

LETTER

The sudden collapse of pollinator communities

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Abstract

Declines in pollinator populations may harm biodiversity and agricultural productivity. Little attention has, however, been paid to the systemic response of mutualistic communities to global environmental change. Using a modelling approach and merging network theory with theory on critical transitions, we show that the scale and nature of critical transitions is likely to be influenced by the architecture of mutualistic networks. Specifically, we show that pollinator populations may collapse suddenly once drivers of pollinator decline reach a critical point. A high connectance and/or nestedness of the mutualistic network increases the capacity of pollinator populations to persist under harsh conditions. However, once a tipping point is reached, pollinator populations collapse simultaneously. Recovering from this single community-wide collapse requires a relatively large improvement of conditions. These findings may have large implications for our view on the sustainability of pollinator communities and the services they provide.

Keywords

Critical transitions, hysteresis, mutualistic networks, nestedness, pollinator decline.

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INTRODUCTION

Widespread declines in wild and domesticated pollinator populations raise concerns about the future of biodiversity and agricultural productivity (Allen-Wardell *et al.* 1998; Diaz *et al.* 2005; Biesmeijer *et al.* 2006; Potts *et al.* 2010; Burkle *et al.* 2013; Garibaldi *et al.* 2013). The majority of flowering plants depend on animals for pollination. Those plants are in turn at the basis of food webs and provide food for livestock and human populations (Klein *et al.* 2007; Ollerton *et al.* 2011). Pollinators thus provide an essential service to ecosystems and humanity. Assessing the potential for further degradation of this service is therefore of great importance.

A considerable effort is being made to identify the potential causes of declining pollinator abundances. Recently, field experiments showed how commonly used insecticides strongly increase pollinator mortality (Henry *et al.* 2012; Whitehorn *et al.* 2012). Habitat destruction, parasites and disease are also seen as important drivers of pollinator decline. Most likely, a mix of those causes increases the mortality of pollinator populations (Diaz *et al.* 2005; Potts *et al.* 2010; Bryden *et al.* 2013).

The impact of a further increase in drivers of pollinator decline will depend strongly on the capacity of plant-pollinator communities to withstand a further increase in those drivers. Determination of the response of natural communities to environmental change is however notably hard, primarily because the response of these relatively complex systems depends on more than the intrinsic properties of species. A central role is likely to be played by the strength, number and nature of interactions between species, and the way in which those interactions are arranged in ecological networks (May 1972; McCann 2000; Bascompte *et al.* 2006; May 2006; Ives

& Carpenter 2007; Scheffer *et al.* 2012). When assessing the impact of a further increase in the drivers of pollinator decline, it is thus of fundamental importance to take the topology of mutualistic networks (i.e. the number and way in which mutualistic interactions are arranged) into account.

Mutualistic networks, such as those made out of the interactions between plants and pollinators, are known to display a high degree of nestedness, i.e. the more specialist species tend to interact with subsets of the species interacting with the more generalist species (see Fig. 1; Bascompte *et al.* 2003; Bascompte & Jordano 2007). Theoretical work has shown that the nestedness of mutualistic networks increases the robustness of plant-pollinator communities to species extinctions (Memmott *et al.* 2004; Burgos *et al.* 2007) and habitat loss (Fortuna & Bascompte 2006), the proportion of coexisting species once an equilibrium is reached (Bastolla *et al.* 2009; Thébault & Fontaine 2010), and the speed at which the community returns to equilibrium after a perturbation (Okuyama & Holland 2008; Thébault & Fontaine 2010).

Little attention, however, is given to the influence of mutualistic network topology on potential critical transitions in the size of pollinator populations. Ecosystems may respond in various ways to changing environmental conditions, such as the change in conditions caused by a further increase in drivers of pollinator decline, which may have profound implications for their resilience to environmental change (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). When conditions change gradually, the state of some systems (e.g. the size of populations) may change likewise, in a smooth, gradual manner. Other systems may respond strongly to change within a narrow range of environmental conditions, but are relatively insensitive to change outside of this range. Particularly sudden shifts may occur when a system has more than one stable state. Such a

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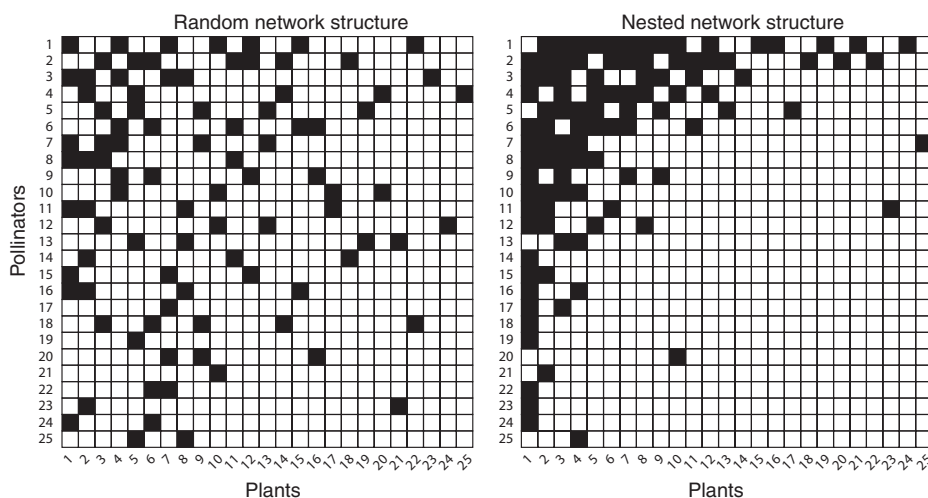


