

# The sudden collapse of pollinator communities

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1 **ABSTRACT**

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

## 13 INTRODUCTION

14 Widespread declines in wild and domesticated pollinator populations raise concerns about the future of  
15 biodiversity and agricultural productivity (Allen-Wardell *et al.* 1998; Diaz *et al.* 2005; Biesmeijer *et al.*  
16 2006; Potts *et al.* 2010; Burkle *et al.* 2013; Garibaldi *et al.* 2013). The majority of flowering plants  
17 depend on animals for pollination. Those plants are in turn at the basis of food webs and provide food  
18 for livestock and human populations (Klein *et al.* 2007; Ollerton *et al.* 2011). Pollinators thus provide  
19 an essential service to ecosystems and humanity. Assessing the potential for further degradation of this  
20 service is therefore of great importance.

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

26 The impact of a further increase in drivers of pollinator decline will depend strongly on the capacity  
27 of plant-pollinator communities to withstand a further increase in those drivers. Determination of the  
28 response of natural communities to environmental change is however notably hard, primarily because the  
29 response of these relatively complex systems depends on more than the intrinsic properties of species. A  
30 central role is likely to be played by the strength, number, and nature of interactions between species,  
31 and the way in which those interactions are arranged in ecological networks (May 1972; McCann 2000;  
32 Bascompte *et al.* 2006; May 2006; Ives & Carpenter 2007; Scheffer *et al.* 2012). When assessing the  
33 impact of a further increase in the drivers of pollinator decline, it is thus of fundamental importance to  
34 take the topology of mutualistic networks (i.e., the number and way in which mutualistic interactions are  
35 arranged) into account.

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

45 Little attention, however, is given to the influence of mutualistic network topology on potential critical  
46 transitions in the size of pollinator populations. Ecosystems may respond in various ways to changing  
47 environmental conditions, such as the change in conditions caused by a further increase in drivers of  
48 pollinator decline, which may have profound implications for their resilience to environmental change  
49 (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). When conditions change gradually, the state of some  
50 systems (e.g., the size of populations) may change likewise, in a smooth, gradual manner. Other systems  
51 may respond strongly to change within a narrow range of environmental conditions, but are relatively  
52 insensitive to change outside of this range. Particularly sudden shifts may occur when a system has  
53 more than one stable state. Such a system cannot change smoothly from a one stable state (e.g., large  
54 population sizes) to an alternative stable state (e.g., small population sizes). Instead, a sudden shift occurs  
55 when environmental conditions pass a critical point. We refer to such shifts as ‘critical transitions’. To  
56 return back to the original state after a critical transition, a return to conditions prior to the transition is  
57 often not sufficient; instead, a larger change in conditions is needed until another critical point is reached  
58 at which the system shifts back to the original state. The existence of a difference between the critical  
59 conditions at which a forward and backward transition occurs, is known as ‘hysteresis’.

60 The notion that alternative stable states exist is supported by observations in a wide variety of  
61 ecological and experimental systems (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Rietkerk *et al.*  
62 2004; Kefi *et al.* 2007; Drake & Griffen 2010; Veraart *et al.* 2011; Hirota *et al.* 2011; Dai *et al.* 2012).  
63 The complexity of many natural communities has however made it hard to develop the existing theory  
64 on alternative stable states further into a framework that helps us to assess their resilience (Scheffer  
65 *et al.* 2012). Here, we try to contribute to the development of such a framework, by merging theory on  
66 alternative stable states with theory on the structure of ecological networks. Specifically, we do this by  
67 examining the potential occurrence of critical transitions in the size of pollinator populations due to a  
68 change in a driver of pollinator decline. Subsequently, we study the way in which the connectance and  
69 nestedness of mutualistic networks may affect the community-wide implications of these shifts between  
70 alternative stable states. This will be done with the help of a mathematical model.

71 **METHODS**

72 **Nestedness algorithm.** Networks with a different degree of nestedness were generated by using an  
 73 algorithm similar to the one described by Medan *et al.* (2007). This algorithm was shown to generate  
 74 networks that are similar to empirically studied plant-pollinator networks (also by Medan *et al.* 2007).  
 75 The algorithm allows us to vary nestedness of networks with a given number of species, connectance and  
 76 fraction of “forbidden links”. Connectance is the fraction of all possible interactions that is occurring in  
 77 the network. Forbidden links are interactions that cannot occur, for example because of a morphological  
 78 or phenological uncoupling (e.g., between late-flowering plant species and early seasonal pollinator species,  
 79 see Jordano *et al.* 2003).

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

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

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

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

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

96 where  $S_P$  is the number of plant species,  $S_A$  is the number of pollinator species and  $N_{ij}$  is the nestedness  
 97 of species pair  $i$  and  $j$ , which is derived as follows:

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

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

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

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

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

$$\frac{dP_i}{dt} = r_i P_i + \frac{\sum_{k=1}^{S_A} \gamma_{ki} A_k}{1 + h_i \sum_{k=1}^{S_A} \gamma_{ki} A_k} P_i - \sum_{j=1}^{S_P} C_{ij} P_j P_i + \mu_P, \quad (3)$$

$$\frac{dA_k}{dt} = (r_k - d_A) A_k + \frac{\sum_{i=1}^{S_P} \gamma_{ik} P_i}{1 + h_k \sum_{i=1}^{S_P} \gamma_{ik} P_i} A_k - \sum_{l=1}^{S_A} C_{kl} A_k A_l + \mu_A,$$

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

117 Population growth is enhanced by mutualistic partners (i.e. the pollinator or plant species providing  
 118 a service or resource to the plant or pollinator population). Like Okuyama & Holland (2008) and Bastolla  
 119 *et al.* (2009), we assume that the beneficial effect of mutualistic partners on population growth saturates  
 120 when the abundance of mutualistic partners is high. The extent of this saturation is determined by half-  
 121 saturation constants  $h$ . We assume mutualistic interactions to be either absent, in which case mutualistic  
 122 interaction strength,  $\gamma$ , is equal to zero, or to be present, in which case the mutualistic interaction strength  
 123 is assumed to depend on the degree of the node benefiting from the interaction in the following manner:

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

124 in which, for each interaction,  $\gamma_0$  is taken from a uniform distribution,  $K_n$  is the number of interactions of  
125 the species befitting from the interaction, and  $t$  determines strength of the trade-off between interaction  
126 strength and number of interactions. Both  $t = 0$  (no trade-off) and  $t = 1$  (full trade-off), represent  
127 “neutral” cases. Assuming no trade-off is neutral in the sense that the strength of mutualistic interactions  
128 is not changed by the topology of the network, while a full trade-off assumes that the gain species have  
129 from their mutualistic interactions is not changed by the topology of the network. Ecological reality is  
130 likely to lie somewhere in between those two extremes. The strength of competition between individuals  
131 of the same species group is determined by  $C$ . We study a system where species do not outcompete each  
132 other when mutualistic partners are absent (as in Van Nes & Scheffer 2004). Intraspecific competition,  
133  $C_{ii}$ , is therefore assumed to be substantially stronger than interspecific competition  $C_{ij}$ . Lastly, a small  
134 immigration factor  $\mu$  is incorporated in order to allow for the (re-)establishment of otherwise extinct  
135 species.  $\mu$  is not supposed to influence the dynamics of the model.

