

# 1 Real-world Interaction Networks Buffer Impact of Small 2 Evolutionary Shifts On Biodiversity

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12 **Keywords:** mutualistic networks, ecosystem stability, community diversity

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## Abstract

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Biodiversity maintenance and community evolution depend on the species interaction network. The “diversity-stability debate” has revealed that the complex interaction structure within real-world ecosystems determines how ecological communities respond to environmental changes, but can have opposite effects depending on the community type. Here we quantify the influence of shifts on community diversity and stability at both the species level and the community level. We use interaction networks from 19 real-world mutualistic communities and simulate shifts to antagonism. We demonstrate that both the placement of the shifting species in the community, as well as the structure of the interaction network as a whole contribute to stability and diversity maintenance under shifts. Our results suggest that the interaction structure of natural communities generally enhances community robustness against small ecological and evolutionary changes, but exacerbates the consequences of large changes.

## 28 **Author Summary**

29 Ecological interaction networks are important determinants of the stability of a community  
30 and influence how the community responds to environmental changes. Network properties  
31 that stabilize antagonistic networks destabilize mutualistic networks and vice versa. Previ-  
32 ous studies of interactions networks all assume that the type of interaction between species  
33 remains the same over time. Interactions between species, however, can shift from mutualistic  
34 to antagonistic and back over evolutionary time. Here we quantify the influence of such shifts  
35 on community diversity and stability at both the species level and the community level. We  
36 show that the location of the shifting species in the community, as well as the structure of the  
37 interaction network as a whole contribute to stability under such shifts. Our results suggest  
38 that the interaction structure of real-world communities generally enhances community ro-  
39 bustness against small ecological and evolutionary changes, but exacerbates the consequences  
40 of large changes.

## 41 **1 Introduction**

42 Forty years ago Robert May theoretically predicted that large complex ecosystems with ran-  
43 dom interactions are unlikely to be stable [1]. Ever since then, a large body of work has been  
44 published investigating various aspects of community structures that can stabilise different  
45 types of ecological communities [2, 3]. Typically such studies have focused on two types of in-  
46 teractions. The first type is antagonistic interaction, such as in producer-consumer or predator-  
47 prey communities [4–6]. These interactions are characterised by one of the species benefiting  
48 from the interaction while the other species suffers a cost. The second type is mutualistic inter-  
49 action, such as plant-pollinator or plant-seed disperser networks [7–10]. Here both interaction  
50 partners benefit from the interaction. Interestingly, the network properties that convey stabil-  
51 ity to antagonistic networks render mutualistic networks unstable and those that make mu-  
52 tualistic networks more stable make antagonistic networks less stable [11]. Recent studies on  
53 theoretical and real-world ecological networks containing both types of interactions showed  
54 that a low ratio of mutualistic to antagonistic interactions can destabilize an otherwise stable  
55 antagonistic community, but a moderate mixture of both interaction types can stabilize popu-  
56 lation dynamics [12–14].

57 These previous studies all assumed that the type of interaction between species remains  
58 the same over time. However, empirical studies have suggested that interaction types within  
59 an ecosystem shift over ecological and evolutionary time [15, 16]. It remains unclear what  
60 effect these interaction type shifts may have on the diversity and stability of an ecosystem.  
61 Here we perform a first step towards understanding how shifts between interaction types in  
62 real-world communities affect biodiversity and community stability at both the species level  
63 and the community level. Mutualists are continuously under the threat of exploitation [17],  
64 and therefore shifts from mutualism to antagonism in such mutualistic communities represent  
65 a relevant case study for the effect of shifts in ecological communities [16].

66 More specifically, we examined 19 previously published real-world plant-pollinator net-  
67 works [7] and applied a species interaction model to study the change in the equilibrium state  
68 of the community. The general strategy was to choose one or several pollinator species in each  
69 network and switch their interactions with all plants to antagonistic. We determine the effects  
70 of these shifts with respect to resistance stability [18], evenness biodiversity [19] and ecological

71 dominance on the shifted species. As proxies for these properties we use the relative Eu-  
72 clidian distance, the relative Shannon Index change, and the relative frequency change of the  
73 shifted species between the two equilibrium states respectively (see Methods). To assess the  
74 importance of network structure, we compared each real-world network with 100 simulated  
75 networks generated by randomizing the interactions.

## 76 **2 Materials and Methods**

77 We determine the effects of shifts of the interaction type in simulated real-world networks  
78 (see Section 2.1). A network is composed of a number of pollinator and plant species. A  
79 specific pollinator only interacts with a subset of plant species (see Figure 1a). This network of  
80 interactions is represented by an adjacency matrix. The strength of the interaction is given by  
81 the interaction model (see Section 2.2).

