A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance

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Abstract

Understanding and predicting species extinctions and coextinctions is a major goal of ecological research in the face of a biodiversity crisis. Typically, models based on network topology are used to simulate coextinctions in mutualistic networks. However, such topological models neglect two key biological features of species interactions: variation in the intrinsic dependence of species on the mutualism, and variation in the relative importance of each interacting partner. By incorporating both types of variation, we developed a stochastic coextinction model capable of simulating extinction cascades far more complex than those observed in previous topological models. Using a set of empirical mutualistic networks, we show that the traditional topological model may either underestimate or overestimate the number and likelihood of coextinctions, depending on the intrinsic dependence of species on the mutualism. More importantly, contrary to topological models, our stochastic model predicts extinction cascades to be more likely in highly connected mutualistic communities.

Keywords

Complexity-stability, extinction cascades, horizontal cascades, seed dispersal, network disassembly, network robustness, pollination, simulation model, stochastic coextinction model, topological co-extinction model.

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INTRODUCTION

Current rates of species extinctions are higher than the background rates inferred from fossil records (Barnosky *et al.* 2011) and are predicted to remain high in the future (Pereira *et al.* 2010). Understanding and predicting the process of extinction is thus a major topic of current ecological research. Because species depend on each other for resources such as food and for processes such as breeding and dispersal, the loss of a single species may drive the coextinction of other species (Dunn 2009; Colwell *et al.* 2012). However, most studies that have examined the magnitude of species extinctions have not taken into account that primary extinctions are likely to lead to further extinctions. Taking coextinctions into account when assessing the magnitude of the current biodiversity crisis leads to higher estimated past and future extinction rates (Koh *et al.* 2004).

Species coextinctions are difficult to investigate empirically, which makes the use of modelling approaches essential to advance our ability to predict future extinction rates (Colwell *et al.* 2012). A long-standing line of research in ecology has focused on the effects of structural properties of model interaction networks on community stability and on the number of coextinctions and their distribution among trophic levels (e.g. Pimm 1979; Borrvall *et al.* 2000; Eklöf & Ebenman 2006). Such approach usually employs dynamical models based on generalised Lotka–Volterra equations, in which primary extinctions in model networks lead to direct and indirect addi-

tional extinctions through complex extinction cascades. However, much effort has recently been devoted to modelling the structure and dynamics of empirical interaction networks (Bascompte *et al.* 2003; Montoya *et al.* 2006; Bascompte & Stouffer 2009). Because dynamical models are computationally intensive and difficult to parameterise, attempts to model coextinctions in real, species-rich interaction networks are usually based on a topological model of coextinctions (Solé & Montoya 2001; Dunne *et al.* 2002; Memmott *et al.* 2004; Pocock *et al.* 2012).

The topological coextinction model (TCM) does not consider population dynamics explicitly and is based on the architecture of species interaction networks (i.e. their topology). The model removes species from the network and assumes that a coextinction occurs when a species has no surviving prey, host or mutualistic partner (e.g. Dunne *et al.* 2002; Memmott *et al.* 2004). The assumption that the coextinction of a species requires the loss of all the species on which it depends places a severe constraint on the complexity of extinction cascades under the TCM. In mutualistic networks, a species that suffers coextinction due to the loss of a partner has, by definition, no other partners left. Therefore, its loss cannot lead to additional extinctions. While species in real mutualistic networks are connected with varying strength to their different partners (Vázquez *et al.* 2005, 2012), this assumption also implies that a species can persist even if only a minor, weakly interacting partner is present. Relaxing the assumption that coextinctions require the loss of all mutualistic partners should

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allow for complex extinction cascades in which primary extinctions in one trophic level indirectly lead to additional extinctions in the same trophic level (i.e. 'horizontal cascades'; Sanders *et al.* 2013). For example, the coextinction of a plant species following the primary loss of a key pollinator species might lead to the extinction of additional pollinator species that depend strongly on the plant, which might in turn lead to the extinction of other plant species, and so on.

In addition to neglecting variation in the interaction strengths between species, the TCM also ignores variation in the intrinsic demographic dependence of species on the services provided by mutualistic partners. In the case of plant-pollinator networks, for example, the TCM ignores that plant species vary in their ability to self-pollinate without the aid of an animal pollinator (Bond 1994), or that pollinators often feed on resources other than floral nectar (Blüthgen 2010). Such variation in species dependence on mutualisms may also occur at the scale of entire assemblages (Kissling *et al.* 2009; Ollerton *et al.* 2011). Relaxing this second assumption may reduce the expected number of coextinctions in some situations and lead to different conclusions regarding which species are most sensitive to coextinctions.

One straightforward consequence of the traditional topological approach to modelling coextinctions in ecological networks is that primary extinctions in highly connected networks are less likely to produce coextinctions, so that increased network connectance leads to increased robustness to extinctions (Dunne *et al.* 2002). This is a necessary consequence of the assumption that coextinctions require the loss of all interacting partners, since such total loss becomes more unlikely when species tend to have more connections. However, one could alternatively argue that extinction cascades triggered by primary extinctions should propagate more easily in highly connected networks, so that increased connectance should lead to decreased robustness to extinctions. Secondary extinctions under the TCM cannot trigger additional extinctions in mutualistic networks. Thus, the positive relationship between network connectance and robustness predicted by the TCM may simply result from the combination of an excessively optimistic assumption and the model's neglect of complex extinction cascades. In fact, Campbell *et al.* (2011, 2012) have recently used a synchronous Boolean model for mutualistic network dynamics to show that highly connected communities are more sensitive to coextinctions. However, while their Boolean model incorporates negative interactions due to morphological mismatch, it focuses on artificial networks and does not consider variation in interaction strengths and in the intrinsic dependence of species on the mutualistic interaction.