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

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

149 In our default approach, we made simulations for communities consisting out of 25 plants and 25  
150 pollinator species. The impact of connectance on the behaviour of the model was tested by varying the  
151 connectance of communities with a random network topology. The impact of nestedness was studied by  
152 comparing networks differing in nestedness, but equal in connectance ( $D=0.15$ ) and fraction of forbidden  
153 links ( $F=0.3$ ). We, however, made sure that the qualitative behaviour of our model does not depend on a  
154 specific number of species, connectance or fraction of forbidden links chosen (see supplementary material  
155 3). For each level of connectance and nestedness, we tested 250 different networks created with the above  
156 algorithm.

157 Unless stated otherwise, parameters were sampled from the following uniform distributions:  $r_i \sim$

158  $U(0.05, 0.35)$ ,  $\gamma_{0,ik} \sim U(0.8, 1.2)$ ,  $h_i \sim U(0.15, 0.3)$ ,  $C_{ii} \sim U(0.8, 1.1)$ ,  $C_{ij} \sim U(0.01, 0.05)$ , or given the  
159 following value:  $t = 0.5$ ,  $\mu = 0.0001$ .

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

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

170 **RESULTS**

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

186 Once the driver of pollinator decline has increased beyond the point where all pollinator populations  
187 have collapsed, a small decrease in mortality rates may not be sufficient for species to recover. As was  
188 the case with the sudden collapses, observed when the driver of pollinator decline,  $d_A$ , was *increased*,  
189 pollinator populations may also recover suddenly when the driver of pollinator decline is *decreased*.  
190 Especially in nested communities, the difference between the first point of recovery and the final point  
191 of collapse can be substantial when compared to randomly structured communities (see figure 3). A  
192 considerable improvement of conditions might thus be necessary before species can recover from collapse,  
193 which is indicative of hysteresis.

194 Multiple points of recovery were typically observed within communities that also exhibited several net-  
195 work collapses. In randomly structured communities, with a connectance of 0.15, for example, multiple  
196 points of sudden recovery were found in 92% of the feasible communities in which also multiple col-  
197 lapses were observed. More than one sudden recovery was however only observed in 21% of the feasible  
198 communities that exhibited one point of collapse.

199 The ranking of species recovery was, in most feasible communities, similar to the order in which  
200 they collapsed. E.g., the species who were the last to collapse when the driver of pollinator decline,  $d_A$ ,  
201 was increased, always recovered before or simultaneously with species that collapsed at a lower value of  
202 pollinator decline, in 79% of randomly structured communities with a connectance of 0.15.

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

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

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

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

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

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

234 **Pollinator persistence under changing environmental conditions.** Network topology influ-  
235 ences not only the probability of a single community-wide collapse; it is also important for the capacity  
236 of pollinator communities to persist under increasingly harsh conditions. Here, we measure this capacity  
237 as the amount of increase in the driver of pollinator decline,  $d_A$ , needed to reach the “final point of  
238 collapse”. This final point of collapse is the point where the last pollinator collapses to extinction (as  
239 indicated in figure 2). Similarly, we can measure the ease of recovery by measuring the value of the driver  
240 of pollinator decline, where the first pollinator recovers from extinction. This would be the “first point  
241 of recovery” (as indicated in figure 3). The points of collapse and recovery as they were found for a  
242 certain value of connectance and nestedness are plotted in figure 5. For each value of connectance and  
243 nestedness, multiple networks were tested.

244 Connectance and nestedness both postpone the final point of collapse. Consequently, the persistence of  
245 the pollinator community to an increase in the driver of pollinator decline,  $d_A$ , increases with connectance  
246 and/or nestedness. Highly connected, and/or nested communities also recover from a collapse at higher  
247 values of the driver of pollinator decline. The distance between the final point of collapse and the first  
248 point of recovery, however, increases with connectance and/or nestedness. This means that a larger  
249 change in the driver of pollinator decline is needed for pollinators to recover, after the final threshold is  
250 passed.

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

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

267 Increased connectance and nestedness both increase the fraction of mutualistic partners shared by  
268 pollinators. The behaviour of highly connected, and/or highly nested communities, is therefore similar  
269 to the behaviour of the two pollinator species who share an interaction with the same plant species  
270 (see figure 6). With increasing connectance the “overlap” in identity of the mutualistic partners of  
271 pollinators is simply increased because a larger number of interactions has to be distributed over an  
272 equal number of plant species. The “rich get richer” mechanism that lies at the basis of the algorithm  
273 we used to generate nested networks, makes pollinators interact with mutualistic partners where many  
274 other pollinators already interact with. With the algorithm we thus achieve a similar increase in overlap  
275 while maintaining the number of interactions equal. As with the two species sharing an interaction with  
276 the same mutualistic partner in figure 6, pollinators who form part of a nested and/or highly connected  
277 community indirectly support each other when stress levels are high. This makes the community survive  
278 higher levels of the driver of pollinator decline,  $d_A$ , but also leads to a simultaneous collapse, because  
279 species depend on each other when stress levels are high.

280 Feasible solutions can be found in two types of regimes. The first regime would be one in which the  
281 combined effect of direct and indirect effects between pollinators is positive. An alternative regime is  
282 one where these net effects are mostly negative. This second regime is only feasible when these negative  
283 effects are relatively equal in strength. With increasing nestedness we move from the second to the first  
284 regime. Intermediate values of nestedness might be less likely to be in either of the two regimes. Some  
285 species have already benefited from the increase in nestedness, while others have not, which leads to an

286 unbalanced community. This may explain why the probability of finding a feasible solution is smallest  
287 for intermediate values of nestedness (see figure 4 and supplementary material 3).

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

304 Our results can be understood intuitively by considering the “net effects” of species on each other and  
305 the way in which these effects are mediated by the topology of mutualistic networks. Pollinators have a  
306 direct negative effect on each other due to competition, while indirect positive effects may occur between  
307 pollinator species who interact with the same plant species. The extent to which pollinators interact  
308 with the same plant species increases with connectance and/or nestedness. A high nestedness of the  
309 mutualistic network may therefore promote the occurrence of indirect positive effects between pollinators.  
310 Earlier work has shown that these indirect positive effects may reduce the effective competition between  
311 pollinators, and promote the coexistence of species in nested communities (Bastolla *et al.* 2009).