82 We study the stability of the real-world networks on four different levels. In a first step,  
83 we examine the effect of the shift of the interaction type of a single species on the network as a  
84 whole, as well as on the shifting species itself (see Section 2.4). This allows us to quantify the  
85 effect of the shifting species' centrality in the network (see Section 2.5) on diversity and stabil-  
86 ity. We also examine the effect of the species centrality on the change of its own abundance.  
87 In a second step, we compare the effect of shifting random species in a real-world network to  
88 equivalent randomized networks using two randomization schemes (see Section 2.6). The first  
89 randomization scheme keeps the connectance constant, while destroying all network struc-  
90 ture. The second scheme keeps both the connectance and the degree distribution constant.  
91 This allows us to tease apart the effects of connectance, degree distribution and higher order  
92 network structure. To quantify the effects of the introduction of an antagonistic interaction on  
93 the network, in a third step, we study the differences between the interaction type shift of a  
94 single species and the extinction of the same species. Finally, in a fourth step, we determine the  
95 robustness of the network to interaction type shifts of multiple species. As for single species,  
96 we quantify the stability and diversity of the network to such shifts. For multiple shifts, we  
97 also quantify the number of secondary extinctions caused by the interaction type shifts.

98 In general, all simulations proceed in the following manner. We first determine the equilib-  
99 rium abundances of each species in the network as reference abundances of a specific network

100 (see Section 2.3). We then shift the interaction type of a single pollinator species. This results  
101 in a new interaction network (see Figure 1b). Finally, we determine the new equilibrium abun-  
102 dances of each of the species and compare these to the reference abundances.

## 103 2.1 Network data

104 We use real world plant-pollinator networks previously published in [7]. The smallest net-  
105 work has 10 plants and 12 pollinators, while the largest has 112 plants and 839 pollinators. A  
106 full list of number of species in each network is given in Supplementary Table S1. The values  
107 of interaction strength between plants and pollinators have been normalized such that bidirec-  
108 tional asymmetry exists [7].

## 109 2.2 Interaction Model

110 We use a multi-species interaction model equivalent to Bascompte *et al.* [7]. For mathematical  
111 tractability, we focus on Holling type I functional responses and show in the Supplementary  
112 Materials that we obtain qualitatively equivalent results in the case of single species shifts  
113 when using a Holling type II functional response. The model with a type I functional response  
114 in the interaction term has the form,

$$\frac{dn_i}{dt} = r_i n_i - s_i n_i^2 + \sum_{i \neq j} a_{ij} n_i n_j = \left( r_i - \sum_j c_i a_{ij} n_j \right) n_i, \quad (1)$$

115 where  $n_i$  is the abundance of species  $i$ ,  $r_i$  is species'  $i$ 's individual growth rate,  $s_i$  a intra-  
116 specific competition term and  $a_{ij}$  is the effect on species  $i$  of the interaction with species  $j$ . We  
117 have incorporated the intra-specific interaction term for a species  $i$  into the interaction matrix,  
118 such that  $a_{ii} = s_i$ . The parameter  $c_i$  represents the magnitude of the payoff of an interaction.  
119 Positive entries in  $\mathbf{A}$  ( $a_{ij} > 0$ ) are interactions where the species  $i$  pays a price for interacting  
120 with  $j$  and negative entries ( $a_{ij} < 0$ ) are interactions where species  $i$  gains a benefit from the  
121 interaction with species  $j$ . Note that the interaction matrix  $\mathbf{A}$  contains both the effects on plants  
122 when they interact with animals, as well as the effects on animals, when they interact with  
123 plants.

124 In this study, we only consider interactions between two species classes (plants and polli-

125 nators). Assuming there are  $N$  species in total, of which  $N_A$  are animals species (pollinators)  
126 and  $N_P$  are plant species, then we can partition the matrix  $\mathbf{A}$  such that the rows and columns  
127  $i \in \{1, 2, \dots, N_A\} = \mathcal{N}_A$  are animal species and  $i \in \{N_A + 1, N_A + 2, \dots, N\} = \mathcal{N}_P$  are plant  
128 species. We neglect inter-specific competition (plant-plant and animal-animal interactions), so  
129  $a_{ij} = 0$  when  $i, j \in \mathcal{N}_X, X \in \{\mathcal{N}_A, \mathcal{N}_P\}$ .

130 To shift the  $k$ -th animal from a mutualist into an antagonist, we multiply the  $k$ -th column  
131 of  $\mathbf{A}$  by  $-1$ . Therefore, the animal still gains the same benefit from interacting with the plants  
132 as before the shift, but the plant now pays a price for each interaction with this animal species.  
133 In terms of a plant-pollinator system, if the interaction strengths are related to the frequency  
134 of visits, then the pollinator still claims the reward for visiting the plant (e.g. gets nectar), but  
135 the plant pays a price for each visit (e.g. damaging of the plant, theft of nectar).

136 We assume that the frequency of visitation is equally proportional to the abundance of any  
137 pollinator species. Thus generalist pollinators distribute their mutualistic interactions across  
138 many different plants, while specialist pollinators visit few plants more frequently. Mathemat-  
139 ically, we assume that the columns of  $\mathbf{A}$  excluding the diagonal sum to 1,

$$\sum_{i \neq j} a_{ij} = 1.$$

140 We consider facultative mutualism, such that  $r_i > 0$  and all species have a positive growth  
141 rate in absence of any mutualistic interaction. Population growth is limited by the intra-specific  
142 competition terms  $s_i$ . For randomly interacting populations, a finite non-trivial steady state  
143 for species  $i$  exists if  $s_i > c_i$  (see Supplementary Materials). We show in the Supplementary  
144 Materials that we obtain qualitatively equivalent results with obligate mutualism.