Here, we describe and evaluate a stochastic model for coextinctions in mutualistic networks which allows for complex extinction cascades and is easily applicable to empirical interaction networks. Our stochastic coextinction model (SCM) incorporates variation in the intrinsic demographic dependence of species on the mutualistic interaction. In addition, by considering the variation in the mutual dependence between every species and each of its mutualistic partners, the SCM relaxes the assumption that the coextinction of a species requires the loss of all of its partners. By contrasting our proposed SCM with the traditional TCM, we demonstrate that the TCM may either underestimate or overestimate the number and likelihood of coextinctions depending on the overall intrinsic dependence of species on the mutualism. Also, while the TCM suggests a positive relationship between network connectance and robustness to species extinctions, the SCM predicts the opposite relationship: highly connected networks are more susceptible to coextinction cascades.

MATERIAL AND METHODS

A Stochastic Coextinction Model for mutualistic networks

We developed a stochastic simulation model for coextinctions in mutualistic networks based on the intrinsic dependence of species on the mutualism and the dependence of species on each of their mutualistic partners. Previously, we briefly presented the model and used it to explore the functional and phylogenetic consequences of plant-pollinator coextinctions (Vieira *et al.* 2013). Here, we provide a more formal presentation of the model followed by a detailed exploration of its properties and predictions.

Let A and B be two sets of species (hereafter 'trophic levels') so that every species in A has mutualistic interactions with one or more species in B, and vice versa. We assume that no direct interaction occurs between species at the same trophic level. We let $P_{ij} = R_i d_{ij}$ be the probability of species i going extinct following the extinction of a mutualistic partner species j. Dependence of i on j (d_{ij}) is defined as the population-level strength of the interaction between i and j divided by the sum of interaction strengths between i and all of its partners. Empirically, d_{ij} may be estimated as the number of visits recorded between species i and j divided by the total number of visits involving species i (Bascompte *et al.* 2006), which is easy to calculate from empirical quantitative interaction matrices. Note that it is not necessary to have $d_{ij} = d_{ji}$. R_i is assumed constant for each species and reflects the intrinsic demographic dependence of species i on the mutualism in question. For example, if species i is a plant, R_i may reflect the extent to which its seed set is limited by cross-pollination (allogamy) and might be inversely related to its degree of self-compatibility or to its ability to reproduce asexually. Since pollinators need not be restricted to consuming floral resources, R_i may also reflect the intrinsic dependence of a pollinator on nectar. This dependence on floral resources for food could be estimated empirically, for example by calculating the proportion of floral resources in the animal's diet. A similar approach could be applied to fruiting plants and seed dispersers.

Simulated extinction cascades in the SCM begin with a single primary extinction at a given trophic level (say, trophic level A). Following the primary extinction, all species from trophic level B have a probability of suffering coextinction according to the equation $P_{ij} = R_i d_{ij}$. For each coextinction in B, if any, all species in A have a probability of going extinct themselves, and so on. Whenever coextinctions lead to no additional extinctions, we assume that the community has reached equilibrium. As the extinction cascade goes on, the dependences d_{ij} are recalculated. For example, species i has dependence $d_{ij} = 1$ when j is its last surviving partner, regardless of the initial value of d_{ij} (as long as it

was not zero). Note that, since P_{ij} may be < 1 when species j is the last surviving partner of species i, species i may persist even if it has lost all of its partners.

We define the *degree* of an extinction cascade as the number of extinction episodes, with each episode involving one or more species, summed across both tropic levels. For example, if the primary loss of a pollinator species leads to the extinction of two plant species, which in turn leads to the loss of four additional pollinator species, we define this event as a *third-degree extinction cascade*. Note that the degree does not necessarily correspond to the *total number of species lost* in the extinction cascade (which is seven in the example above).

Compensation-mediated persistence under the TCM and the SCM

The SCM and the TCM postulate different rules for determining the outcome of primary extinctions (i.e. whether or not coextinctions occur). Those rules may be interpreted in terms of assumptions regarding the ability of species to compensate the loss of a mutualistic partner and thus persist. The TCM assumes, often implicitly, that a species is able to compensate the loss of a partner by interacting more frequently with its remaining partners. For example, if a plant species loses one of its seed dispersers, other species of seed dispersers should interact more frequently with the plant due to reduced interspecific competition in the absence of the extinct seed disperser. If a pollinator loses one of its partner plant species, it might compensate the loss by visiting its remaining plant species more frequently. Such compensatory mechanisms, which also include evolutionary responses, might explain part of the difference between the large numbers of coextinctions predicted by models and the small number of coextinction events observed empirically (Dunn *et al.* 2009). The TCM assumes that compensation-mediated persistence occurs independently of how important the extinct partner was in terms of relative interaction strengths. The SCM, in turn, may be interpreted as having a more flexible attitude towards the possibility of compensation-mediated persistence: it is likely when the extinct species was a minor partner, and becomes unlikely when a remaining species was highly dependent on its extinct partner. For example, assume species i ($R_i = 1$) has dependences $d_{ij} = 0.05$ on species j and $d_{ik} = 0.8$ on species k. The probability of species i surviving the loss of species j is $(1 - P_{ij}) = 0.95$, that is, persistence via compensation is very likely, since the amount of mutualistic service that needs to be compensated is small. The probability of species i persisting after the loss of species k is much lower $(1 - P_{ij}) = 0.2$ which may be interpreted as a low probability of compensation-mediated persistence. For example, the remaining partners of species i might not be abundant enough to compensate for the large amount of mutualistic service lost due to the extinction of species k. Under the TCM, however, compensation-mediated persistence of species i would be equally probable after the loss of either species j or species k.