312 In this study, we show that the relative strength of indirect facilitation between pollinators becomes  
313 stronger as the driver of pollinator decline,  $d_A$ , increases (see figure 6). This corresponds to the increas-  
314 ingly popular ‘stress-gradient hypothesis’ which suggests that facilitative effects grow in importance as  
315 environmental stress increases (Bertness & Callaway 1994; Holmgren *et al.* 1997; He *et al.* 2013). A high  
316 nestedness of mutualistic networks may therefore not only minimize effective competition to a level re-  
317 quired for species coexistence; under stressful conditions, it may even promote strong indirect facilitation  
318 between pollinators.

319 We found that pollinators who are part of highly connected and/or nested communities can maintain  
320 themselves substantially longer than pollinators who are part of communities with a low nestedness as  
321 the driver of pollinator decline,  $d_A$ , is increased. This large persistence of pollinator populations under

322 increasingly stressful conditions is, most likely, the result of the aforementioned indirect facilitation.  
323 Pollinator species who are part of either a highly nested or highly connected community can maintain  
324 themselves under stressful conditions because they indirectly support each other.

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

336 Our findings may have large implications for our view on the sustainability of natural communities and  
337 the ecosystem services provided by them. Based on the insurance hypothesis, one expects ecosystems  
338 services to be more reliable when supported by a large number of species (Naeem & Li 1997; Yachi  
339 & Loreau 1999). Functional redundancy of species is often seen as a valuable ‘commodity’, because  
340 it makes ecosystems more reliable in terms of the ecosystem services they provide (see Naeem & Li  
341 1997). Our analysis, however, illustrates that the functional overlap of pollinators, which is related to  
342 the connectivity and/or nestedness of mutualistic networks, may simultaneously increase the risk for a  
343 single community-wide collapse. A valuable ecosystem service, namely pollination, can therefore be lost  
344 suddenly, despite the fact that it is provided by a large number of species who are, when taking only  
345 their intrinsic properties into account, not equally sensitive to the driver of pollinator decline,  $d_A$ .

346 Our study is one of many small steps needed to bring theory on critical transitions and the structure  
347 of ecological networks together and we realize that this paper raises new questions that require further  
348 exploration. First, even though our model is substantially more complex than many others that study  
349 critical transitions, it is constrained to mutualistically interacting plant-pollinator communities. Multiple  
350 types of interactions co-occur in natural communities (Melián *et al.* 2009), and future studies should  
351 explore how the structuring of multiple types of interactions affect critical transitions. Secondly, our  
352 results underline the importance of developing early-warning signals for critical transitions in ecological  
353 networks (Scheffer *et al.* 2009). Third and finally, as the mechanisms we describe are generic, it is possible  
354 that a similar trade-off between persistence under severe conditions and potential for a systemic collapse

355 occurs in other systems as well. This is reinforced by previous studies finding notable similarities between  
356 the structure of mutualistic networks and that of financial systems (Uzzi 1996; May *et al.* 2008; Saavedra  
357 *et al.* 2008; Haldane & May 2011; Saavedra *et al.* 2011).

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363 **FIGURE CAPTIONS**

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

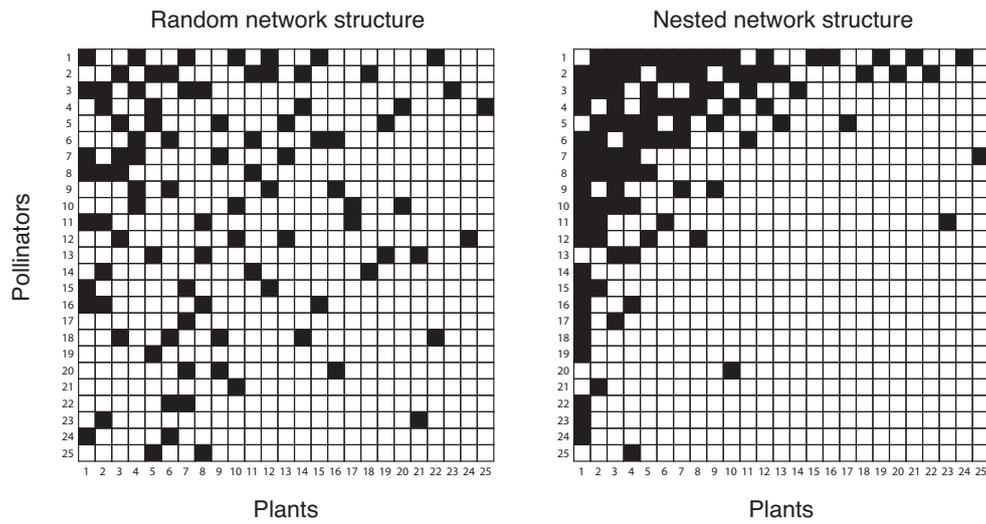
367 Figure 2: The collapse of pollinator populations when the driver of pollinator decline,  $d_A$ , affecting growth  
368 and/or mortality of pollinators, is gradually increased from zero to one. Results are shown for a random  
369 (left) and a nested (right,  $N=0.6$ ) network. Connectance of both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

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

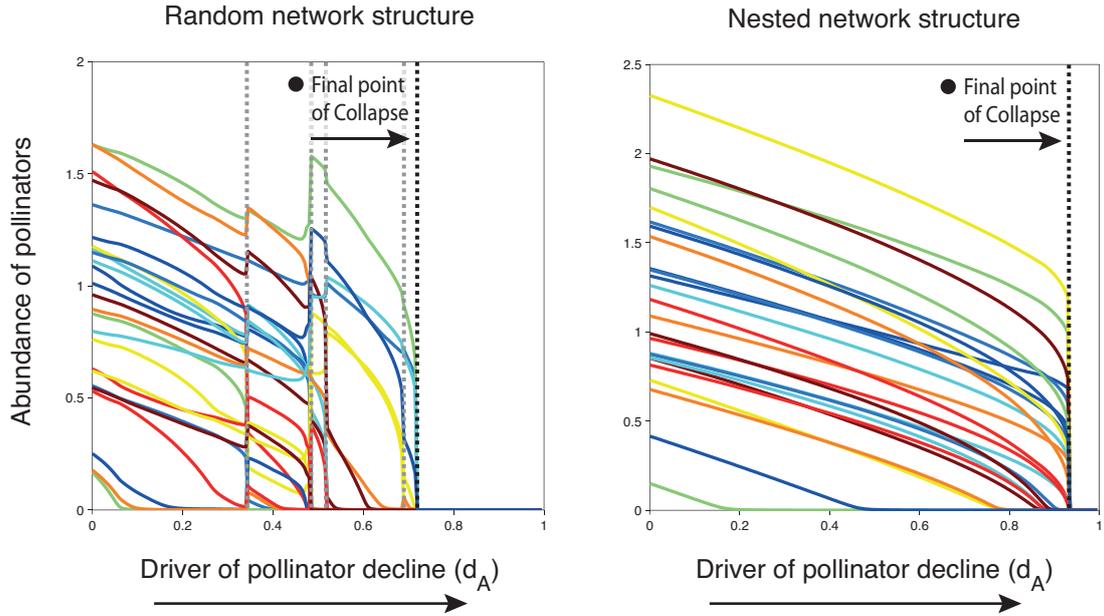
377 Figure 4: The number of collapses observed in randomly structured communities with different levels  
378 of connectance (left), and in communities with increasingly nested network topologies with a fixed con-  
379 nectance of 0.15 and fraction of forbidden links of 0.3 (right). The coloured bars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