Figure 1 Matrix representations of a randomly structured network (left) and a nested network (right, $N = 0.6$). Filled squares indicate interactions between species. Column and row numbers correspond to individual plant and pollinator species. Species are ordered based upon their number of interactions.

system cannot change smoothly from a one stable state (e.g. large population sizes) to an alternative stable state (e.g. small population sizes). Instead, a sudden shift occurs when environmental conditions pass a critical point. We refer to such shifts as ‘critical transitions’. To return back to the original state after a critical transition, a return to conditions prior to the transition is often not sufficient; instead, a larger change in conditions is needed until another critical point is reached at which the system shifts back to the original state. The existence of a difference between the critical conditions at which a forward and backward transition occurs, is known as ‘hysteresis’.

The notion that alternative stable states exist is supported by observations in a wide variety of ecological and experimental systems (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Rietkerk *et al.* 2004; Kefi *et al.* 2007; Drake & Griffen 2010; Veraart *et al.* 2011; Hirota *et al.* 2011; Dai *et al.* 2012). The complexity of many natural communities has however made it hard to develop the existing theory on alternative stable states further into a framework that helps us to assess their resilience (Scheffer *et al.* 2012). Here, we try to contribute to the development of such a framework, by merging theory on alternative stable states with theory on the structure of ecological networks. Specifically, we do this by examining the potential occurrence of critical transitions in the size of pollinator populations due to a change in a driver of pollinator decline. Subsequently, we study the way in which the connectance and nestedness of mutualistic networks may affect the community-wide implications of these shifts between alternative stable states. This will be done with the help of a mathematical model.

METHODS

Nestedness algorithm

Networks with a different degree of nestedness were generated using an algorithm similar to the one described by Medan *et al.* (2007). This algorithm was shown to generate networks that are similar to empirically studied plant-pollinator networks (also by Medan *et al.* 2007). The algorithm allows us to vary nestedness

of networks with a given number of species, connectance and fraction of ‘forbidden links’. Connectance is the fraction of all possible interactions that is occurring in the network. Forbidden links are interactions that cannot occur, for example because of a morphological or phenological uncoupling (e.g. between late-flowering plant species and early seasonal pollinator species, see Jordano *et al.* 2003).

Initially, the algorithm assigns with a predefined probability mutualistic interactions and forbidden links between two species groups. This results in a network with a random structure, of which the probability of having an interaction corresponds to the connectance of the network and the probability of a forbidden link to the fraction of forbidden links. In case any of the species has no interactions, a new randomly structured network is generated.

In order to generate nested networks, interactions are rearranged within the network. During each iteration, the algorithm randomly selects an interaction between two species a and b . This interaction is changed into an interaction between species a and randomly selected species c , when this species has more interactions than species b . During the iterative process, species thus start to interact more with species that already have many interactions. This ‘rich get richer’ mechanism increases the nestedness of the network. Iterations are continued until a desired nestedness is reached.

Two exceptions to the above mentioned rule exist. The interaction is not changed from an interaction with species b to an interaction with species c , when species b has only one interaction, or when the interaction between species a and c is forbidden. This ensures that each species remains having at least one interaction, and that the identity of forbidden links is not changed by the algorithm.

We derive the nestedness of the entire network, N , as in Bastolla *et al.* (2009):

$$N = \frac{\sum_{i < j}^{S_P} N_{ij} + \sum_{i < j}^{S_A} N_{ij}}{\frac{S_P(S_P-1)}{2} + \frac{S_A(S_A-1)}{2}}, \quad (1)$$

where the first sum is across all pairs of plant species, the second sum is across all pairs of pollinator species, S_P is the

number of plant species, and S_A is the number of pollinator species. N_{ij} is the nestedness of species pair i and j , which is derived as follows:

$$N_{ij} = \frac{n_{ij}}{\min(n_i, n_j)}, \quad (2)$$

where n_{ij} is the number of times species i and j interact with the same mutualistic partner, n_i is the number of interactions of species i and n_j is the number of interactions of species j .

All networks generated with the procedure above were checked for the potential presence of more than one component (i.e. a group of species that is completely disconnected from the rest of the network). If more than one component was found, the network was dismissed from our analysis, and replaced with a newly generated network, consisting of only one component.

Model of mutualistically interacting species

In an attempt to disentangle the relationship between network structure and the response of plant-pollinator communities to environmental change, we studied the impact of mutualistic network topology on the behaviour of a dynamic model. Our dynamic model describes two mutualistically interacting species groups: plants and pollinators. Species belonging to the same group are in direct competition with each other, while mutualistic interactions occur between species belonging to a different group. The pollinators are subjected to a gradual change in mortality and/or growth rate, caused by a change in one of the drivers of pollinator decline.