Simulations with empirical data

To explore the behaviour of our SCM using empirical data, we used 27 quantitative mutualistic networks (14 pollination

and 13 seed dispersal networks) from a variety of biomes and geographic regions. A quantitative mutualistic network is described by an interaction matrix whose entries a_{ij} contain the number of times animal species i was recorded interacting with plant species j. Interaction frequency can be used as a surrogate for the total effect of each mutualistic interaction on the interacting pair of species (Vázquez *et al.* 2005). We obtained the data from previous compilations by Rezende *et al.* (2007) and by Vieira *et al.* (2013) (see Table S1 for details and sources).

We simulated extinction cascades in the empirical mutualistic networks according to the SCM. In each simulation, the original network was subjected to a single extinction cascade in which the initial, primarily extinct species was chosen randomly from either trophic level and coextinctions occurred according to the equation $P_{ij} = R_i \, d_{ij}$. Starting d_{ij} values were calculated from the original interaction matrices. R_i was assumed to be equal for all species and was uniformly sampled in each simulation from three intervals representing low $(0 < R_i \le 0.3)$, intermediate $(0.3 < R_i \le 0.6)$ and high $(0.6 < R_i \le 1)$ intrinsic demographic dependence on the mutualistic interaction for persistence. For each network, we performed 10^4 simulations for each interval of R_i and constructed empirical frequency distributions for the total number of extinctions in an extinction cascade. We also quantified the degree of each extinction cascade and constructed its corresponding frequency distribution. From this frequency distribution, we calculated, for each network and R_i level, the probability that a primary extinction would result in second-, third- and fourth-degree-or-higher extinction cascades.

In addition to performing simulations under the SCM, we used simulations to obtain the frequency distribution for the total number of extinctions under the TCM, which constrains the coextinction of a species to the loss of all of its mutualistic partners. From this distribution, we calculated the probability that a primary extinction would result in a second-degree extinction cascade under the TCM (note that third-degree-or-higher cascades are impossible under this model). Finally, we assessed the relationship between network connectance and the probability of a primary extinction resulting in additional extinctions (hereafter the probability of an extinction cascade) for both models. Although descriptors of network structure (e.g. connectance, nestedness, modularity) are often correlated with each other, we focused on connectance because there is a clear potential mechanistic link between connectance and the probability of coextinctions in mutualistic networks under our model: high connectance implies that more pathways are available for the effects of primary extinctions to propagate across the network.

We implemented all simulations and analyses in R (R Development Core Team 2013). Code for the simulations is available as Supporting Information and instructions are provided in the Appendix S1.

RESULTS

Probability and degree of extinction cascades

Frequency distributions of the total number of extinctions and the degree of extinction cascades in empirical mutualistic
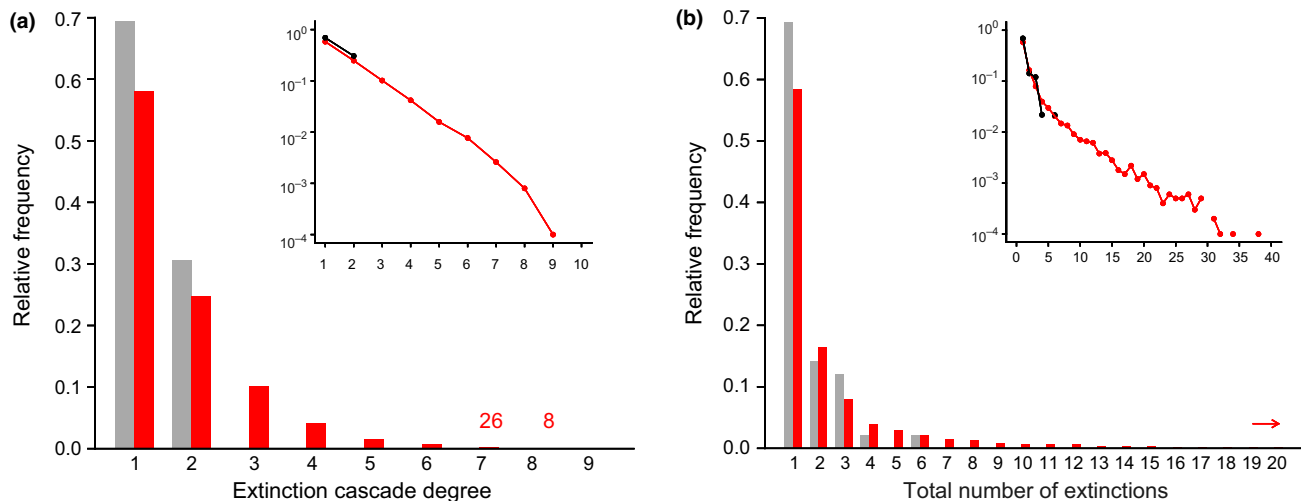
Figure 1 Typical frequency distributions of the degree (a) and total number of extinctions (b) of extinction cascades simulated in an empirical mutualistic network ('Albrecht' network, 49 species, see Table S1) using the topological coextinction model (grey bars and black points) and the stochastic coextinction model (SCM; red bars and points) under high values of R_i. Red numbers indicate the number of observations for rare, extremely large degree values obtained under the SCM. The red arrow indicates large observed values of total number of extinctions that were omitted to improve visualisation. Inset plots show the same data with a logarithmic y-axis.

networks are illustrated in Fig. 1 for the TCM and the SCM. While the TCM is constrained to produce coextinction cascades with a maximum degree of two (Fig. 1a), the SCM was able to produce cascades of degrees up to 7, 12 and 19, for low, medium and high values of the R_i parameter respectively. Under the SCM, the frequency distribution of extinction cascade degrees was highly skewed, with most primary extinctions leading to an extinction cascade of degree one (i.e. no additional extinctions) or two, and occasional primary extinctions leading to complex, high-degree extinction cascades (Fig. 1a).