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

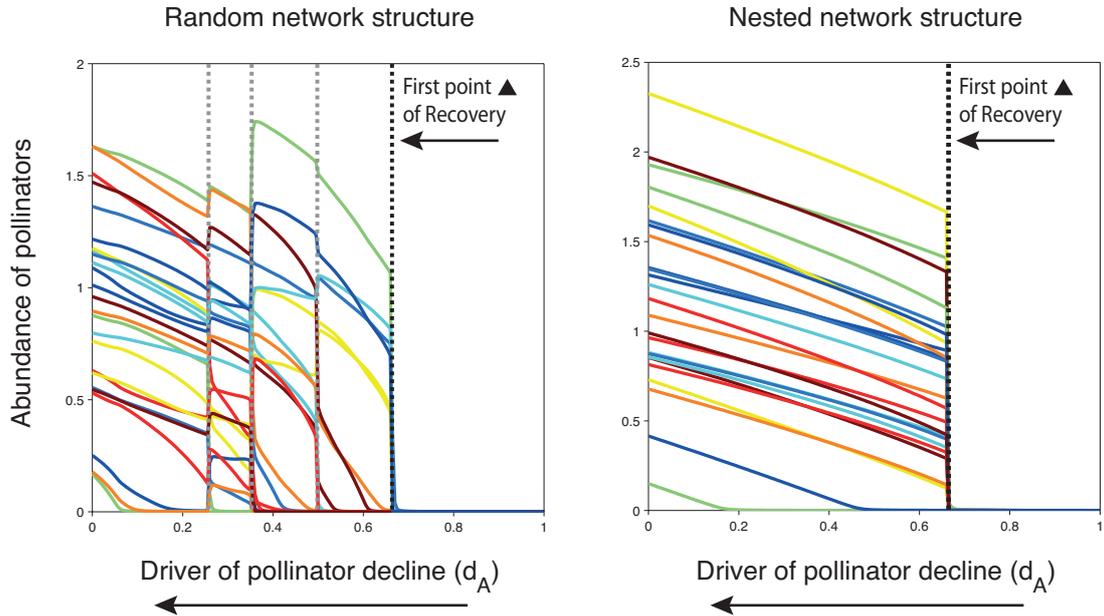
387 Figure 6: The net effect of species on each other while the driver of pollinator decline increases. Pol-  
388 linators that share a mutualistic partner have an increasingly positive effect on each other and collapse  
389 simultaneously. Pollinators that do not share mutualistic partners have an increasingly negative effect on  
390 each other and collapse independently. A. A simple network of mutualistic interactions between plants  
391 and pollinators. Pollinator A1 and A2 share mutualistic partner P1, while pollinator A3 does not share its  
392 mutualistic partner P2. Dashed lines indicate net-relationships between pollinators. Although pollinators  
393 are in direct competition with each other, net-positive relationships may exist between pollinator A1 and  
394 A2. B. Net effect ( $dA_k/dr_l$ ) of pollinator species on each other. In blue the net effects of pollinators A1  
395 and A2 on each other. In green the net-relationships between pollinator A3 and the other two pollinators.  
396 C. Abundance of pollinators A1 and A2 (blue), and pollinator A3 (red).



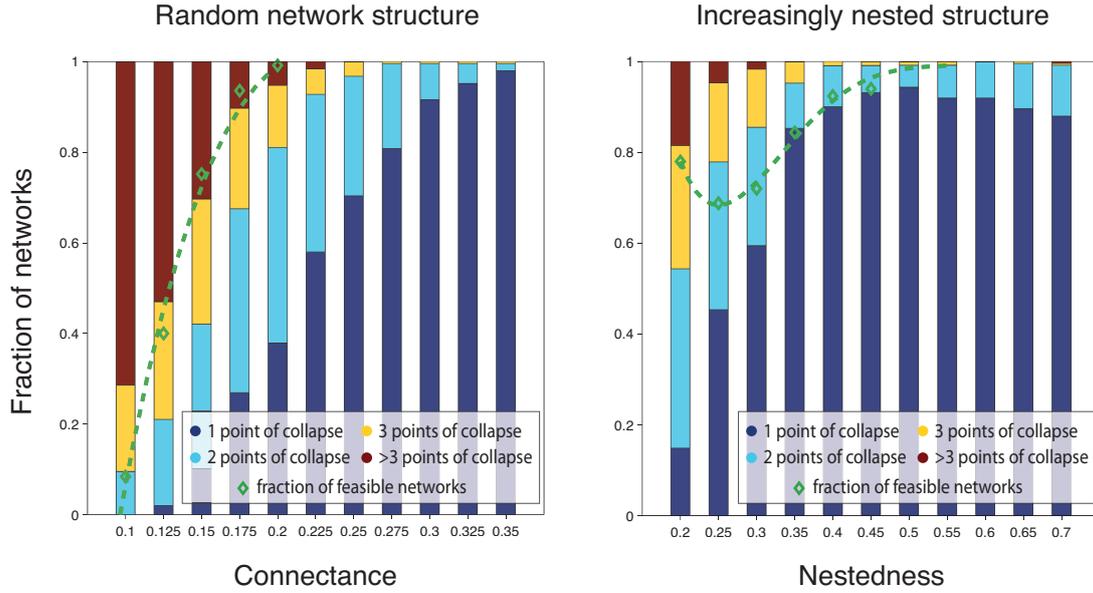
**Figure 1:** Matrix representations of a randomly structured network (left) and a nested network (right,  $N=0.6$ ). Filled squares indicate interactions between species. Column and row numbers correspond to individual plant and animal species. Species are ordered based upon their number of interactions.