The model, describing a group of S_P plant species and S_A pollinator species, is as follows:

$$\begin{aligned} \frac{dP_i}{dt} &= r_i P_i + \frac{\sum_{k=1}^{S_A} \gamma_{ik} A_k}{1 + h_i \sum_{k=1}^{S_A} \gamma_{ik} A_k} P_i - \sum_{j=1}^{S_P} C_{ij} P_j P_i + \mu P_i, \\ \frac{dA_k}{dt} &= (r_k - d_A) A_k + \frac{\sum_{i=1}^{S_P} \gamma_{ki} P_i}{1 + h_k \sum_{i=1}^{S_P} \gamma_{ki} P_i} A_k - \sum_{l=1}^{S_A} C_{kl} A_l A_k + \mu A_k, \end{aligned} \quad (3)$$

where P_i represents the abundance of plant species i and A_k represents the abundance of pollinator species k . Intrinsic growth rates, i.e. the growth independent from mutualistic and competitive interactions, are represented by r , which is species specific and can either be positive or negative. A general reduction of pollinator growth rates or increase in pollinator mortality rates, affecting all pollinator species, is included with driver of pollinator decline, d_A .

Population growth is enhanced by mutualistic partners (i.e. the pollinator or plant species providing a service or resource to the plant or pollinator population). Like Okuyama & Holland (2008) and Bastolla *et al.* (2009), we assume that the beneficial effect of mutualistic partners on population growth saturates when the abundance of mutualistic partners is high. The extent of this saturation is determined by half-saturation constant h . We assume mutualistic interactions to be either absent, in which case mutualistic interaction strength, γ , is equal to zero, or to be present, in which case the mutualistic

interaction strength is assumed to depend on the degree of the node benefiting from the interaction in the following manner:

$$\gamma_{mn} = \frac{\gamma_0}{K_n^t}, \quad (4)$$

in which, for each interaction, γ_0 is taken from a uniform distribution, K_n is the number of interactions of the species befitting from the interaction and t determines strength of the trade-off between interaction strength and number of interactions. Both $t = 0$ (no trade-off) and $t = 1$ (full trade-off) represent 'neutral' cases. Assuming no trade-off is neutral in the sense that the strength of mutualistic interactions is not changed by the topology of the network, while a full trade-off assumes that the, on average, gain species have from their mutualistic interactions is not changed by the topology of the network. Ecological reality is likely to lie somewhere in between those two extremes. The strength of competition between individuals of the same species group is determined by C . We study a system where species do not outcompete each other when mutualistic partners are absent (as in Van Nes & Scheffer 2004). Intraspecific competition, C_{ii} , is therefore assumed to be substantially stronger than interspecific competition C_{ij} . Lastly, a small immigration factor μ is incorporated in order to allow for the (re-)establishment of otherwise extinct species. μ is not supposed to influence the dynamics of the model.

Simulations and parameter settings

We examined the response of pollinator populations to increasingly harsh conditions by gradually increasing the driver of pollinator decline, d_A . This gradual increase was simulated by a stepwise increase in the driver of pollinator decline, with step size 0.01. For each step, we ran our model until equilibrium was reached, by applying a Runge–Kutta method that numerically solves our model. We increased the driver of pollinator decline past the point where all pollinator species are extinct (i.e. have an abundance lower than 0.01). After this point was reached, we simulated improving conditions by gradually decreasing the driver of pollinator decline, again with a step size of 0.01. This allowed us to check for hysteresis.

We scanned for the occurrence of sudden changes in pollinator abundance within a small range of change in the driver of pollinator decline. We defined a 'sudden change' as a change in pollinator abundance that was larger than 0.2 over an increase or decrease in the driver of pollinator decline of 0.01 (one step in our simulations). This allowed us to differentiate between a sudden and a gradual extinction or recovery of pollinator populations.

In our default approach, we made simulations for communities consisting out of 25 plants and 25 pollinator species. The impact of connectance on the behaviour of the model was tested by varying the connectance of communities with a random network topology. The impact of nestedness was studied by comparing networks differing in nestedness, but equal in connectance ($D = 0.15$) and fraction of forbidden links ($F = 0.3$). We, however, made sure that the qualitative behaviour of our model does not depend on a specific number of species, connectance or fraction of forbidden links chosen

(see supplementary material 3). For each level of connectance and nestedness, we tested 250 different networks created with the above algorithm.

Unless stated otherwise, parameters were sampled from the following uniform distributions: $r_i \sim U(0.05, 0.35)$, $\gamma_{0,mm} \sim U(0.8, 1.2)$, $h_i \sim U(0.15, 0.3)$, $C_{ii} \sim U(0.8, 1.1)$, $C_{ij} \sim U(0.01, 0.05)$, or given the following values: $t = 0.5$, $\mu = 0.0001$.

The feasibility of networks

In order to allow for partial collapses of the plant-pollinator community, a substantial variation in growth rate, competition and mutualistic interaction strength is needed. As a result of this variation, we did not always find a feasible solution, where the abundances of all species were higher than 0.01. If no feasible solution was found for a certain network, parameters were re-sampled until a feasible solution was found. If after 500 attempts no solution was found, the network was discarded as non-feasible.

The net effect of species on each other

Net relationships between pollinators were studied by numerically determining the influence of a small change in growth rate of species l on the abundance of species k (dA_k/dr_l). If an increase in growth rate of species l leads to an increased abundance of species k , the net effect of species l on species k is positive (following Stone & Roberts 1991).