The probability of an extinction cascade under our SCM is either lower or higher than expected from the TCM, depending on the intrinsic demographic dependence of species on the mutualistic interaction (i.e. the value of R_i) (Fig. 2a). For most networks (74%) under low R_i, the probability of an extinction cascade was lower under the SCM than under the TCM (Fig. 2a). Under intermediate R_i, on the other hand, most networks (85%) had a higher probability of suffering an extinction cascade under the SCM. For high values of R_i, all mutualistic networks had a higher probability of suffering an extinction cascade under the SCM (Fig. 2a). Averaging across all 27 empirical mutualistic networks on which we performed simulations, the probability that a primary extinction would result in an extinction cascade was 0.15 ± 0.09 (mean $\pm$ SD) under the TCM. Under the SCM, extinction cascades occurred on average with probabilities 0.10 ± 0.02, 0.23 ± 0.6 and 0.32 ± 0.10 for low, intermediate and high values of R_i respectively. For three networks, the probability of an extinction cascade under the TCM was zero; no single primary extinction left any other species completely disconnected.

Under the SCM, extinction cascades of second-, third- and fourth-degree or higher were increasingly likely to occur as the value or R_i increased (Fig. 3). Extinction cascades of second-degree or higher were relatively common even when

R_i was low, and their probability of occurrence averaged across all 27 mutualistic networks was about 0.1. However, they were on average about three times as likely to occur for high values of R_i. This effect is even stronger for third- and fourth-degree-or-higher cascades, which occur with negligible probability under low values of R_i but become relatively common under high values of R_i (Fig. 3). High values of R_i thus tend to increase not only the likelihood of extinction cascades but also their average complexity (in terms of their degree).

Total number of extinctions

Under both models, the frequency distribution of the total number of extinctions per primary extinction was highly skewed, with most primary extinctions leading to zero or a few additional extinctions and occasional primary extinctions leading to a larger number of extinctions (Fig. 1b). The mean number of extinctions per primary extinction under the SCM is either lower or higher than expected from the TCM, depending on the value of R_i (Fig. 2b). For low values of R_i, our model predicted 3.5–27.1% fewer extinctions for most mutualistic networks (85%) and 4.7–18.5% more extinctions for the remaining four networks. On the other hand, for intermediate and high values of R_i, our SCM predicted a higher number of extinctions per primary extinction for all mutualistic networks (Fig. 2b). Under intermediate and high values of R_i, the mean number of extinctions was respectively 1.06–1.77 and 1.65–3.27 times the corresponding mean under the TCM. The same relative differences between models occurred for the mean proportion of species lost after a single primary extinction (Fig. 2c).

Connectance vs. probability of extinction cascades

Under the TCM, highly connected networks had a lower probability of suffering extinction cascades (Spearman's corre-
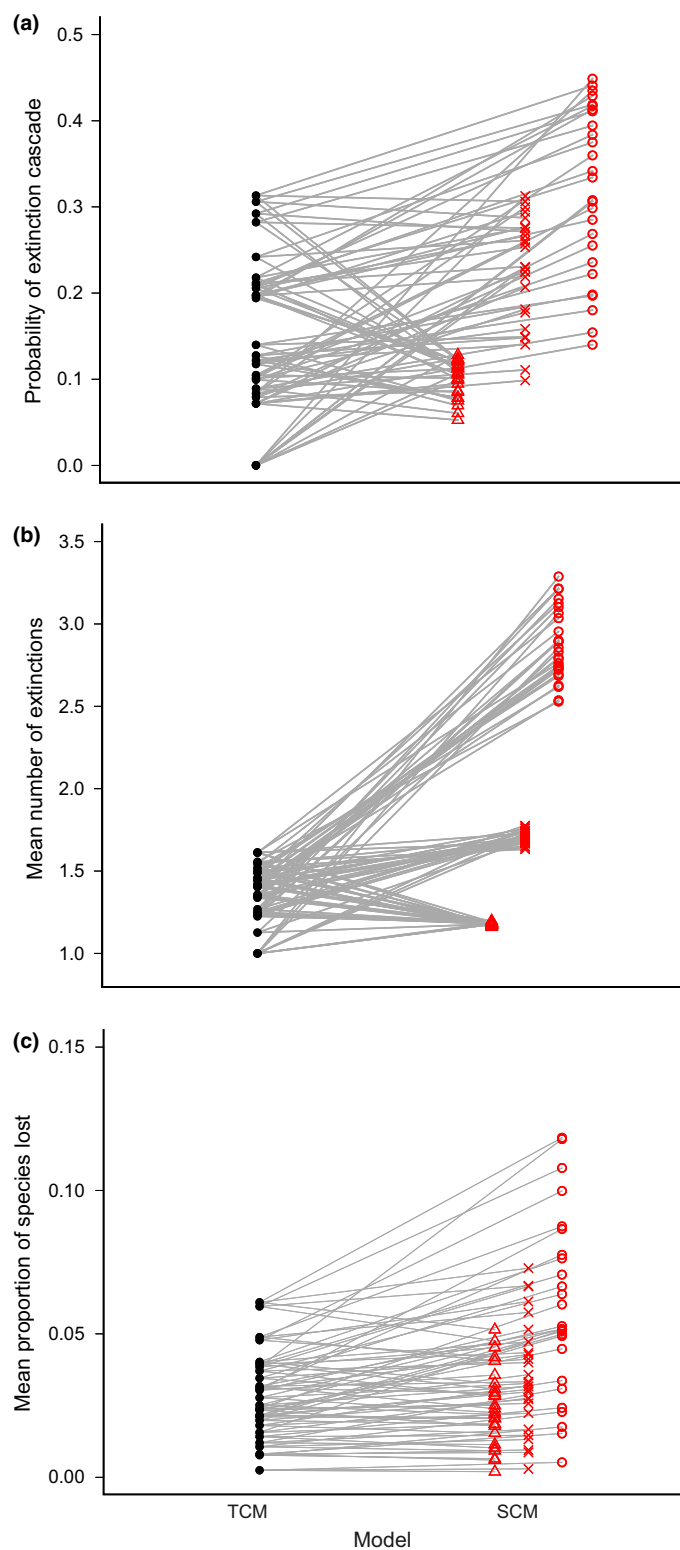
(a)