### 145 2.3 Determining the equilibrium abundances

146 We find the non-trivial equilibrium state of a system with interaction matrix  $\mathbf{A}$  by solving  
147 the nonlinear system of equations  $d\mathbf{n}/dt = 0$  (Equation 1). This is equivalent to finding the  
148 solution to the linear system of equations  $\mathbf{A}\bar{\mathbf{n}} = \mathbf{r}$ .

149 A species  $i$  is extinct at equilibrium if it has an equilibrium abundance  $\bar{n}_i \leq 0$ . These  
150 negative abundances, however, can influence the equilibrium abundances of the other species.  
151 We therefore extract a sub-matrix  $A'$  where the  $i$ -th row and column are deleted and find the

152 equilibrium abundances of this subsystem  $\mathbf{n}^*$ . We repeat this procedure until all remaining  
153 species have an abundance  $\bar{n}'_i > 0$ .

## 154 2.4 Stability and diversity measures

155 We use three measures to determine the effect of interaction shifts on the stability and diversity  
156 of the network: (1) relative Euclidian distance; (2) relative frequency change of the shifting  
157 animal; and (3) the relative Shannon index change of the equilibria.

158 **Relative Euclidian distance.** The relative Euclidian distance  $\delta$  measures how much the abun-  
159 dances of the different species change from before to after the shift of one or more animal  
160 species from mutualists to antagonists. If  $n_i$  is the abundance at equilibrium of species  $i$  before  
161 the shift and  $n_i^*$  is the abundance at equilibrium of species  $i$  after the shift, then the relative  
162 Euclidian distance is,

$$\delta = \frac{\sqrt{\sum_{i=1}^N (n_i^* - n_i)^2}}{\sqrt{\sum_{i=1}^N n_i^2}}. \quad (2)$$

163 **Relative frequency change of the shifting animal.** The relative change in an animal's fre-  
164 quency  $\Delta f_i$  measures the relative benefit or price an animal gains or pays if that animal shifts  
165 from being a mutualist to an antagonist,

$$\Delta f_i = \frac{f_i^* - f_i}{f_i}, \quad (3)$$

166 where  $f_i$  is the relative of abundance of the animal species in the current ecosystem,

$$f_i = \frac{n_i}{\sum_i n_i}.$$

167 **Relative Shannon index change.** The relative Shannon index change  $\Delta s$  measures how much  
168 diversity is affected by the shift of one or more animals from pure mutualists to antagonists,

$$\Delta s = \frac{-\sum_{i=1}^N f_i^* \ln f_i^*}{-\sum_{i=1}^N f_i \ln f_i} - 1. \quad (4)$$

## 169 2.5 Network measures

170 Centrality measures determine the importance of an individual species in the network. Here  
171 we use two centrality measures that capture different aspect of the species placement in the  
172 network [20].

173 **Degree centrality.** We measure the importance of single species within one network by its de-  
174 gree centrality  $k_i$ , which is defined as the number of interactions  $K_i$  with other species divided  
175 by the total number of species,

$$k_i = \frac{K_i}{N}. \quad (5)$$

176 **Betweenness centrality.** An alternative measure of centrality of a single species is its be-  
177 tweenness. The betweenness of species  $i$  is defined as the number of shortest paths between  
178 any two nodes  $l$  and  $m$  that pass through  $i$  divided by the total number of shortest paths be-  
179 tween  $l$  and  $m$ . We calculate betweenness centrality using the algorithm implemented in the  
180 igraph library [21].

181 **Nestedness measure** We measure nestedness using the established NODF measure [22]. In  
182 order to account for network properties such as the total number of interaction that can also  
183 influence nestedness, we use a relative measure of nestedness,

$$N^* = \frac{N - \langle N_R \rangle}{\langle N_R \rangle}. \quad (6)$$

184 Here  $N = \frac{\sum N_{\text{paired}}}{n(n-1)/2 + m(m-1)/2}$  is the NODF measure defined in [22] and  $\langle N_R \rangle$  is the NODF  
185 nestedness of an interaction matrix obtained by shuffling the interactions, averaged over 100  
186 randomizations (see section 2.6).

## 187 2.6 Randomizations

188 We compare the effects of shifting from mutualists to antagonists in the real network to ran-  
189 domized networks with equal number of plant and animal species. The randomized networks  
190 have the same number of plant-animal interactions. We employ two randomization schemes.  
191 In the first scheme, all interactions are distributed randomly between plants and animals. To

192 guarantee that all animals interact with at least one plant and vice-versa, a single interaction  
193 partner is first assigned to each animal/plant. The remaining interactions are then randomly  
194 placed to animal-plant pairs. This randomizes both the degree distribution as well any other  
195 higher-order structure of the network. In the second scheme, the degrees of each animal and  
196 plant are retained, but the interaction partners are randomized. In this scheme, only the higher-  
197 order structure is randomized.