RESULTS

The majority of pollinator populations collapse suddenly to extinction once the driver of pollinator decline, d_A , reaches a critical value. These sudden collapses occur due to a positive feedback mechanism that results from the positive interactions between plants and pollinators. A large pollinator population size enhances the growth and thus the population size of plants, which in turn enhances the growth of the pollinator populations. As the strength of the driver pollinator decline, d_A , increases, this positive feedback mechanism maintains pollinator populations under conditions where they cannot recover from extinction (see supplementary material 1). Under these conditions, multiple alternative stable states may therefore exist, varying from a state where all pollinator populations are present to a state where some or all pollinator species are extinct. As the strength of the driver of pollinator decline, d_A , increases further, a critical point is reached at which the strength of this feedback mechanism is no longer sufficient to maintain pollinator populations. At this point, a critical transition occurs, leading to the sudden collapse of some or all pollinator populations. In communities with a random network topology and a relatively low connectance, we typically observe several partial collapses involving the extinction of few species. Nested communities with an equal connectance, however, tend to exhibit only one point of collapse, involving the extinction of the entire community (see Fig. 2).

Once the driver of pollinator decline has increased beyond the point where all pollinator populations have collapsed, a

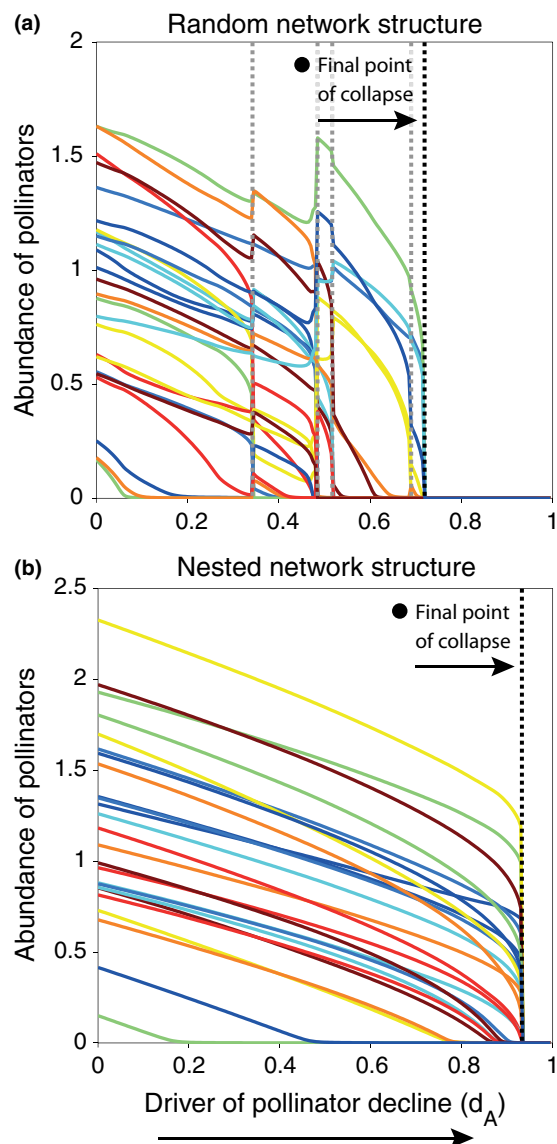


Figure 2 The collapse of pollinator populations when the driver of pollinator decline, d_A , affecting growth and/or mortality of pollinators, is gradually increased from zero to one. Results are shown for a random (a) and a nested (b, $N = 0.6$) network. Connectance of both networks is equal ($D = 0.15$). Several extinction events precede the final collapse of the randomly structured plant-pollinator community, while the nested community exhibits only one point of community-wide collapse.

small decrease in mortality rates may not be sufficient for species to recover. As was the case with the sudden collapses, observed when the driver of pollinator decline, d_A , was increased, pollinator populations may also recover suddenly when the driver of pollinator decline is decreased (see Fig. 3). Especially in nested communities, the difference between the first point of recovery and the final point of collapse can be substantial when compared to randomly structured communities. A considerable improvement of conditions might thus be necessary before species can recover from collapse, which is indicative of hysteresis.

Multiple points of recovery were typically observed within communities that also exhibited several network collapses. In

