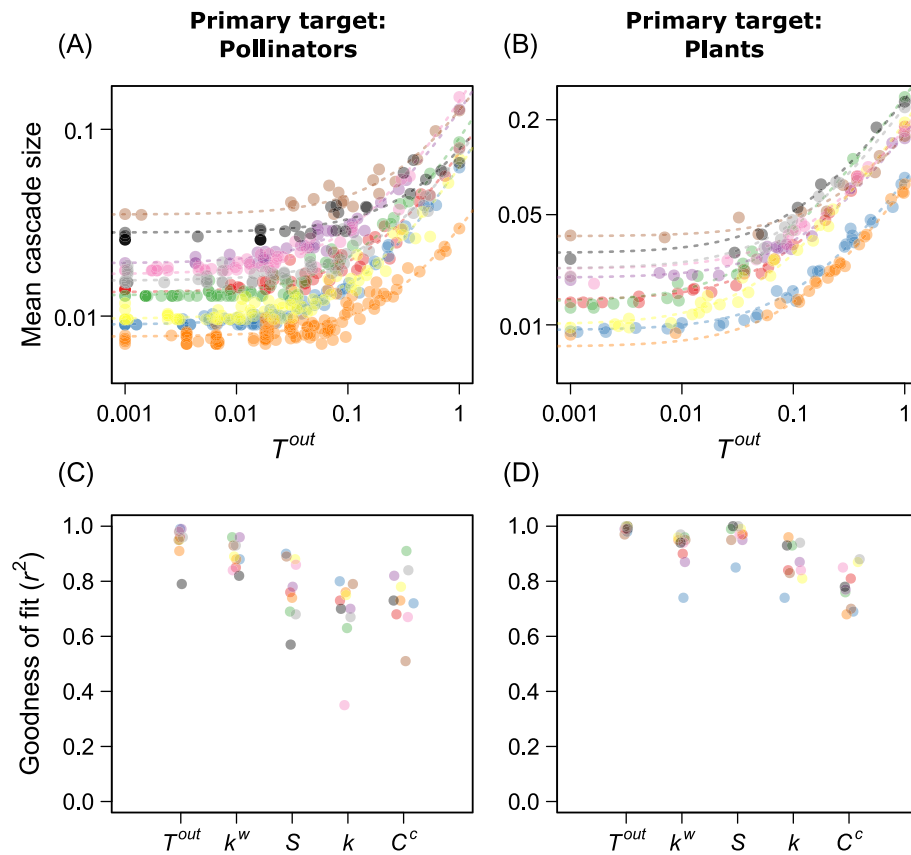
Reports

Fig. 3. Determinants of mean cascade size for 10 plant–pollinator networks. Top panels show the relationship between the mean proportion of species that went extinct in a cascade (100 simulations assuming $R = 0.5$) and T^{out} of each target species. Bottom panels show the fit of models relating mean cascade size to different species-level topological descriptors: T^{out}, species degree (k), weighted degree (k^w), closeness centrality (C^c), and species strength (S). (A) and (C) show results for the removal of pollinators and (B) and (D) the results after removing plants. Different networks are represented by different colors.

the multiple direct and indirect paths connecting species were we able to predict a species' vulnerability to the cascading effects of an extinction event. Third, uncertainty in coextinction patterns was greater for networks where all species are connected by short paths. In such networks, there are many equivalent paths over which cascading effects may propagate (Vieira and Almeida-Neto 2015). Thus, species respond to an extinction in similar ways, making it more difficult to estimate which species are more vulnerable.

Local extinctions will often have appreciable effects on the species' direct partners. The loss of pollinators may lead to pollen limitation of their partners, resulting in reproductive failure, reduced fruit/seed set, or lower germination success (Burd 1994, Ashman et al. 2004, Anderson et al. 2011). Correspondingly, the reduced availability of floral resources may cause declines in pollinator abundance (Scheper et al. 2014) and diversity (Carvell et al. 2006). Even if the loss of a species does not trigger subsequent extinctions, it may cause cascading effects with demographic impacts on multiple species (Säterberg et al. 2013). Our findings show that

understanding these far-reaching consequences of extinctions requires looking beyond direct links. Informed estimations of the consequences of species loss that incorporate the structural complexity of ecological systems are critical for the conservation and management of biodiversity (Moir et al. 2010).