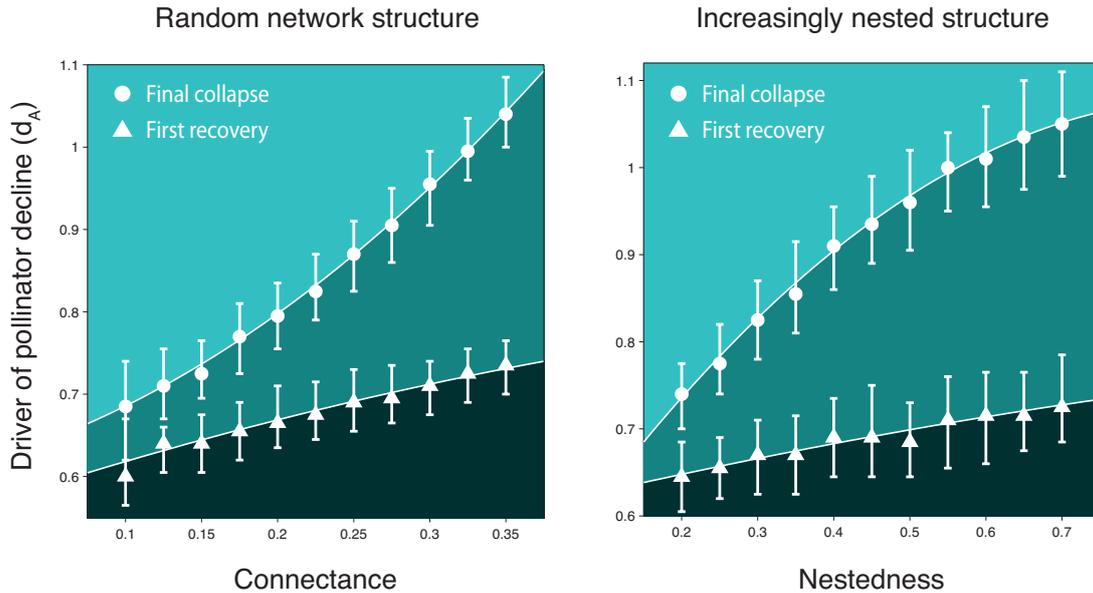
**Figure 2:** The collapse of pollinator populations when the driver of pollinator decline,  $d_A$ , affecting growth and/or mortality of pollinators, is gradually increased from zero to one. Results are shown for a random (left) and a nested (right,  $N=0.6$ ) network. Connectance of both networks is 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.



**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 figure 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.

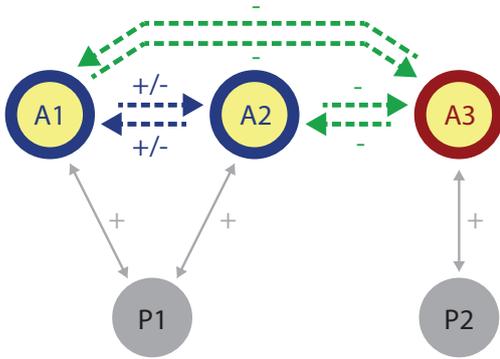


**Figure 4:** The number of collapses observed in randomly structured communities with different levels of connectance (left), and in communities with increasingly nested network topologies with a fixed connectance of 0.15 and fraction of forbidden links of 0.3 (right). The coloured bars represent the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



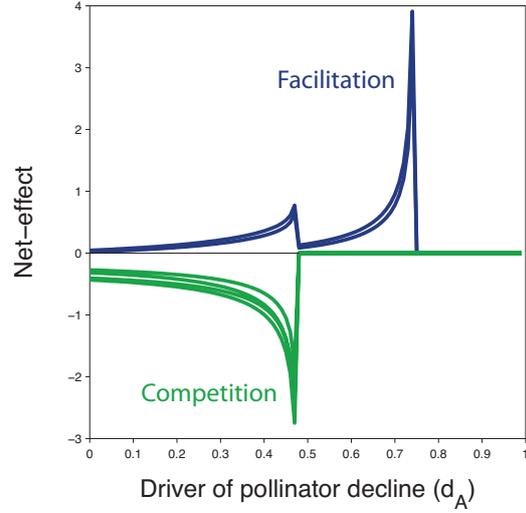
**Figure 5:** Points of collapse (circles) when the driver of pollinator decline,  $d_A$ , is increased, and points of recovery (triangles) when the driver of pollinator decline,  $d_A$ , is decreased. As in figure 4, results are shown for randomly structured networks that vary in connectance (left), 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.

**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.

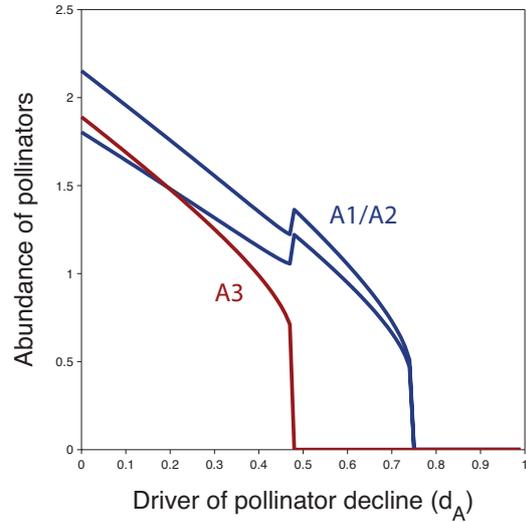


**A.** A simple network of mutualistic interactions between plants and pollinators. Pollinator A1 and A2 share mutualistic partner P1, while pollinator A3 does not share its mutualistic partner P2. Dashed lines indicate net-relationships between pollinators. Although pollinators are in direct competition with each other, net-positive relationships may exist between pollinator A1 and A2.

**parameter settings:**  $r_i \sim U(0.15, 0.25)$ ,  $\gamma_{0,ik} \sim U(0.9, 1.1)$ ,  $t = 0.5$ ,  $h_i \sim U(0.5, 0.6)$ ,  $C_{ii} \sim U(0.4, 0.6)$ ,  $C_{ij} \sim U(0.025, 0.075)$ , and  $\mu = 0.0001$ .

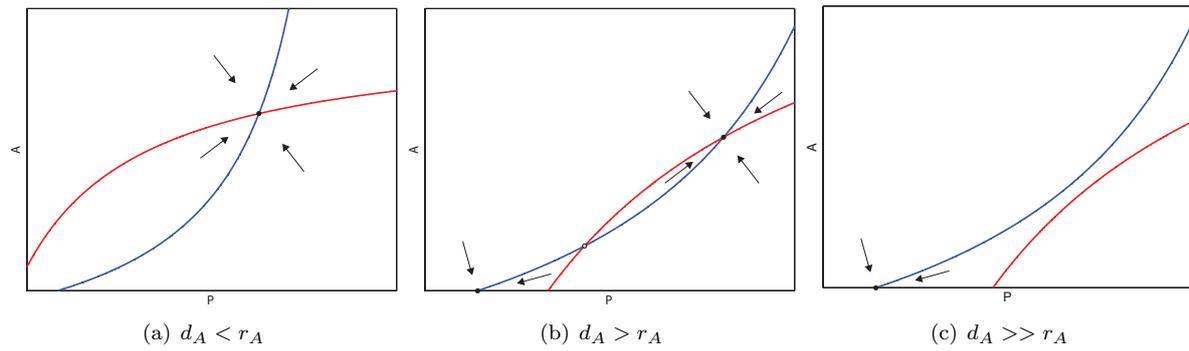


**B.** Net effect ( $dA_k/dr_l$ ) of pollinator species on each other. In blue the net effects of pollinators A1 and A2 on each other. In green the net-relationships between pollinator A3 and the other two pollinators



