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16 **Abstract**

- 17 1. Understanding the processes driving ecological resilience, defined as the extent to
18 which systems retain their structure while absorbing perturbations, is a central
19 challenge for theoretical and applied ecologists. Plant-insect assemblages are well-
20 suited for the study of ecological resilience as they are species-rich and encompass
21 a variety of ecological interactions that correspond to essential ecosystem
22 functions.
- 23
- 24 2. The mechanisms affecting community response to perturbations depend on both
25 the natural history and the structure of ecological interactions. Natural history
26 attributes of interspecific interactions, *e.g.* whether they are mutualistic or
27 antagonistic, may affect ecological resilience by controlling the demographic
28 feedbacks driving ecological dynamics at the community level. Interaction
29 generalisation may also affect resilience, by defining opportunities for interaction
30 rewiring, the extent to which species are able to switch interactions in fluctuating
31 environments. These natural history attributes may also interact with network
32 structure to affect ecological resilience.
- 33
- 34 3. Using adaptive network models, we investigated the resilience of plant-pollinator
35 and plant-herbivore networks to species loss. We specifically investigated how
36 fundamental natural history differences between these systems, namely the
37 demographic consequences of the interaction and their level of generalisation –
38 mediating rewiring opportunities - affects the resilience of dynamic ecological
39 networks to extinctions. We also create a broad reference for the effect of network
40 structure on resilience using theoretical networks.

41

42 4. When network structure was static, pollination networks tended to be less resilient
43 than herbivory networks; this was is related to their high levels of nestedness and
44 the reciprocally positive feedbacks that define mutualisms, which made
45 coextinction cascades more likely and longer in plant-pollinator assemblages. When
46 considering interaction rewiring, the high generalisation and the structure of
47 pollination networks boosted their resilience to extinctions, which approached those
48 of herbivory networks. Finally, results using theoretical networks suggested that the
49 empirical structure of herbivory networks may protect them from collapse.

50

51 5. Understanding the ecological and evolutionary processes driving interaction
52 rewiring is key to understanding the resilience of plant-insect assemblages.
53 Accounting for rewiring requires ecologists to combine natural history with
54 network models that incorporate feedbacks between species abundances, traits and
55 interaction patterns. This combination will elucidate how perturbations propagate
56 at community-level, reshaping biodiversity structure and ecosystem functions.

57

58

59 **Key-words** antagonism, cascade length, coevolutionary networks, forbidden links,
60 interaction rewire, mutualistic network, robustness

61 **Introduction**

62 Ecological resilience can be defined as the ability of a system to maintain its structure,
63 functioning and internal feedbacks when absorbing perturbations (Holling, 1973, 1996).
64 Ecological interactions drive community resilience to perturbations by connecting biodiversity
65 structure with ecosystem functioning. The loss of species and interactions trigger structural
66 changes that can propagate through several trophic levels, reshaping community organisation
67 and eroding ecosystem functions (Janzen, 1974; Jordano, 2016). Assessing community
68 resilience to the loss of species and interactions can help explain how extinctions disassemble
69 the interaction structure of ecological communities and may also reveal strategies for
70 biodiversity restoration (Tylianakis et al., 2018). Plant-insect interactions are excellent model
71 systems to study the mechanisms shaping community resilience to extinctions as they
72 encompass a diversity of natural histories, which reflect their relevance for ecosystem functions
73 (Coley et al., 2006; Del-Claro et al., 1996; Requier et al., 2015; Shepherd & Chapman, 1998).

74 Networks are powerful tools to investigate how ecological communities are structured
75 and how such structures affect their resilience. Ecological networks representing different
76 interaction types show recurrent structural patterns. For instance, antagonistic networks
77 involving insect herbivores and plants are often modular, *i.e.* include sets of species that interact
78 more frequently among themselves than with other species in the assemblage (Cagnolo et al.,
79 2011; Thébault & Fontaine, 2010). On the other hand, networks depicting free-living
80 mutualisms, such as plant-pollinator interactions, are highly nested (Bascompte et al., 2003;
81 but see Olesen et al., 2007), *i.e.* present a highly connected core of generalist species to which
82 specialist species are connected. Networks' structural patterns partially result from the
83 contrasting natural history attributes of interaction types (Guimarães et al., 2007), which affect
84 their dynamics and resilience in different ways (Burgos et al., 2007; Dunne et al., 2002;
85 Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010; Vieira & Almeida-Neto, 2015).