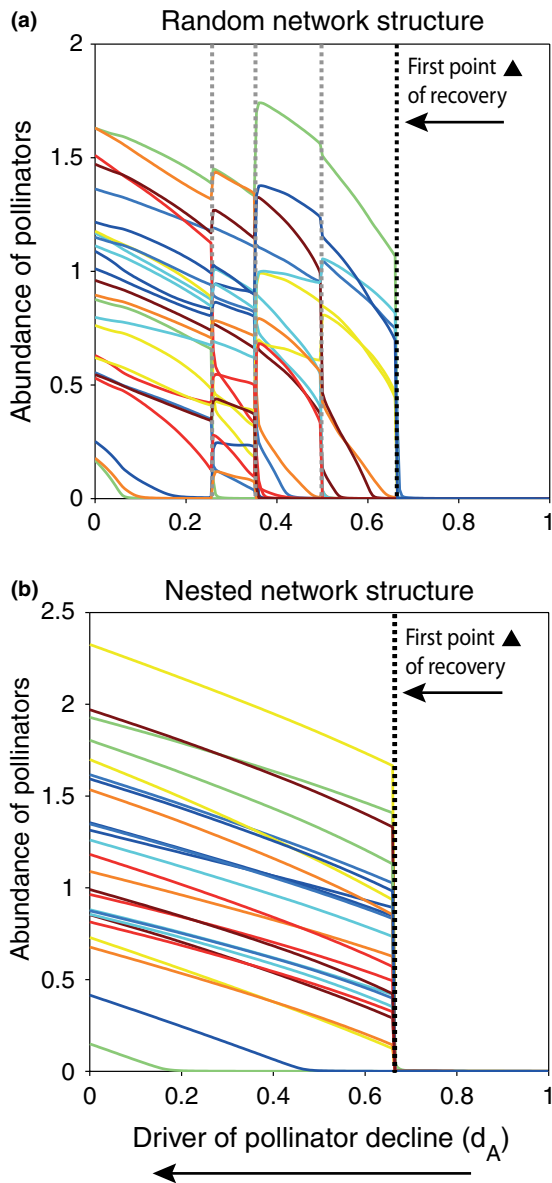


Figure 3 The recovery of pollinator populations when the driver of pollinator decline, d_A , is gradually decreased from one to zero. The points of recovery are not necessarily equal to the points of collapse (see Fig. 2). Especially in the nested community a large difference is observed between the final point of collapse and the first point of recovery. A substantial reduction of the driver of pollinator decline might thus be necessary for pollinator populations to recover from a collapse.

randomly structured communities, with a connectance of 0.15, multiple points of sudden recovery were found in 92% of the feasible communities in which also multiple collapses were observed. More than one sudden recovery was however only observed in 21% of the feasible communities that exhibited one point of collapse.

The ranking of species recovery was, in most feasible communities, similar to the order in which they collapsed. For example, the species who were the last to collapse when the driver of pollinator decline, d_A , was increased, always recovered before or simultaneously with species that collapsed at a lower value of pollinator decline, in 79% of

randomly structured communities with a connectance of 0.15.

Further, sudden changes in the pollinator community always coincided with sudden changes in the plant community (see supplementary material 2).

The potential for a single community-wide collapse

The probability of having a single community-wide collapse, instead of having several partial collapses, is strongly influenced by the connectance and/or nestedness of mutualistic networks. The fraction of networks, equal in connectance and nestedness, in which a single community-wide collapse was observed, can be seen as a measure of this probability.

The left panel of Fig. 4 shows the impact of connectance on the number of collapses that occur when the driver of pollinator decline, d_A , is increased. As the connectance of randomly structured communities increases, the fraction of communities that exhibit only one single point of community-wide collapse grows, until eventually almost no partial collapses are observed.

In the right panel of Fig. 4, we show what happens when the nestedness of communities with a connectance of 0.15 is increased. A small increase in nestedness from 0.2 to 0.25 is already sufficient to observe a substantial decrease in the occurrence of partial collapses. When nestedness is increased further, almost no partial collapses are observed any more. Consequently, by increasing the nestedness, we thus observe a strong reduction in the occurrence of partial collapses, even though the connectance of those networks was fixed.

The cases where we did find a partial collapse in a highly nested community represent an extreme case where a large fraction of specialists interacts only with one single generalist. This generalist may, together with the specialists associated to it, collapse independent of the rest of a highly nested community.

As described in the Methods section, we needed a substantial variation in growth rate, competition and mutualistic interaction strength in order to allow for partial collapses of the plant-pollinator community. As a result of this variation, the parameters drawn from uniform distributions did not always give a feasible solution. A large fraction of randomly structured networks with a connectance of 0.15, however, gave a feasible solution, and the majority of them also showed partial collapses. Surprisingly, the feasibility of networks was lowest for intermediate values of nestedness. Feasible solutions were thus most easily found in networks that were either fully random, or fully nested (see Fig. 4 and supplementary material 3). Networks for which it was hard to find a feasible solution, often had a small fraction of species that, during all attempts made to find a feasible solution, could not coexist with all others. Non-feasibility was thus almost always a property of this small fraction of species, rather than a property of the community as a whole.

Pollinator persistence under changing environmental conditions

Network topology influences not only the probability of a single community-wide collapse; it is also important for the

capacity of pollinator communities to persist under increasingly harsh conditions. Here, we measure this capacity as the amount of increase in the driver of pollinator decline, d_A , needed to reach the ‘final point of collapse’. This final point of collapse is the point at which the last pollinator collapses to extinction (as indicated in Fig. 2). Similarly, we can measure the ease of recovery by measuring the value of the driver of pollinator decline, where the first pollinator recovers from

extinction. This would be the ‘first point of recovery’ (as indicated in Fig. 3). The points of collapse and recovery as they were found for a certain value of connectance and nestedness are plotted in Fig. 5. For each value of connectance and nestedness, multiple networks were tested.

Connectance and nestedness both postpone the final point of collapse. Consequently, the persistence of the pollinator community to an increase in the driver of pollinator decline,