## 198 2.7 Residual measures.

199 When species are removed from the community (i.e. extinctions) their abundances are arti-  
200 ficially set to zero. This is a different perturbation than shifts to antagonism, since in shifts  
201 the interactions are modified and in extinctions the abundances are modified. In such cases,  
202 the distance measures may be artificially inflated due to the removal of a single species. For  
203 example, if species  $k$  is removed its abundance is set to zero, while if it shifts it may persist  
204 with a non-zero abundance, leading to a smaller change in the case of shifts. We therefore con-  
205 sider residual measures of  $\delta$ ,  $\Delta s$  and  $\Delta f$ , which are calculated equivalently to explained above  
206 without considering the shifted/removed species,

$$\delta^{(-k)} = \frac{\sqrt{\sum_{i \neq k} (n_i^* - n_i)^2}}{\sqrt{\sum_{i \neq k} n_i^2}}, \quad (7)$$

$$\Delta s^{(-k)} = \frac{-\sum_{i \neq k} f_i^{*,(-k)} \ln f_i^{*,(-k)}}{-\sum_{i \neq k} f_i^{(-k)} \ln f_i^{(-k)}} - 1, \quad (8)$$

207 where  $f_i^{(-k)} = \frac{n_i}{\sum_{i \neq k} n_i}$ .

## 208 3 Results

### 209 3.1 Single shifts

210 **Response to single shifts.** Shifting the interaction type of a single pollinator species changed  
211 the equilibrium abundances of all the species but did not result in any secondary extinctions  
212 of either plants nor pollinators. As a result of the introduction of antagonistic interactions,  
213 however, the total sum over the abundance of all species decreases. The relative Euclidian

214 distance,  $\delta$ , between the equilibrium states before and after the single shift is smallest when the  
215 shifting species has a low centrality and increases with the centrality of the species (Figure 2  
216 and Table 1). The relative Shannon index change,  $\Delta s$ , is always negative for single shifts. The  
217 magnitude of the relative Shannon index change,  $|\Delta s|$ , is smallest for low centrality species  
218 and increases with species centrality. The relative abundance frequency change of the shifting  
219 species is either positive or negative. It is largest for low centrality species and decreases  
220 with increasing centrality. The rank correlation between the centrality and both  $\delta$  and  $|\Delta s|$  is  
221 significantly positive within each network and independent of the centrality measure (Table 1).  
222 We also qualitatively find the same correlations between the centrality and distance measures  
223 for weak and strong intraspecific competition (see Supplementary Materials).

224 **Real networks versus randomizations.** To assess the effect of network structure of the sta-  
225 bility to shifts, we compared the median value of the three distance measures for all possible  
226 single species shifts in real-world and corresponding randomized networks (mean value over  
227 100 randomizations). The median relative Euclidian distance and the median magnitude of  
228 the relative Shannon index change are higher in the randomized networks than the real-world  
229 networks (Figure 3a-b). Conversely, the relative frequency change of the antagonistic species  
230 is generally larger in real-world than in randomized networks (Figure 3c). These results are  
231 consistent for both randomization schemes, though the effect is smaller when the degree dis-  
232 tribution is kept constant and only the higher order structure is randomized. Weak and strong  
233 interactions did not qualitatively influence these results (see Supplementary Materials).

234 **Influence of nestedness.** We then determined the role of nestedness on the stability to shifts.  
235 In agreement with previous findings [8], networks with more species are more nested than  
236 networks containing less species (Supplementary Figure S1). We find that the median relative  
237 Euclidian distance  $\delta$  decreases both with number of species (Spearman's  $\rho = -0.984$ ,  $p = 3.20 \cdot$   
238  $10^{-14}$ ) and nestedness (Spearman's  $\rho = -0.753$ ,  $p = 0.000305$ ), but increases with connectance  
239 (Spearman's  $\rho = 0.921$ ,  $p = 1.50 \cdot 10^{-6}$ ). The magnitude of the median relative Shannon index  
240 change  $\Delta s$  also decreases with number of species (Spearman's  $\rho = -0.947$ ,  $p = 7.86 \cdot 10^{-13}$ )  
241 and nestedness (Spearman's  $\rho = -0.707$ ,  $p = 0.00101$ ), and also increases with connectance  
242 (Spearman's  $\rho = 0.863$ ,  $p < 10^{-15}$ ). The median relative frequency change  $\Delta f$  increases with

243 number of species (Spearman's  $\rho = 0.548$ ,  $p = 0.0152$ ) and nestedness (Spearman's  $\rho = 0.496$ ,  
244  $p = 0.0323$ ), but decreases with connectance (Spearman's  $\rho = -0.574$ ,  $p = 0.0116$ ).

245 Since, however, number of species, connectance and nestedness are not necessarily in-  
246 dependent (Figure S1), we also perform an ANOVA with all three factors. When analyzed  
247 together, only the number of species ( $F = 75.8$ ,  $p = 3 \cdot 10^{-7}$ ,  $df = 1$ ) and the connectance  
248 ( $F = 5.98$ ,  $p = 0.0273$ ,  $df = 1$ ) are significant. The normalized NODF no longer has a significant  
249 effect ( $F = 0.147$ ,  $p = 0.707$ ,  $df = 1$ ).