(b)

(c)

Figure 2 Probability of extinction cascades (a), their mean total number of extinctions (b) and the mean proportion of species lost (c) in 27 empirical mutualistic networks. Lines connect values obtained for the same network. Black: topological coextinction model (TCM). Red: stochastic coextinction model (SCM). Triangles: low R_i. Crosses: Intermediate R_i. Open circles: high R_i.
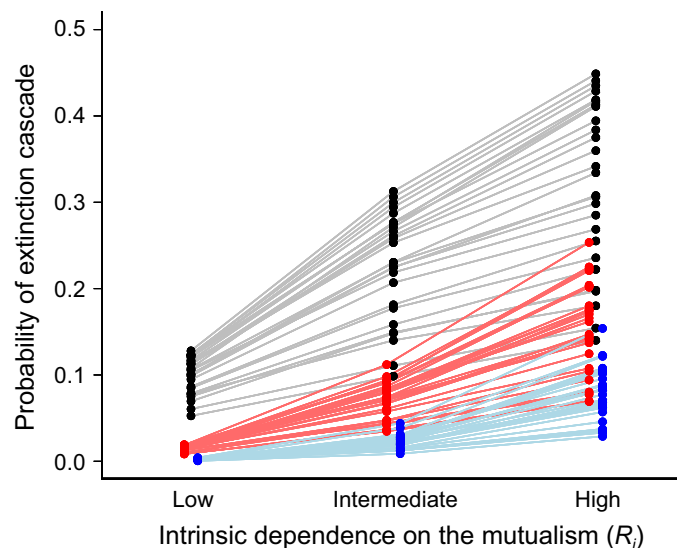

Figure 3 Probability of extinction cascades of second-(black), third-(red) and fourth-degree-or-higher (blue) under the stochastic coextinction model as a function of the R_i parameter. Lines connect observations taken from the same mutualistic network.

lation: rs $= -0.35$, one-tailed $P = 0.036$; Fig. 4). Under the SCM, no relationship between network connectance and probability of second-degree-or-higher extinction cascades was found for low values of R_i (rs $= 0.31$, one-tailed $P = 0.056$; Fig. 5a). On the other hand, for intermediate and high values of R_i, highly connected networks had a higher probability of suffering extinction cascades (intermediate R_i: rs $= 0.38$, one-tailed $P = 0.025$; high R_i: rs $= 0.36$, one-tailed $P = 0.032$; Fig. 5b, c). The positive effect of connectance was even stron-
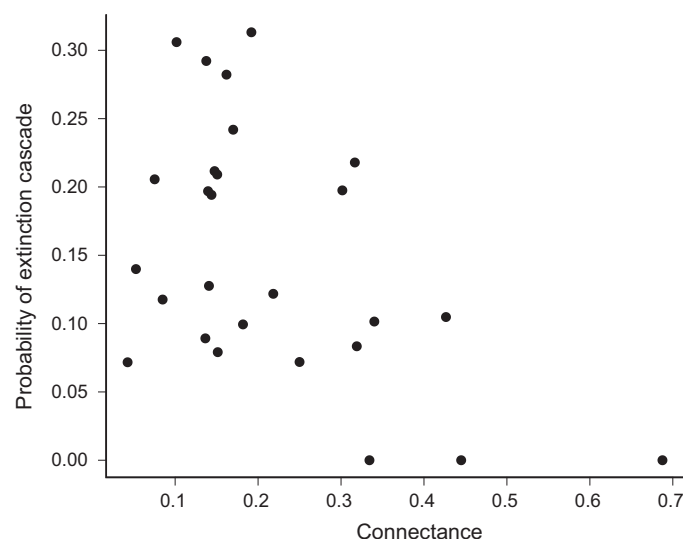