86 Ecological networks are dynamic systems and we are only beginning to understand how
87 incorporating dynamics into network studies affects our understanding of biodiversity
88 resilience (Costa et al., 2018; Gilljam et al., 2015; Ramos-Jiliberto et al., 2012; Valdovinos et
89 al., 2016). Adaptive network models (ANMs) are a class of dynamic models that can account
90 for two naturally observable sources of ecological community dynamics: the local dynamics of
91 species' abundances over time, and topological dynamics, referring to alterations in network
92 structure that result from changes in species composition and interaction switches, hereafter
93 referred to as rewiring (Gross & Blasius, 2008). In ANMs there is feedback between these two
94 in-built sources of dynamics, allowing us to investigate how the contrasting dynamical
95 properties of different plant-insect systems affect their resilience.

96 Mutualisms and antagonisms have contrasting demographic effects that could modulate
97 the long-term persistence of community structure in different ways. These population-level
98 feedbacks that result from interactions are a fundamental natural history attribute potentially
99 affecting the resilience of these systems (Thébault & Fontaine, 2010). In mutualisms, such as
100 pollination, species exploit each other with reciprocal net fitness benefits. The reciprocity of
101 mutualisms may increase the probability and length of extinction cascades because plant
102 population declines would lead to declines in pollinators, leading to further declines in plants
103 (Vieira & Almeida-Neto, 2015). In herbivory, however, as only herbivores benefit from the
104 interaction, plant declines would lead to herbivore declines, but not the inverse, constraining
105 the frequency and length of extinction cascades. Such contrasting population feedbacks are
106 therefore likely key determinants of plant-insect network persistence (Thébault & Fontaine,
107 2010) and hence resilience (Holling, 1973).

108 Species abundances continuously affect and are affected by species interactions (Poisot
109 et al., 2015). Interaction rewiring is widespread in free-living mutualisms, such as pollination
110 (Kaiser-Bunbury et al., 2010), given their high levels of generalisation that lead to flexibility

111 in interaction partners (Bascompte & Jordano, 2013). Interaction rewiring between plants and
112 pollinators occurs over time (CaraDonna et al., 2017) and space (Carstensen et al., 2014;
113 Trøjelsgaard et al., 2015), both as a consequence of, or despite, changes in species abundances
114 (Carstensen et al., 2014; MacLeod et al., 2016; Trøjelsgaard et al., 2015). In contrast, whilst
115 rewiring occurs in plant-herbivore interactions (Auerbach & Simberloff, 1988; Murphy &
116 Feeny, 2006), host switches are often phylogenetically constrained involving mostly
117 congeneric plant species (Novotny & Basset, 2005; but see Agosta, 2006). Difference in the
118 pervasiveness of interaction rewiring between pollination and herbivory systems could result
119 from their distinct levels of generalisation – which is embedded on the structure of these
120 networks (Fontaine et al., 2009), as plant defences impose selection on herbivores favouring
121 specialisation (Thompson, 2005).

122 We combine ANMs and empirical network data to investigate how three properties that
123 differ between pollination and herbivory networks – their network structure (Objective 1),
124 demographic feedbacks (Objective 2), and levels of generalisation (Objective 3) - affect their
125 resilience to species loss. Network robustness is an easy to interpret metric (Memmott et al.,
126 2004), that quantifies how structurally resilient, *i.e.* able to maintain its structure and structuring
127 feedbacks (Holling, 1973; Walker et al., 2004), ecological networks are to the loss of species.
128 We predict that the reciprocally positive demographic feedbacks between plant and insect
129 populations in pollination networks will result in longer and more frequent coextinction
130 cascades in pollination than in herbivory networks, reducing their resilience. We also predict
131 rewiring opportunities to be more limited in herbivory, as a result of their high degree of
132 specialisation, reducing their resilience. Finally, we investigate how the structure of plant-
133 insect networks interacts with population feedbacks and rewiring opportunities to affect
134 network resilience. We complement our analysis with theoretical networks to deepen our
135 understanding on the relationship between network structure and resilience. By accounting for

136 the dynamic nature of ecological systems, and by systematically controlling for the effect of
137 network structure, demographic feedbacks and interaction generalisation, we hope to shed light
138 on how these processes interact to affect the resilience of plant-insect systems to species loss.