### 250 3.2 Shifts to antagonism versus extinctions

251 We compared the relative Euclidian distance and the relative Shannon index change when a  
252 single species shifts to antagonism to the case where the same species is removed, i.e. goes  
253 extinct (Figure 4). As the extinction of a species in itself represents a strong change in the  
254 distribution of species abundances, even without considering the secondary effects of this ex-  
255 tinction on other species, we only consider the change in the species excluding the antago-  
256 nistic/extinct species (Supplementary Matrials). Interaction type shifts affect the community  
257 more strongly than the removal of a mutualist, both with respect to relative Euclidian distance  
258 ( $\rho = -0.571$ ,  $p < 10^{-16}$ ) and relative Shannon index change ( $\rho = -0.406$ ,  $p < 10^{-16}$ ). Moreover,  
259 we find that the difference in effects between interaction type shifts and extinctions decreases  
260 with the centrality of the shifted/removed species. The effect of weak and strong intra-specific  
261 competition is shown in Supplementary Figures S7.

### 262 3.3 Multiple shifts

263 We then assessed how networks respond to shifts of multiple species. For a small number of  
264 shifts, both the relative Euclidian distance and the Shannon index change is smaller in real-  
265 world than randomized networks (similar to single species shifts). To this end we compared  
266  $\delta$  and  $\Delta s$  in real and randomized networks when shifting different fraction of randomly cho-  
267 sen pollinators. As the number of shifted species increases, the effect on real-world networks  
268 becomes considerably larger than in randomized networks (Figure 5; we also observe this  
269 reversal in the case of species removals, see Supplementary Figure S3). When a sufficient  
270 number of pollinators are shifted, we started to observe secondary extinctions. The number

271 of such secondary extinctions is considerably larger in the real-world networks than random-  
272 ized networks (Supplementary Figure S2). We observe an initial increase in the number of  
273 secondary extinctions with the number of shifted species. However, when almost all species  
274 shift to antagonism then the number of secondary extinctions decreases again (Supplementary  
275 Figure S2).

## 276 **4 Discussion**

277 More centrally located species, as measured by a higher degree or betweenness centrality, pay  
278 a higher cost when shifting to antagonism, while species towards the periphery of the network,  
279 lower degree centrality, pay a smaller cost or even benefit from shifting (Figure 2). Similarly,  
280 the relative change in Shannon Index and the relative Euclidian distance increase with the cen-  
281 trality of the shifted species (Figure 2). This confirms the importance of generalists in main-  
282 taining diversity and stability [23, 24]. Together, this implies that shifts of species at the edge  
283 of the network are more likely to occur, both because of the advantage to the species itself, as  
284 well as the smaller effect on the community.

285 The effect of a single pollinator species shift to antagonism, however, also strongly depends  
286 on network structure (Figure 3). The total change in equilibrium abundances and species even-  
287 ness is larger in randomized than in real-world networks. The relative effect on the shifting  
288 species, however, is mostly positive (i.e. the shifting species increases its abundance relative to  
289 all other species) and its magnitude is generally larger in real-world than in randomized net-  
290 works. Overall, these results have three implications. Firstly, real-world mutualistic networks  
291 have an intrinsic structure that reduces the effect on the whole community caused by shifts  
292 to antagonism. Secondly, real-world networks, in contrast to randomized networks, maintain  
293 evenness biodiversity better under shifts. Thirdly, real-world networks enhance the benefit the  
294 shifting species receives compared to all the other species in the network.

295 These results are generally consistent when all network structure is destroyed, and also  
296 when the degree distribution of the network is kept constant, although the effect is smaller in  
297 the latter case. Thus, the degree distribution can only in part explain the difference between  
298 real-world and randomized networks. This is consistent with previous reports that the degree  
299 distribution can be a predictor of network stability, but its effect must be teased apart from the

300 effects from other higher-order network structure [25, 26].

301 Mutualistic communities are often strongly nested [27], which could explain the differ-  
302 ence between real-world and randomized networks that is not due to differences in the de-  
303 gree distribution. We found that the median values of the relative Euclidian distance and the  
304 magnitude of the relative Shannon index change both decrease with relative nestedness (Sup-  
305 plementary Figure S1). The effect of relative nestedness, however, becomes non-significant  
306 once community size is taken into account. Therefore it is unclear whether the robustness of  
307 real-world networks is a direct consequence of their nested architecture or other higher-order  
308 network structure.

309 An alternative perturbation to which the stability of an ecological community can be mea-  
310 sured is the extinction or removal of a species [28, 29]. Interaction type shifts have a greater  
311 effect on the community than extinctions. Even for the most centrally located species, interac-  
312 tion type shifts lead to more than 50% larger changes compared to extinctions. Thus although  
313 interaction type shifts lead to greater changes than removals, ecological communities are com-  
314 paratively more robust to shifts in central species than to extinctions.