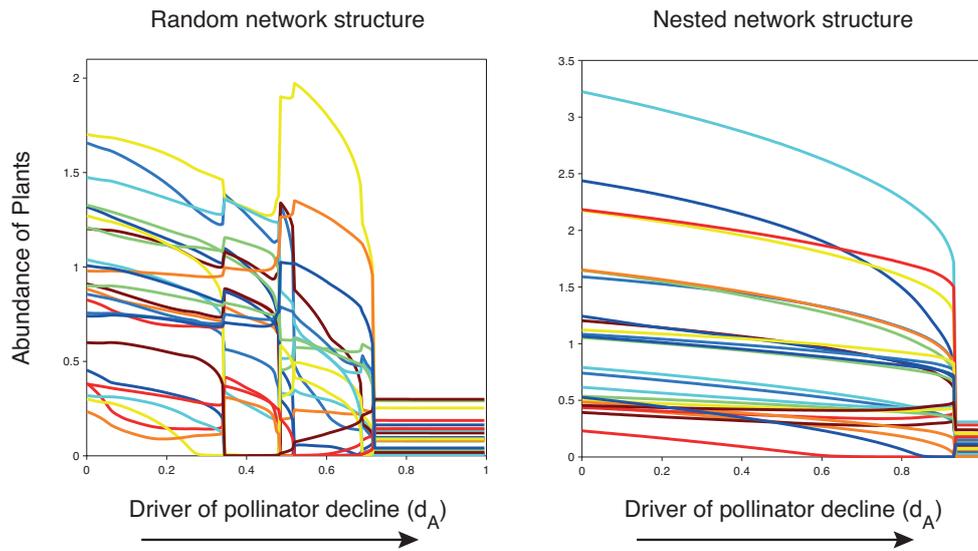
**C.** Abundance of pollinators A1 and A2 (blue), and pollinator A3 (red).

SUPPLEMENTARY MATERIAL 1

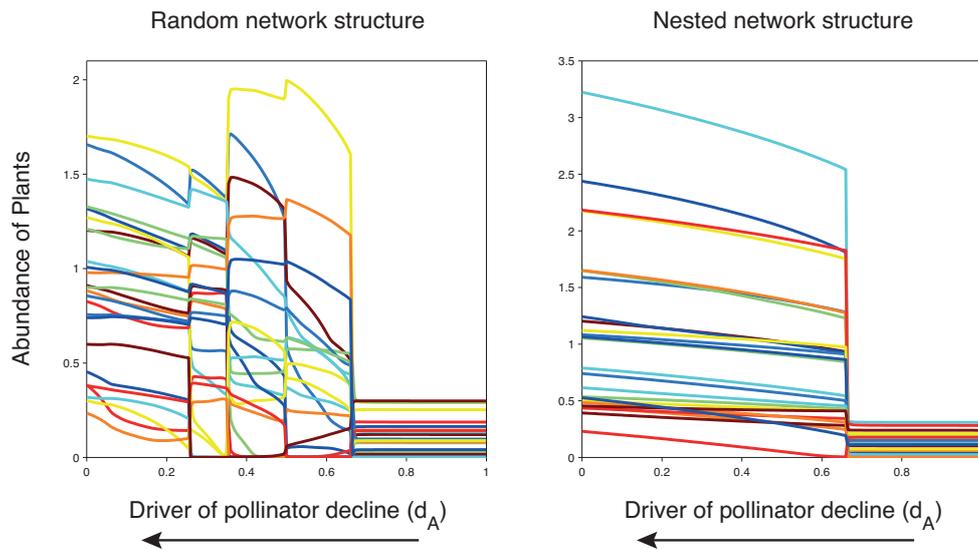


**Figure S1:** Nullclines of two mutualistically interacting species. Filled dots indicate stable equilibria, open dots indicate unstable equilibria. Fundamentally different configurations exist when (a) the driver of pollinator decline,  $d_A$ , is smaller than intrinsic growth rate  $r_A$ , (b) when the driver of pollinator decline,  $d_A$ , is bigger than intrinsic growth rate  $r_A$  and, (c) when the driver of pollinator decline,  $d_A$ , is substantially larger than intrinsic growth rate  $r_A$ . By increasing the driver of pollinator decline,  $d_A$ , we change from a regime with one stable state, presented in *a*, to the regime with two alternative stable states presented in *b*, until eventually a tipping point is reached where pollinators collapse to extinction. For a further analysis of models with two mutualistically interacting species see May (1978), Dean (1983), and Wright (1989).

SUPPLEMENTARY MATERIAL 2



**Figure S2:** Collapse of plant populations when *increasing* the mortality  $d_A$  of pollinators. Results are shown for a random (left) and a nested (right,  $N=0.6$ ) network. Parameter settings are the same as in figure 2.



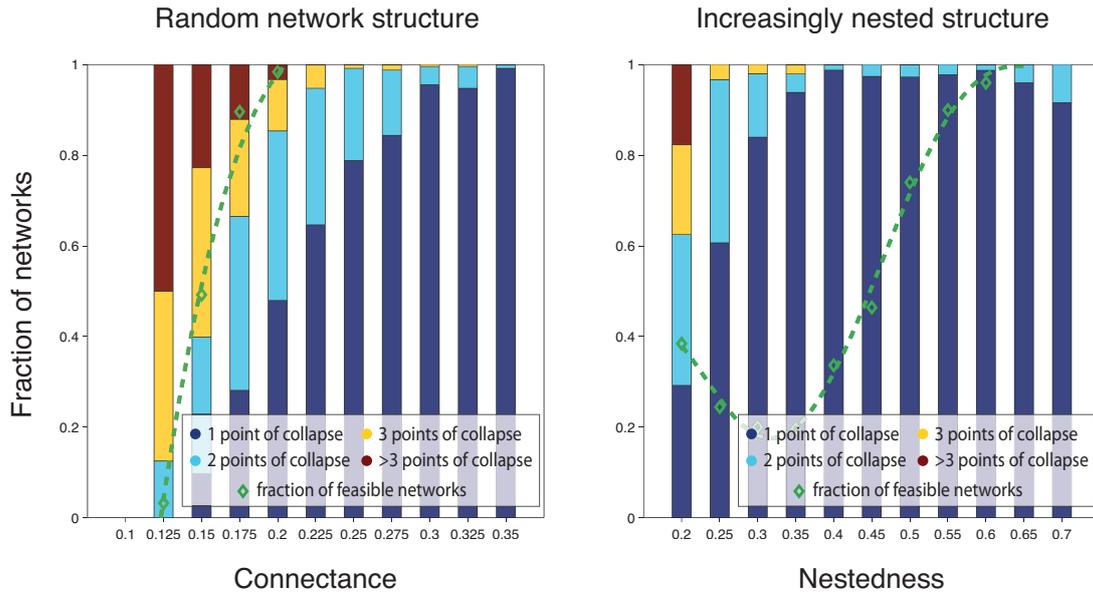
**Figure S3:** Re-establishment of plant populations when *decreasing* the mortality of pollinators  $d_A$ . Results are shown for a random (left) and a nested (right,  $N=0.6$ ) network. Parameter settings are the same as in figure 3.