139

140 **Material and methods**

141 We first describe our simulation procedure and model - specifically, how the ANM
142 incorporates local and topological dynamics. We then present our network dataset, composed
143 of empirical and theoretical networks, simulation scenarios and statistical analyses.

144

145 *Simulation overview*

146 We simulate coextinction cascades following primary extinctions of one randomly removed
147 plant species (Fig. 1). One cascade encompasses all secondary extinctions following a primary
148 extinction, including species from both trophic levels. We removed plants as primary
149 extinctions because plants positively affect insect populations in both pollination and herbivory
150 systems, while the inverse is not true, facilitating the comparison of network collapse between
151 interaction types. Following a primary extinction (Fig. 1; steps I and II), insect species
152 interacting with the extinct plant have the opportunity to rewire their interactions (step III; see
153 *Rewiring algorithm – Topological dynamics*). After changes in network structure due to species
154 loss and rewiring, species abundances are recomputed (numerically solving equation 1, see
155 below) and coextinctions recorded (steps IV and V). Coextinctions can either be abundance-
156 related when abundances approach zero – emulating the process by which rare species are at a
157 higher extinction risk (Pimm et al., 1988) - or interaction-related when species are no longer
158 linked to other species in the network mimicking most models of network robustness. Plants in
159 herbivory networks can remain in the system even if disconnected. We used simulated
160 abundance data (see *Model – Local dynamics*) allowing us to compare two study systems that

161 differ in sampling methods and therefore interaction frequencies, by isolating the elements
162 under investigation: network structure, demographic feedbacks and interaction generalisation.
163 Coextinctions are treated similarly to primary extinctions: the secondary extinction of a plant
164 (step II), gives the insects feeding on that plant the opportunity of rewiring. If insects are lost
165 (step VI), plants do not rewire as rewiring is a direct result of insects' behavioural change.
166 Species abundances are recalculated after changes in network structure and further
167 coextinctions are computed. Coextinction cascades end when (co)extinctions lead to no further
168 coextinctions, and a new cascade starts.

169

170 *Model – Local dynamics*

171 We use the model developed by Suweis et al. (2013). Interaction networks and matrices (\mathbf{M})
172 are interchangeable structures. In \mathbf{M} , a matrix corresponding to a bipartite network, each animal
173 species, $A = \{A_1, A_2, A_3 \dots A_{SA}\}$, is a row, each plant species, $P = \{P_1, P_2, P_3 \dots P_{SP}\}$ is a column
174 and $m_{ij} = 1$ when insect i and plant j interact, and $m_{ij} = 0$ otherwise. Species richness in the
175 network is $SM = SA + SP$, where SA and SP are insect and plant richness. At the beginning of
176 each simulation run, we randomly sampled species abundances from a lognormal distribution
177 with mean $\mu = 1$ and standard deviation $\sigma = 1$ (different σ values do not qualitatively affect
178 results, Fig. S1). Coupling species abundances with network structure – *i.e.* distributing species
179 abundances in accordance with their number of interactions – produces similar results
180 (Supplementary Material). A random sample of 100,000 abundance values ranged from 0.039
181 to 173.68, while abundance-related coextinctions happened if values reached 0.001 or lower
182 values. During simulation, species abundances are an outcome of interactions established with
183 other species. In pollination networks, plants and animals are positively affected by
184 interactions, whereas in herbivory networks only animals benefit, and plants are negatively

185 affected by animals. The population dynamics of species i can be described as a function of the
 186 per capita effects of ecological interactions on its abundance x_i :

$$187 \quad \frac{dx_i}{dt} = x_i \left(a_i + \sum_j^{SM} \mathbf{T}_{ij} x_j \right) \quad \text{eqn 1}$$

188 where a_i describes the intrinsic growth rate of species i in the absence of interactions, \mathbf{T}_{ij}
 189 represents the effects of species j on i , and x_j is the abundance of species j . We assumed a type
 190 I functional response for both interaction types.