315 Even though the structure of real-world mutualistic networks enhances their robustness  
316 against single shifts, the opposite is the case for multiple shifts, i.e. they are more sensitive  
317 to multiple shifts than randomized networks. Mougi & Kondoh [14] previously showed that  
318 adding mutualistic interactions to predator-prey networks can stabilize the community, but  
319 that too many mutualistic interactions decreases the stability again. Here, we replace mu-  
320 tualistic interactions with antagonistic ones and find that changing only a small number of  
321 interactions drastically destabilizes real-world networks. As more and more interactions are  
322 shifted, stability is regained. Equivalently, Allesina & Tang [13] showed that a large number  
323 of weak mutualistic interactions has a destabilizing effect on antagonistic communities. Thus,  
324 these results are in agreement, and the effect of mixed-effects is similar, whether one starts  
325 with naturally stable antagonistic networks or a naturally stable mutualistic network.

326 Due to the general nested architecture of real-world mutualistic communities [27], there are  
327 more specialists than generalists in these communities. These specialists have a lower degree  
328 centrality and are more likely to benefit from shifting their interaction type but will have less  
329 of an effect on the whole community. Thus the species that contribute most to the stability of

330 the community (i.e. generalists) are also those which are most prohibited from shifting their  
331 interaction type. Generalist species have also been shown to be less tolerant to a decrease in the  
332 strength of the mutualistic interactions [30]. These results offer an additional explanation why  
333 in phylogenetic studies of mutualistic communities specialists are more likely to “disappear”  
334 from the community [16, 24]. While extinctions have been the usual explanation, we propose  
335 that interaction type shifts could also be a driver of this observation.

336 Exploitation represents an important challenge for mutualistic communities since cooper-  
337 ation between unrelated individuals is particularly susceptible to cheating [17, 31]. The effect  
338 of such cheating has been well studied in the case of two-species interactions, but it is not  
339 clear how these changes propagate through the complex interaction networks characterising  
340 real ecological communities. The interaction type shifts studied here can be seen as the result  
341 of successfully invading cheaters. Overall, our results indicate that real-world networks pro-  
342 mote the shifting of a typical single species more strongly compared to random community  
343 assemblies, but these networks are structured in a way that buffers the effect of interaction  
344 type shifts of single species on the community as a whole. This increased resistance of real-  
345 world networks to single species shifts compared to random assemblies wanes and is even-  
346 tually reversed as the number of shifting species increases. This indicates that the structure  
347 of real-world networks may protect these communities from small perturbations such as sin-  
348 gle species shifts, but can exacerbate the consequences of large perturbations such as multiple  
349 species shifts. This property of real-world networks might be especially relevant as the cur-  
350 rently on-going anthropogenic changes may lead to the type of large-scale perturbations to  
351 which ecological communities are particularly sensitive according to our findings.

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427 **List of Tables**

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507  $r_i = 0.4$ ,  $c_i = 1$ .

Table 1: Rank correlation (Spearman's  $\rho$ ) between the centrality measures and the distance measures in the case of single shifts within each network. Parameters:  $r_i = 0.4$ ,  $s_i = 1.5$ ,  $c_i = 1$ . A double asterisk signifies  $p < 0.01$ , a single asterisk  $p < 0.05$ .

Network	Betweenness centrality			Degree centrality		
	$\delta$	$ \Delta s $	$\Delta f$	$\delta$	$ \Delta s $	$\Delta f$
1	0.861**	0.819**	-0.626**	0.881**	0.845**	-0.652**
2	0.709**	0.658**	-0.416**	0.707**	0.658**	-0.41**
3	0.617**	0.597**	-0.445**	0.597**	0.578**	-0.422**
4	0.63**	0.609**	-0.434**	0.623**	0.6**	-0.417**
5	0.714**	0.692**	-0.535**	0.737**	0.714**	-0.557**
6	0.63**	0.617**	-0.427**	0.632**	0.62**	-0.428**
7	0.679**	0.656**	-0.427**	0.679**	0.657**	-0.423**
8	0.612**	0.6**	-0.438**	0.606**	0.594**	-0.426**
9	0.684**	0.666**	-0.465**	0.693**	0.674**	-0.47**
10	0.563*	0.564*	-0.219	0.567*	0.567*	-0.212
11	0.592**	0.55**	-0.368*	0.602**	0.564**	-0.374*
12	0.843**	0.755**	-0.749*	0.867**	0.791**	-0.788**
13	0.705**	0.684**	-0.395**	0.722**	0.698**	-0.403**
14	0.955**	0.944**	-0.908**	0.963**	0.955**	-0.912**
15	0.741**	0.688**	-0.509**	0.737**	0.686**	-0.514**
16	0.679**	0.646**	-0.484**	0.677**	0.645**	-0.472**
17	0.747**	0.743**	-0.611**	0.751**	0.746**	-0.607**
18	0.83**	0.786**	-0.747**	0.834**	0.789**	-0.749**
19	0.598**	0.593**	-0.415**	0.595**	0.59**	-0.407**