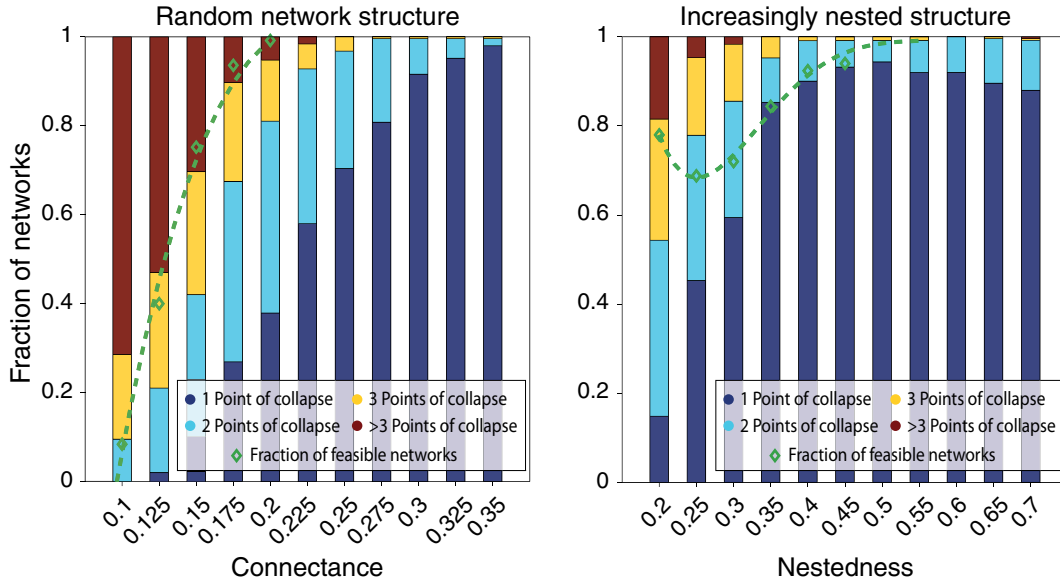


Figure 4 The number of collapses observed in randomly structured communities with different levels of connectance (left), and in communities with increasingly nested network topologies with a fixed connectance of 0.15 and fraction of forbidden links of 0.3 (right). The coloured bars represent the fraction of feasible networks in which a certain number of collapses is found. The fraction of networks for which feasible solutions are found is indicated with the green diamonds.

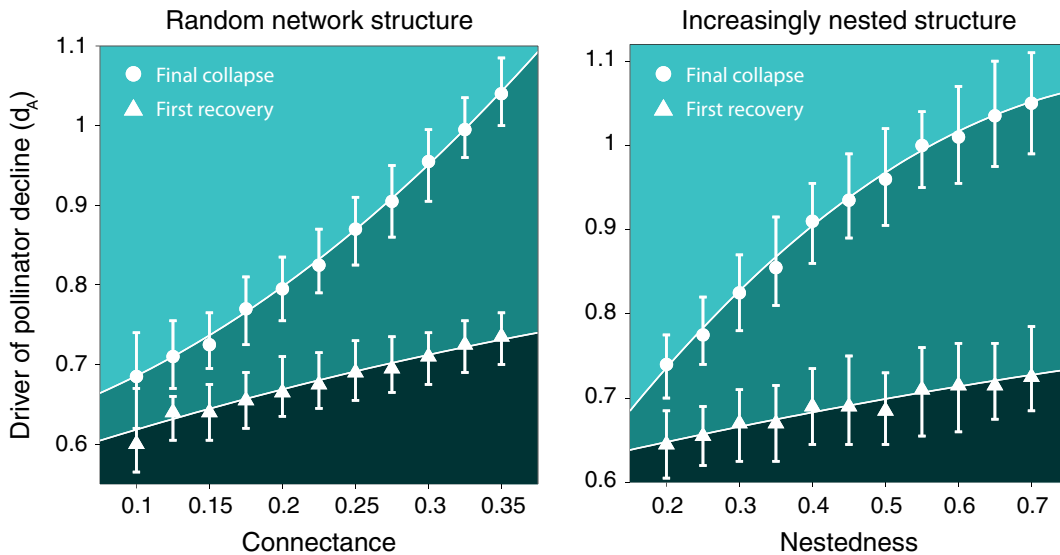


Figure 5 Points of collapse (circles) when the driver of pollinator decline, d_A , is increased, and points of recovery (triangles) when the driver of pollinator decline, d_A , is decreased. As in Fig. 4, results are shown for randomly structured networks that vary in connectance (left), and for increasingly nested networks with a connectance of 0.15 and fraction of forbidden links of 0.3 (right). In case of multiple collapses and/or recoveries, the final point of collapse and the first point of recovery was plotted.

d_A , increases with connectance and/or nestedness. Highly connected, and/or nested communities also recover from a collapse at higher values of the driver of pollinator decline. The distance between the final point of collapse and the first point of recovery, however, increases with connectance and/or nestedness. This means that a larger change in the driver of pollinator

decline is needed for pollinators to recover, after the final threshold is passed.

The net effect of species on each other

Our results show that the connectance and/or nestedness of mutualistic networks affects the stability of pollinator communities in various ways. The different aspects of stability discussed so far are the fraction of networks in which feasible solutions are found, the number of collapses and persistence of pollinator populations when the driver of pollinator decline, d_A , is increased, and the ease of recovery when the driver of pollinator decline, d_A , is decreased. Fortunately, these very different implications of network topology can all be understood when studying the ‘net effects’ of species on each other.

Pollinators have a direct negative effect on each other due to competition. An indirect positive effect between pollinators may however occur when pollinator species interact with the same plant species. It is the interplay between these direct and indirect effects that ultimately determines the net effect of pollinators on each other (Bastolla *et al.* 2009). In Fig. 6, two pollinators interacting with the same plant species are shown to have an increasingly strong positive effect on each other. Not surprisingly, these pollinators can endure a larger increase in the driver of pollinator decline, d_A , than the pollinator not benefiting from this facilitation (also shown in Fig. 6). Once the tipping point is reached, the two pollinators interacting with the same plant species, however, collapse simultaneously, because they both depend on the same plant species.