Network analyses often focus on direct links or short paths, assuming these are the easiest route for effects to spread (Borrett et al. 2007). However, the main implication of the network organization of ecological systems is that species have indirect connections to other species by several alternative paths, all of which contribute to ecosystem functioning. Ecological networks have many more indirect than direct paths connecting species, and perturbations may propagate through paths of any length (Guimarães et al. 2017). We show that by examining these multiple paths, even complex dynamics such as extinction cascades are predictable. In a broader context, our results on extinction dynamics add to the mounting evidence that we need to investigate long indirect paths to understand the dynamics of disparate complex phenomena, such as evolutionary dynamics (Guimarães
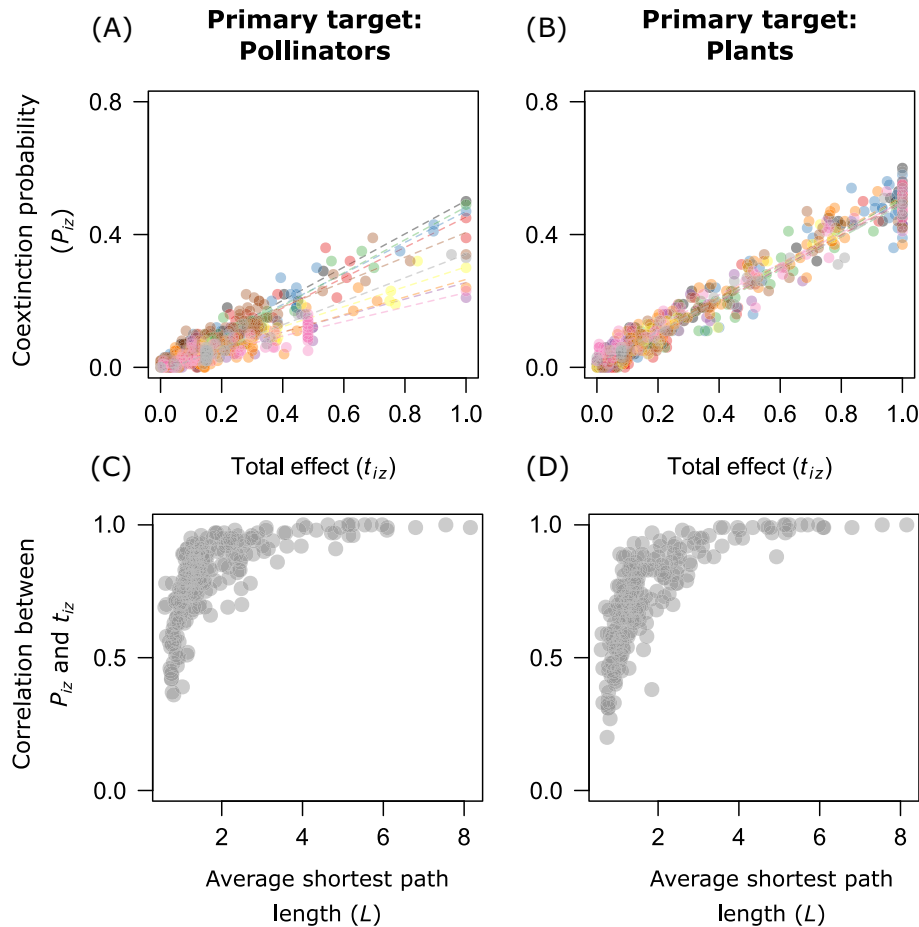
Fig. 4. Predicting coextinction probability. Top panels show the probability of coextinction, P_{iz}, of each species i following the extinction of a pollinator (A) or plant (B) z, as a function of the total effects z exerts upon i (t_{iz}). The target was the species with the largest T^{out} in the network (100 simulations; $R = 0.5$). Different colors represent the 10 different plant–pollinator networks. Bottom panels show the relationship between the strength of the association between P_{iz} and t_{iz}, measured by Spearman's correlation ρ, and average shortest path length (L) in simulated networks. (C) and (D) represent the removal of pollinators or plants, respectively.

et al. 2017, 2018), cultural spread in social networks (Fowler and Christakis 2010), and the dynamics of financial markets (Haldane and May 2011).

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