Figure 4 Probability of a primary extinction resulting in an extinction cascade under the topological coextinction model for 27 mutualistic networks as a function of network connectance.
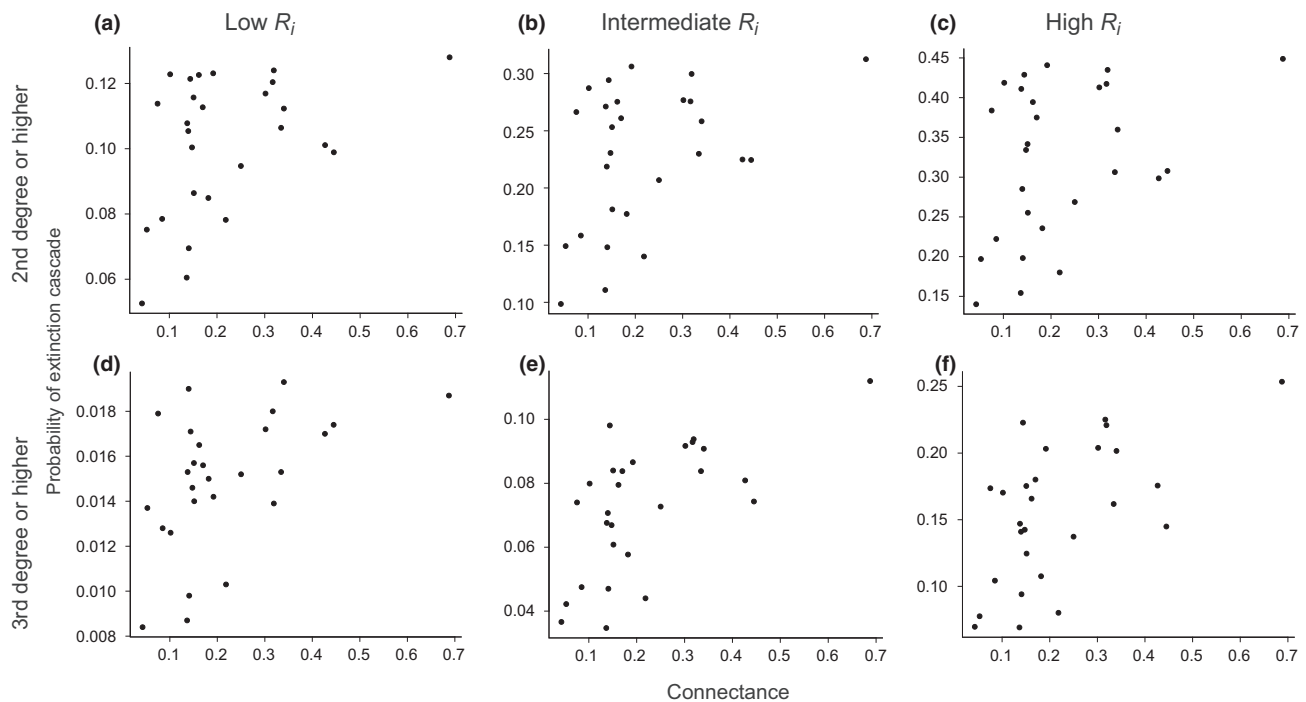
Figure 5 Probability of extinction cascades under the stochastic coextinction model for 27 mutualistic networks as a function of network connectance. (a–c): second-degree-or-higher cascades under low (a), intermediate (b) and high (c) values of R_i. (d–f): third-degree-or-higher cascades under low (d), intermediate (e) and high (f) values of R_i.

ger and occurred for all levels of R_i when only third-degree-or-higher cascades were considered (low R_i: rs = 0.49, one-tailed P = 0.004; intermediate R_i: rs = 0.57, one-tailed P < 0.001; high R_i: rs = 0.53, one-tailed P = 0.002; Fig. 5 d–

Figure 6 Correlation coefficient (Spearman's ρ) between network connectance and probability of extinction cascade under the stochastic coextinction model for different levels of species dependence on mutualistic interactions (i.e. values of R_i). Each correlation coefficient was calculated for the same set of 27 empirical mutualistic networks. Black: second-degree-or-higher cascades. Red: third-degree-or-higher cascades. Blue: fourth-degree-or-higher-cascades.

f). Overall, the relationship was stronger for more complex extinction cascades, but was relatively constant with respect to the value of R_i, except for fourth-degree-or-higher cascades, for which it peaked at an intermediate level of R_i (Fig. 6).
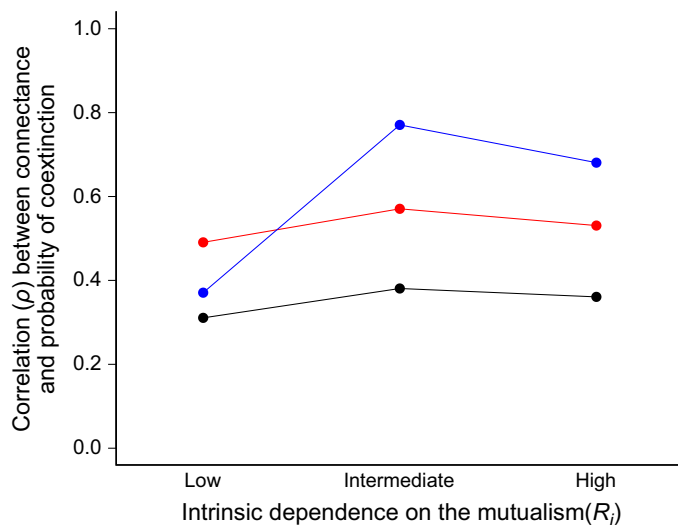
DISCUSSION