Increased connectance and nestedness both increase the fraction of mutualistic partners shared by pollinators. The behaviour of highly connected, and/or highly nested communities, is therefore similar to the behaviour of the two pollinator species who share an interaction with the same plant species (see Fig. 6). With increasing connectance the ‘overlap’ in identity of the mutualistic partners of pollinators is simply increased because a larger number of interactions has to be distributed over an equal number of plant species. The ‘rich get richer’ mechanism that lies at the basis of the algorithm we used to generate nested networks, makes pollinators interact with mutualistic partners where many other pollinators already interact with. With the algorithm we thus achieve a similar increase in overlap while maintaining the number of

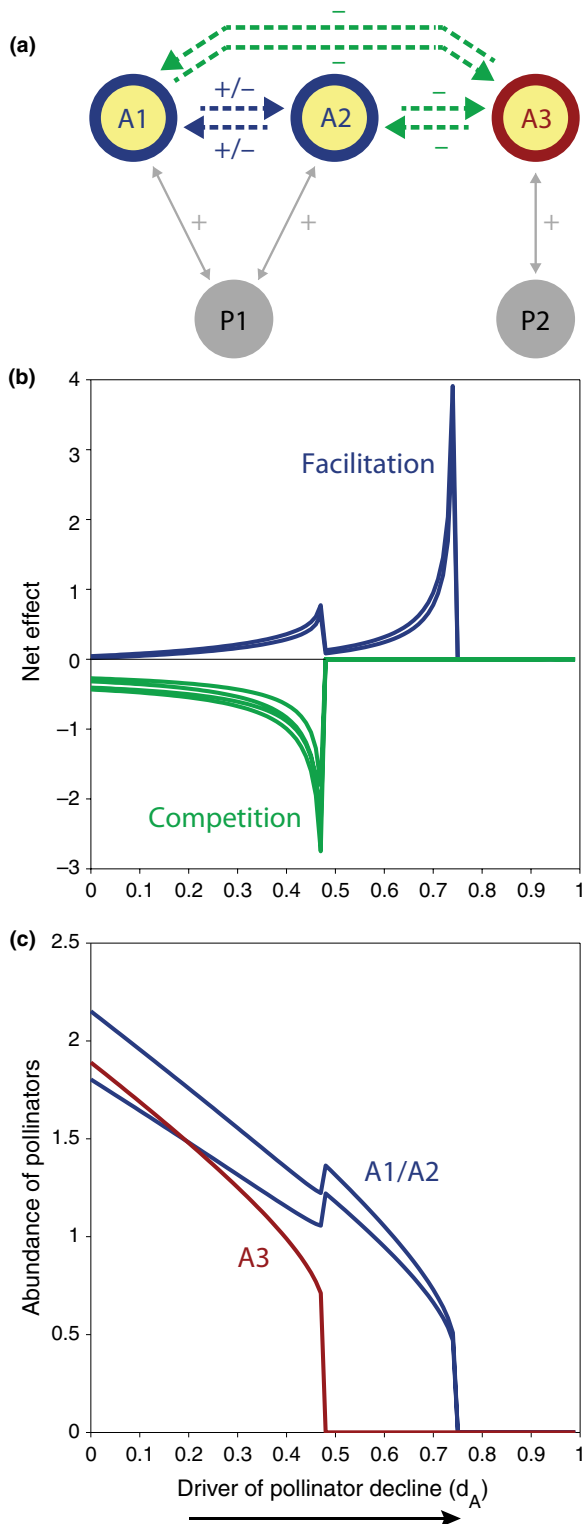


Figure 6 The net effect of species on each other while the driver of pollinator decline increases. Pollinators that share a mutualistic partner have an increasingly positive effect on each other and collapse simultaneously. Pollinators that do not share mutualistic partners have an increasingly negative effect on each other and collapse independently. (a) A simple network of mutualistic interactions between plants and pollinators. Pollinator A1 and A2 share mutualistic partner P1, while pollinator A3 does not share its mutualistic partner P2. Dashed lines indicate net relationships between pollinators. Although pollinators are in direct competition with each other, net positive relationships may exist between pollinator A1 and A2. (b) Net effect (dA_k/dr_i) of pollinator species on each other. In blue, the net effects of pollinators A1 and A2 on each other. In green, the net relationships between pollinator A3 and the other two pollinators. (c) Abundance of pollinators A1 and A2 (blue) and pollinator A3 (red).

interactions equal. As with the two species sharing an interaction with the same mutualistic partner in Fig. 6, pollinators who form part of a nested and/or highly connected community indirectly support each other when stress levels are high. This makes the community survive higher levels of the driver of pollinator decline, d_A , but also leads to a simultaneous collapse, because species depend on each other when stress levels are high.

Feasible solutions can be found in two types of regimes. The first regime would be one in which the combined effect of direct and indirect effects between pollinators is positive. An alternative regime is one where these net effects are mostly negative. This second regime is only feasible when these negative effects are relatively equal in strength. With increasing nestedness we move from the second to the first regime. Intermediate values of nestedness might be less likely to be in either of the two regimes. Some species have already benefited from the increase in nestedness, while others have not, which leads to an unbalanced community. This may explain why the probability of finding a feasible solution is smallest for intermediate values of nestedness (see Fig. 4 and supplementary material 3).