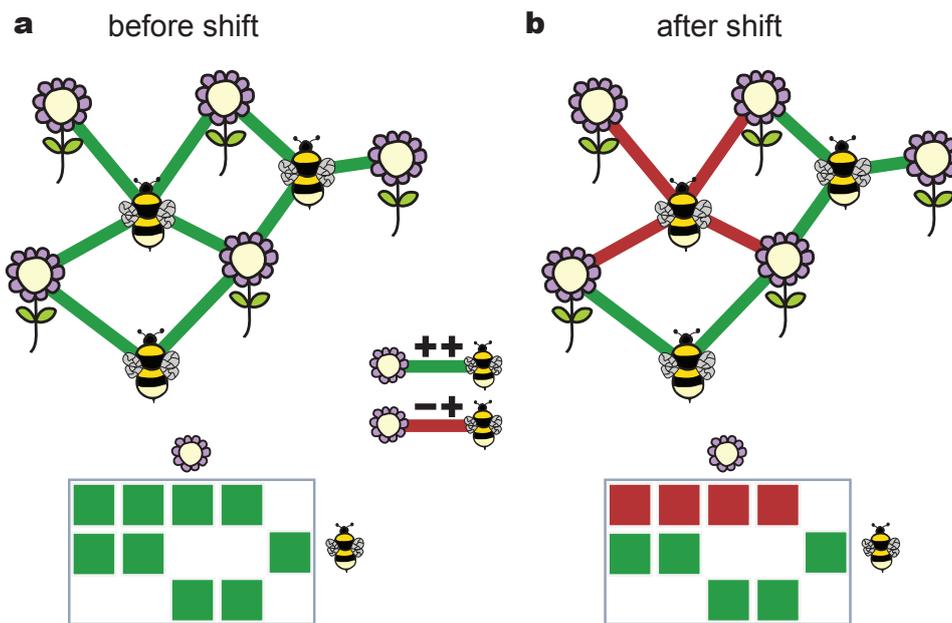


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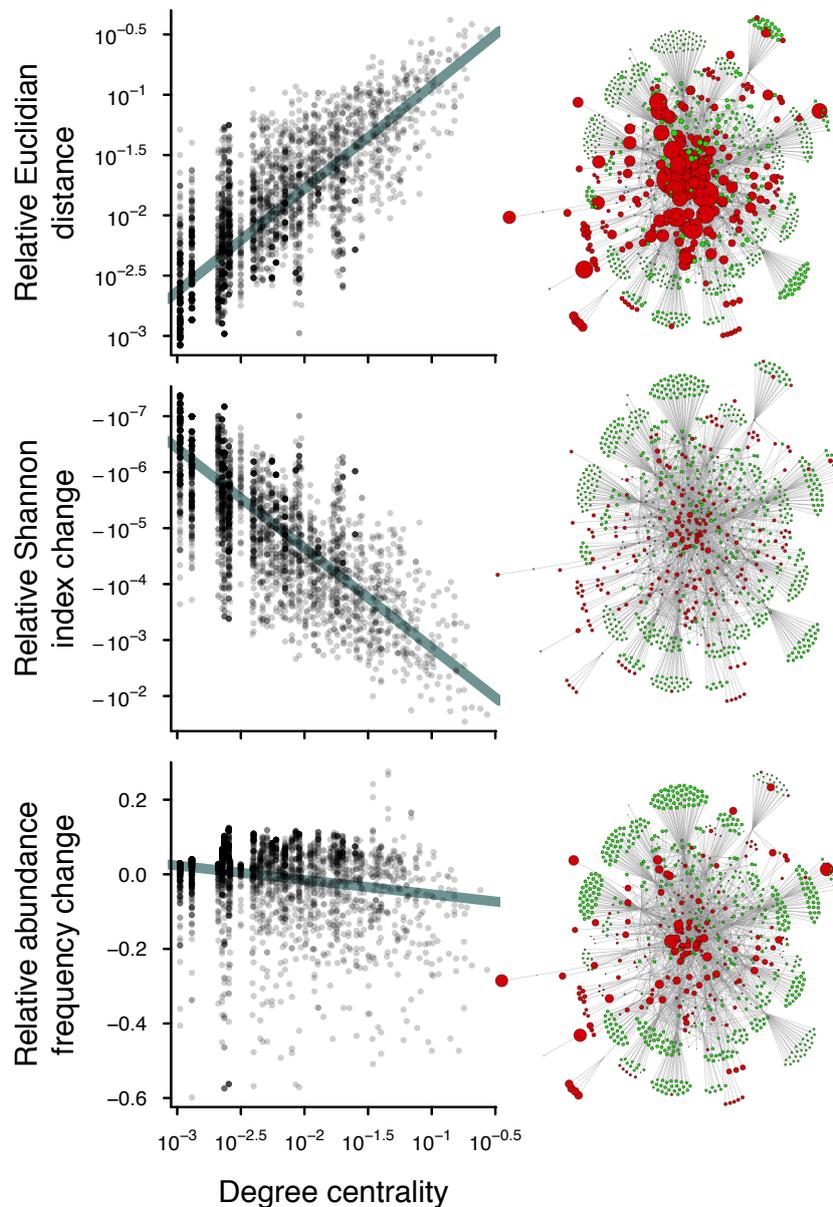