The use of the topological coextinction model to simulate the dynamics of mutualistic networks has provided valuable insights into the effect of extinction scenarios (Memmott *et al.* 2004), animal behaviour (Kaiser-Bunbury *et al.* 2010) and climate change (Memmott *et al.* 2007) on the overall robustness of such networks. The TCM has also been used to assess the consequences of the collapse of mutualistic networks (Rezende *et al.* 2007). Here, we build on this approach by adding two dimensions of biological realism previously neglected by the TCM: variation in the dependence of species on their different mutualistic partners and variation in the degree to which species depend on the mutualism itself for persistence. By relaxing assumptions built into the earlier topological approach, we developed a Stochastic Coextinction Model that produces complex extinction cascades in which species losses in one trophic level may lead to indirect additional losses of species at the same trophic level (i.e. 'horizontal' coextinctions; Sanders *et al.* 2013). This increase in model complexity comes at a moderate cost in terms of additional parameters. Dependence of species on their different mutualistic partners (i.e. d_{ij} values) can be readily estimated from quantitative interaction matrices, and the intrinsic demographic dependence

on the mutualistic interaction (i.e. the R_i parameter) might be estimated in many ways. Some examples include using self-pollination indices to assess the dependence of plants on animal pollination (Brys & Jacquemyn 2011), or estimating the level of frugivory in seed dispersers to assess their dependence on fruiting plants (Kissling *et al.* 2009; Mello *et al.* 2011).

Differences between the TCM and our SCM must be interpreted in the light of variation in the intrinsic demographic dependence of species on mutualistic services for persistence (Bond 1994). Our results indicate that, in addition to underestimating the complexity of extinction cascades, the TCM may either underestimate or overestimate the expected number of extinctions per primary extinction, depending on the intrinsic demographic dependence of species on the mutualism. According to our SCM, when species are highly dependent on pollination or seed dispersal interactions for persistence, extinction cascades are more likely to occur, are often more complex and tend to result in a larger number of extinctions. On the other hand, when species depend little on the mutualism, persistence after the loss of all partners becomes likely under the SCM, so that it predicts fewer extinctions than the TCM. Because natural assemblages may vary in the overall extent to which the species in them depend on mutualistic interactions for persistence (Kissling *et al.* 2009; Ollerton *et al.* 2011), estimating the community-wide intrinsic dependence of species on mutualistic interactions for persistence is imperative for assessing the relative robustness of different mutualistic communities to species extinctions.

In this study, we considered variation in the intrinsic dependence on the mutualism only at the scale of entire mutualistic networks. However, it is possible to obtain empirical estimates for different species in the same community. In combination with data on the relative dependence of species on each of their partners, this might allow us to estimate the sensitivity of each species to coextinction due to the loss of its mutualistic partners. Species highly dependent on mutualistic interactions for survival or reproduction (e.g. self-incompatible dioecious plant species, oligolectic bees) should be highly susceptible to coextinctions. Such effect may be particularly extreme if those species tend to have few mutualistic partners in the network. Using intra-network variation in species dependence on the mutualism to estimate each species susceptibility to coextinction would also allow us to predict the order in which species would be lost during the collapse of mutualistic networks and therefore the intensity of the corresponding decline in biodiversity and ecosystem services (Rezende *et al.* 2007; Vieira *et al.* 2013).

Applying the TCM to a large set of empirical food webs, Dunne *et al.* (2002) showed that high network connectance leads to high robustness against secondary extinctions. Our results have extended that conclusion for mutualistic networks under the TCM. However, when complex extinction cascades were simulated according to our SCM, we found the opposite relationship: primary extinctions were more likely to trigger extinction cascades in highly connected networks. Broadly, this adds to the complexity-stability debate (May 1973; Pimm 1984; McCann 2000; Rooney & McCann 2012). While theoretical work supports the idea that high

connectance decreases the population stability of ecological communities to small perturbations (May 1973; Allesina & Tang 2012), food web studies based on Lotka–Volterra models have found either negative (Pimm 1979) or positive (Eklöf & Ebenman 2006) effects of connectance on network robustness to large perturbations (e.g. primary extinctions). Considering mutualistic networks and using a different, probabilistic approach, our results suggest that high network connectance makes it easier for the effects of primary extinctions to propagate across the network and lead to the extinction of species many links away. Our SCM therefore predicts that highly connected communities of mutualists are more likely to experience changes in species composition following primary extinctions than less connected communities. This result is similar to the one obtained by using a synchronous Boolean model for coextinctions in mutualistic networks (Campbell *et al.* 2011, 2012). That model differs from the SCM in most of its features, for example by adopting a deterministic framework, considering negative interactions between partners and by ignoring both sources of biological variation incorporated by the SCM. However, one important similarity is that both the SCM and the synchronous Boolean model relax the assumption that coextinctions require the loss of all mutualistic partners. Relaxing this extreme assumption seems to be the key feature driving complex extinction cascades and a negative relationship between network connectance and robustness in mutualistic systems. Convergence on this negative relationship from two very different modelling paradigms suggests an important theoretical prediction on the robustness of mutualistic systems that is worthy of empirical investigation.

Topological criteria have been used to simulate coextinctions in other kinds of interaction networks, such as predator-prey food webs (Solé & Montoya 2001; Dunne *et al.* 2002; Petchey *et al.* 2008; Dunne & Williams 2009) as well as non-biological networks (Albert *et al.* 2000). Recently, Bayesian techniques have been used to model complex dynamics in empirical food webs while taking into account variation in interaction strengths and without the need to implement Lotka–Volterra dynamical models (Eklöf *et al.* 2013). However, while the Bayesian approach is elegant and computationally simpler since it requires no replicated simulations, it cannot be applied to intrinsically cyclic interaction networks such as mutualistic networks.