### SUPPLEMENTARY MATERIAL 3

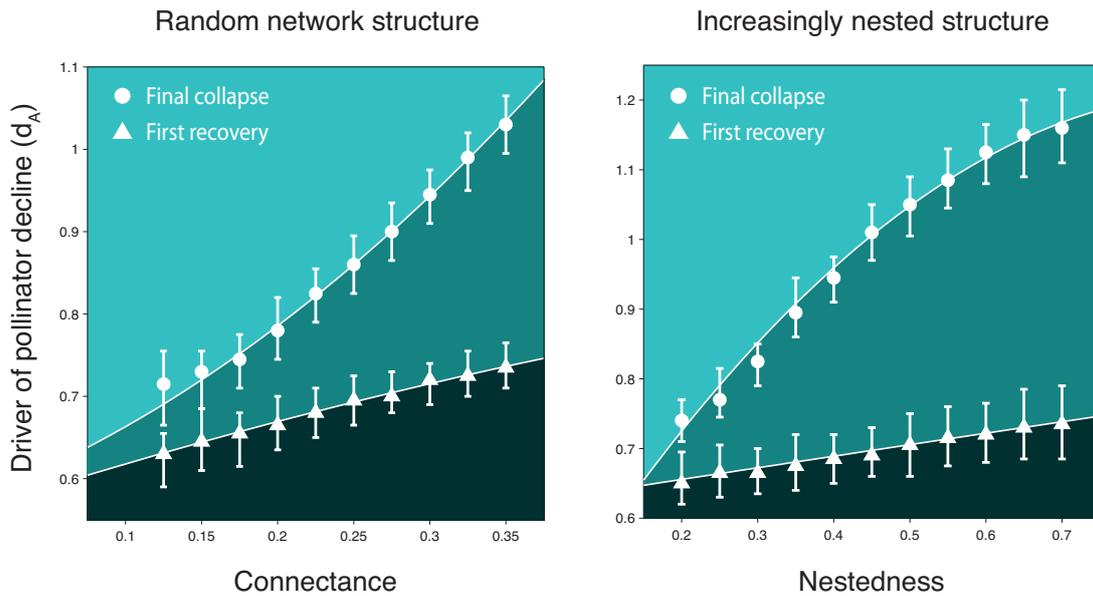
397 We tested the extent to which our results depend on the specific number of species, connectance or  
398 fraction of forbidden links chosen (see figure S6, S7, S4 and S5).

399 Furthermore, we show in figure S8 and S9 what our results look like if we do not allow any species to  
400 have less than 2 partners during any step of the algorithm we used to generate nested networks.

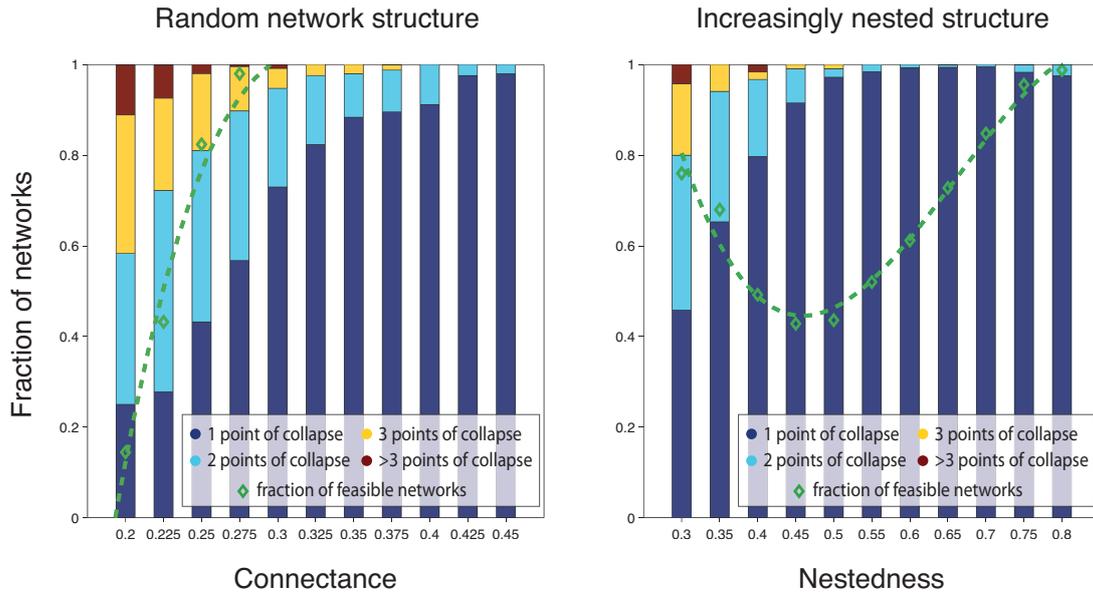
401 We only found qualitative differences in the behaviour of our model.



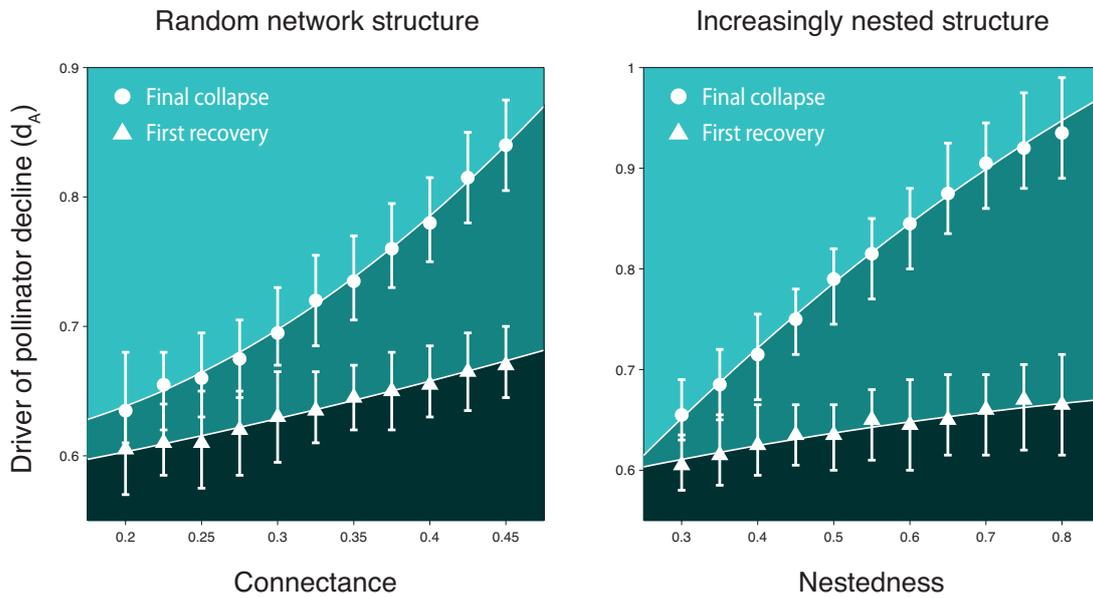
**Figure S4:** Results when using the same parameter settings as in figure 4, only now the community consists out of 35 plant and 35 pollinator species. As in figure 4, the coloured bars represent the fractions of feasible networks in which a certain number of collapses is found. The fraction of networks in which feasible solutions are found is indicated with the green diamonds.