Figure 2: Effect of degree centrality on the different stability measures. Relative Euclidian distance change (top), relative Shannon index change (middle) and relative frequency change (bottom) as a function of the degree centrality of the shifting species for all networks combined. Each point represents a single shifted pollinator species. The model parameters are:  $s_i = 1.5$ ;  $r_i = 0.4$ ;  $c_i = 1$ . The networks figures to the right of the plots give a qualitative impression of the dependence of the measures on centrality for the plant-pollinator dataset from Kibune Forest, Kyoto, Japan [7, 32]. Grey nodes correspond to plant species and coloured nodes to pollinator species. Green animal species increase their relative abundance when shifting to antagonism and red species decrease their relative abundance. The size of the nodes is proportional to the magnitude of the respective measure.

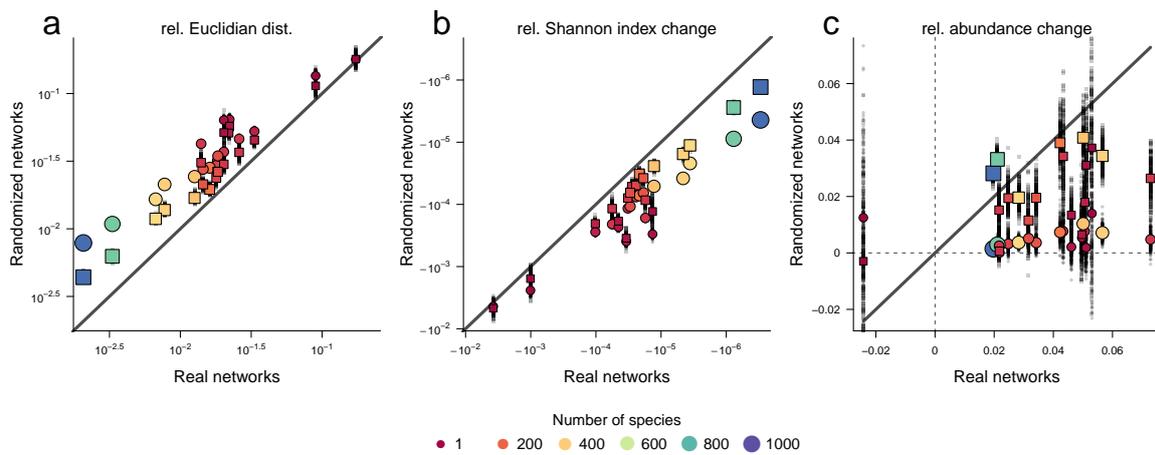


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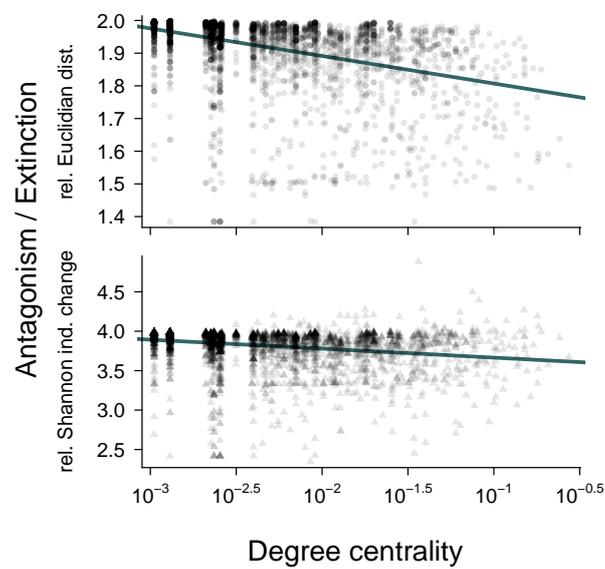


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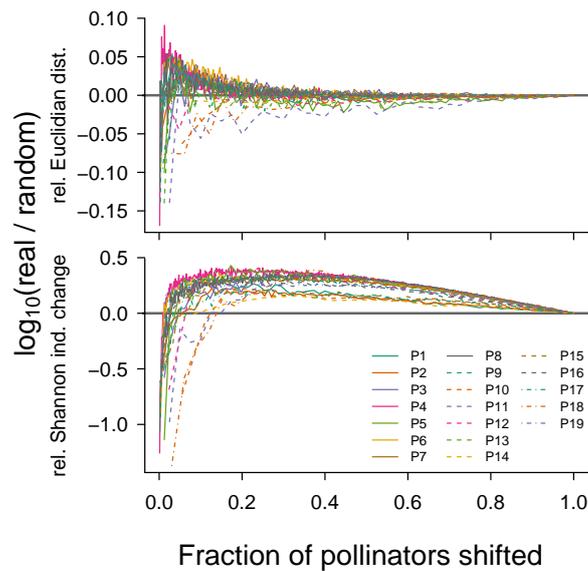


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