The SCM takes an important step towards incorporating complex dynamics into models of network disassembly in natural, species-rich mutualistic communities, while integrating important sources of biological variation in species interactions. Because it represents a powerful improvement over the traditional topological approach while retaining its conceptual and computational simplicity, we propose the SCM as a novel modelling paradigm to investigate the dynamics of mutualistic communities in both theoretical and applied research. In particular, it may lead ecologists and conservation biologists to reconsider the widely accepted positive relationship between connectance and robustness in mutualistic networks, and to search for mechanisms allowing the persistence of highly interconnected mutualistic communities.

AUTHORSHIP

MCV and MAN developed the model and designed the study, MCV compiled network data, implemented the code for the simulations and performed the statistical analyses. MCV wrote the first draft of the manuscript, and both authors contributed substantially to revisions.

REFERENCES

Albert, R., Jeong, H. & Barabási, A.L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B. *et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.

Bascompte, J. & Stouffer, D.B. (2009). The assembly and disassembly of ecological networks. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 1781–1787.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proc. Natl Acad. Sci. USA*, 100, 9383–9387.

Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431–433.

Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic Appl. Ecol.*, 11, 185–195.

Bond, W.J. (1994). Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans. R. Soc. B Biol. Sci.*, 344, 83–90.

Borrvall, C., Ebenman, B. & Jonsson, T. (2000). Biodiversity lessens the risk of cascading extinction in model food webs. *Ecol. Lett.*, 3, 131–136.

Brys, R. & Jacquemyn, H. (2011). Variation in the functioning of autonomous self-pollination, pollinator services and floral traits in three *Centaurium* species. *Ann. Bot.*, 107, 917–925.

Campbell, C., Yang, S., Albert, R. & Shea, K. (2011). A network model for plant-pollinator community assembly. *PNAS*, 108, 197–202.

Campbell, C., Yang, S., Shea, K. & Albert, R. (2012). Topology of plant-pollinator networks that are vulnerable to collapse from species extinction. *Phys. Rev. E*, 86, 021924 (8).

Colwell, R.K., Dunn, R.R. & Harris, N.C. (2012). Coextinction and persistence of dependent species in a changing world. *Annu. Rev. Ecol. Evol. Syst.*, 43, 183–203.

Dunn, R.R. (2009). Coextinction: anecdotes, models and speculation. In *Holocene Extinctions*. (ed Turvey, S.T.). Oxford University Press, New, York, pp. 167–180.

Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009). The sixth mass coextinction: are most endangered species parasites and mutualists? *Proc. R. Soc. B*, 276, 3037–3045.

Dunne, J.A. & Williams, R.J. (2009). Cascading extinctions and community collapse in model food webs. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 1711–1723.

Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, 5, 558–567.

Eklöf, A. & Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *J. Anim. Ecol.*, 75, 239–246.

Eklöf, A., Tang, S. & Allesina, S. (2013). Secondary extinctions in food webs: a Bayesian network approach. *Methods Ecol. Evol.*, 4, 760–770.

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.*, 13, 442–452.

Kissling, W.D., Böhning-Gaese, K. & Jetz, W. (2009). The global distribution of frugivory in birds. *Glob. Ecol. Biogeogr.*, 18, 150–162.

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C. & Smith, V.S. (2004). Species coextinctions and the biodiversity crisis. *Science*, 305, 1632–1634.

May, R.M. (1973). *Stability and complexity in model ecosystems.* Princeton University Press, Princeton.

McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228–233.

Mello, M.A.R., Marquitti, F.M.D., Guimarães, P.R., Kalko, E.K.V., Jordano, P. & Aguiar, M.A.M. (2011). The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS ONE*, 6, e17395.

Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B Biol. Sci.*, 271, 2605–2611.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecol. Lett.*, 10, 710–717.

Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442, 259–264.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F. *et al.* (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496–1501.

Petchey, O.L., Eklöf, A., Borrvall, C. & Ebenman, B. (2008). Trophically unique species are vulnerable to cascading extinction. *Am. Nat.*, 171, 568–579.

Pimm, S.L. (1979). Complexity and stability: another look at MacArthur's original hypothesis. *Oikos*, 33, 351–357.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326.

Pocock, M.J.O., Evans, D.M. & Memmott, J. (2012). The robustness and restoration of a network of ecological networks. *Science*, 335, 973–977.

R Development Core Team. (2013).R: A language and environment for statistical computing. Available at: http://www.R-project.org/. Last accessed 8 November 2014.

Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P. & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448, 925–928.

Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends Ecol. Evol.*, 27, 40–46.

Sanders, D., Sutter, L. & van Veen, F.J.F. (2013). The loss of indirect interactions leads to cascading extinctions of carnivores. *Ecol. Lett.*, 16, 664–669.

Solé, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. B Biol. Sci.*, 268, 2039–2045.

Vázquez, D.P., Morris, W.F. & Jordano, P. (2005). Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.*, 8, 1088–1094.

Vázquez, D.P., Lomáscolo, S.B., Maldonado, M.B., Chacoff, N.P., Dorado, J., Stevani, E.L. *et al.* (2012). The strength of plant-pollinator interactions. *Ecology*, 93, 719–725.

Vieira, M.C., Cianciaruso, M.V. & Almeida-Neto, M. (2013). Plant-pollinator coextinctions and the loss of plant functional and phylogenetic diversity. *PLoS ONE*, 8, e81242.

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