DISCUSSION

Studies addressing the occurrence of critical transitions between alternative stable states in ecosystems have provided us with myriad examples of potential positive feedback mechanisms that might lay at the basis of them (May 1977; Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Rietkerk *et al.* 2004; Kefi *et al.* 2007; Hirota *et al.* 2011). These positive feedback mechanisms propel change towards an alternative stable state when environmental conditions pass a critical point (e.g. when a decline in population size reduces the growth of a population). It has, however, been challenging to understand how such mechanisms may affect the response of structurally complex systems, such as plant-pollinator communities, to changing environmental conditions (Scheffer *et al.* 2012). In this article, we try to address this challenge by merging theory on alternative stable states with theory on the structure of ecological networks. Specifically, we show that pollinator populations may collapse suddenly to extinction, due to a positive feedback mechanism that results from the positive interactions between plants and pollinators. Each pollinator population described with our model is engaged in a unique positive feedback mechanism, of which the strength may vary substantially. Here, we show that such local positive feedback mechanisms may nonetheless provide the potential for a single community-wide collapse of pollinator populations, depending on the topology of mutualistic networks.

Our results can be understood intuitively by considering the 'net effects' of species on each other and the way in which these effects are mediated by the topology of mutualistic networks. Pollinators have a direct negative effect on each other due to competition, while indirect positive effects may occur between pollinator species that interact with the same plant species. The extent to which pollinators interact with the same plant species increases with connectance and/or nestedness. A high nestedness of the mutualistic network may therefore

promote the occurrence of indirect positive effects between pollinators. Earlier work has shown that these indirect positive effects may reduce the effective competition between pollinators, and promote the coexistence of species in nested communities (Bastolla *et al.* 2009).

In this study, we show that the relative strength of indirect facilitation between pollinators becomes stronger as the driver of pollinator decline, d_A , increases (see Fig. 6). This corresponds to the increasingly popular 'stress-gradient hypothesis' which suggests that facilitative effects grow in importance as environmental stress increases (Bertness & Callaway 1994; Holmgren *et al.* 1997; He *et al.* 2013). A high nestedness of mutualistic networks may therefore not only minimise effective competition to a level required for species coexistence; under stressful conditions, it may even promote strong indirect facilitation between pollinators.

We found that pollinators who are part of highly connected and/or nested communities can maintain themselves substantially longer than pollinators who are part of communities with a low nestedness as the driver of pollinator decline, d_A , is increased. This large persistence of pollinator populations under increasingly stressful conditions is, most likely, the result of the aforementioned indirect facilitation. Pollinator species who are part of either a highly nested or highly connected community can maintain themselves under stressful conditions because they indirectly support each other.

On the other hand, when species can survive under stressful conditions because they indirectly support each other, they also increasingly depend on each other as conditions get more stressful. As a consequence, pollinators collapse simultaneously once the driver of pollinator decline, d_A , passes a critical point. What we see in our model is therefore a surprising relationship between the capacity of species to coexist, to survive under stressful conditions, and the risk for a single community-wide collapse. They are all the result of the indirect positive effects, which are promoted by a high connectance and/or nestedness of mutualistic networks. Importantly, once collapsed, highly connected and/or nested communities may not necessarily recover more easily. In fact, our model shows the contrary. Recovery of pollinator populations who form part of highly nested communities require a quite large decrease in the driver of pollinator decline, d_A , in comparison to pollinator populations who form part of communities with a low nestedness.

Our findings may have large implications for our view on the sustainability of natural communities and the ecosystem services provided by them. Based on the insurance hypothesis, one expects ecosystems services to be more reliable when supported by a large number of species (Naeem & Li 1997; Yachi & Loreau 1999). Functional redundancy of species is often seen as a valuable 'commodity', because it makes ecosystems more reliable in terms of the ecosystem services they provide (see Naeem & Li 1997). Our analysis, however, illustrates that the functional overlap of pollinators, which is related to the connectivity and/or nestedness of mutualistic networks, may simultaneously increase the risk for a single community-wide collapse. A valuable ecosystem service, namely pollination, can therefore be lost suddenly, despite the fact that it is provided by a large number of species who are, when taking only

their intrinsic properties into account, not equally sensitive to the driver of pollinator decline, d_A .

Our study is one of many small steps needed to bring theory on critical transitions and the structure of ecological networks together and we realise that this paper raises new questions that require further exploration. First, even though our model is substantially more complex than many others that study critical transitions, it is constrained to mutualistically interacting plant-pollinator communities. Multiple types of interactions co-occur in natural communities (Melián *et al.* 2009), and future studies should explore how the structuring of multiple types of interactions affect critical transitions. Second, our results underline the importance of developing early-warning signals for critical transitions in ecological networks (Scheffer *et al.* 2009). Third and finally, as the mechanisms we describe are generic, it is possible that a similar trade-off between persistence under severe conditions and potential for a systemic collapse occurs in other systems as well. This is reinforced by previous studies finding notable similarities between the structure of mutualistic networks and that of financial systems (Uzzi 1996; May *et al.* 2008; Saavedra *et al.* 2008; Haldane & May 2011; Saavedra *et al.* 2011).

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AUTHORSHIP

Simulations and data analysis were performed by Jelle Lever. A first draft of the manuscript was prepared by Jelle Lever. All authors contributed to the design of the research, discussed data, and contributed to writing the final manuscript.

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