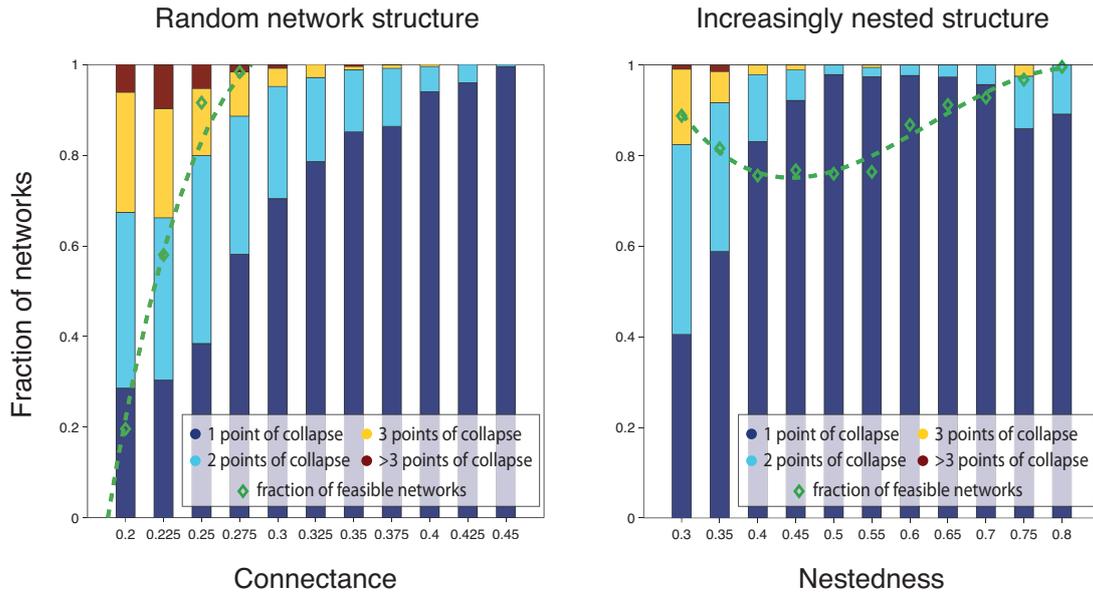
**Figure S5:** Points of collapse (circles) when the driver of pollinator decline,  $d_A$ , is increased, and points of recovery (triangles) when the driver of pollinator decline,  $d_A$ , is decreased. In case of multiple collapses and/or recoveries, the final point of collapse and the first point of recovery was plotted. Parameter settings are as in figure S4.



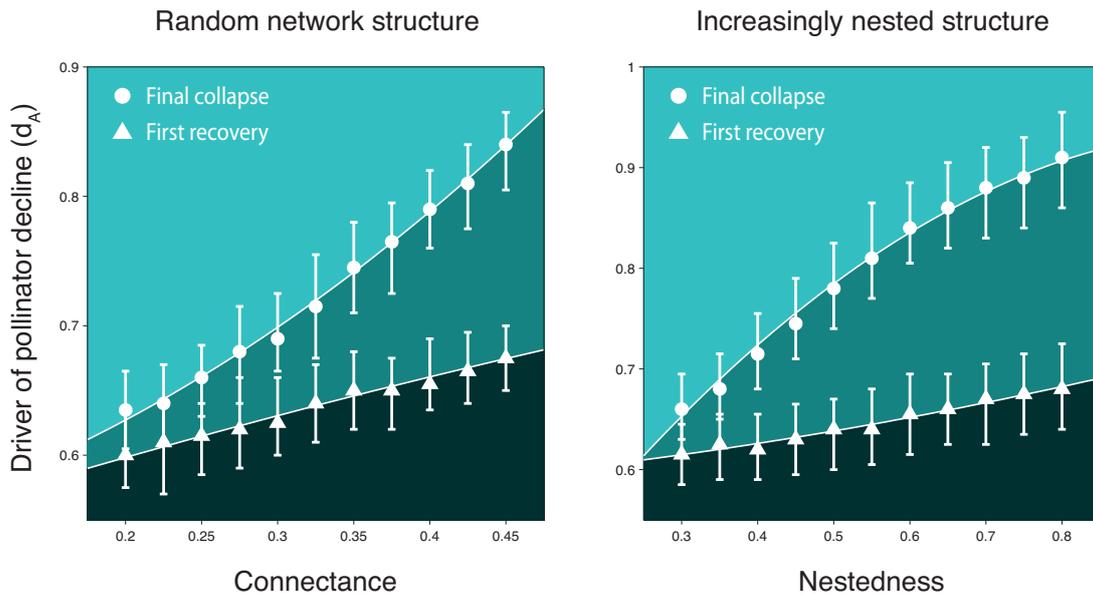
**Figure S6:** Results when using the same parameter settings as in figure 4, only now competition between species is a bit stronger,  $C_{ij} \sim U(0.025, 0.075)$ , and in communities with increasingly nested network topologies (right panel), the connectance is fixed to 0.25, and the fraction of forbidden links is fixed to 0.25. As in figure 4, the coloured bars represent the fractions of feasible networks in which a certain number of collapses is found. The fraction of networks in which feasible solutions are found is indicated with the green diamonds.



**Figure S7:** 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. In case of multiple collapses and/or recoveries, the final point of collapse and the first point of recovery was plotted. Parameter settings are as in figure S6.



**Figure S8:** Results when using the same parameter settings as in figure S6, only now each species has at least two interactions. As in figure S6, the coloured bars represent the fractions of feasible networks in which a certain number of collapses is found. The fraction of networks in which feasible solutions are found is indicated with the green diamonds.



**Figure S9:** 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. In case of multiple collapses and/or recoveries, the final point of collapse and the first point of recovery was plotted. Parameter settings are as in figure S8.

## REFERENCES SUPPLEMENTARY MATERIAL

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