191 Matrix \mathbf{T} of dimensions $SM \times SM$, stores information on the per capita effects of each
 192 interaction on species abundances (\mathbf{T}_{ij} in equation 1):

$$193 \quad \mathbf{T} = \begin{bmatrix} \mathbf{\Omega}_{AA} & \mathbf{\Gamma}_{AP} \\ \mathbf{\Gamma}_{PA} & \mathbf{\Omega}_{PP} \end{bmatrix} = \begin{bmatrix} d & \omega_{1,2} & \cdots & \omega_{1,S_A} & \gamma_{1,S_A+1} & \cdots & \cdots & \gamma_{1,S_M} \\ \omega_{2,1} & d & \cdots & \cdots & \gamma_{2,S_A+1} & \cdots & \cdots & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \omega_{S_A,1} & \vdots & \cdots & d & \gamma_{S_A,S_A+1} & \cdots & \cdots & \gamma_{S_A,S_M} \\ \gamma_{S_A+1,1} & \cdots & \cdots & \cdots & d & \omega_{S_A+1,S_A+2} & \cdots & \omega_{S_A+1,S_M} \\ \gamma_{S_A+2,1} & \cdots & \cdots & \cdots & \cdots & d & \cdots & \omega_{S_A+2,S_M} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \gamma_{S_M,1} & \cdots & \cdots & \cdots & \omega_{S_M,S_A+1} & \cdots & \cdots & d \end{bmatrix} \quad \text{eqn 2}$$

194 where $\mathbf{\Gamma}_{AP}$ and $\mathbf{\Gamma}_{PA}$ describe the per capita effects of pollination or herbivory on species
 195 abundances, and $\mathbf{\Omega}_{AA}$ and $\mathbf{\Omega}_{PP}$ summarise the per capita effects of competition. Diagonal
 196 elements represent intraspecific competition, $d_{ii} = -1$. $\mathbf{\Gamma}_{AP}$ is built from \mathbf{M} : considering a pair
 197 of species $i \{i \in A\}$ and $j \{j \in P\}$ that interact ($m_{ij} = 1$), if the effect of j on the abundance of i is
 198 positive, $\gamma_{ij} \sim |\mathcal{N}(\mu, \sigma)|$; if it is negative, $\gamma_{ij} \sim -|\mathcal{N}(\mu, \sigma)|$; where $\mathcal{N}(\mu, \sigma)$ is a normal distribution
 199 ($\mu = 0, \sigma = 0.1$). Within $\mathbf{\Gamma}_{PA}$, the effect of species i on the abundance of j is defined by a different
 200 number: $\gamma_{ji} \sim |\mathcal{N}(\mu, \sigma)|$ if the effect of the interaction is positive and $\gamma_{ji} \sim -|\mathcal{N}(\mu, \sigma)|$ if it is
 201 negative. Therefore, pollination is symmetrical regarding its sign, but not its value (Bascompte
 202 & Jordano, 2013), whilst herbivory is asymmetric in sign and value. Both $\mathbf{\Omega}_{AA}$ and $\mathbf{\Omega}_{PP}$ were
 203 set to zero, assuming there is no interspecific competition (see Appendix S1 for scenarios
 204 incorporating competition). Species intrinsic growth rates were defined at the beginning of

205 each simulation as $\vec{a} = \mathbf{T} \cdot \vec{x}$, assuming negative values for all groups but for plants in
206 herbivory networks (Thébault & Fontaine, 2010).

207

208 *Rewiring algorithm – Topological dynamics*

209 Rewiring opportunities are defined by a matrix of forbidden links, \mathbf{R} , calculated from \mathbf{M} . At
210 the beginning of each simulation, we calculated the Jaccard similarity of interactions between
211 all networks' insect pairs. As interactions are partly determined by species attributes such as
212 morphology, physiology and phenology (Cipollini & Peterson, 2018; Cornell & Hawkins,
213 2003; Olesen et al., 2011; Stang et al., 2006), we assume that species with high interaction
214 similarity are likely to share those attributes and, therefore, to establish similar interactions.
215 Thus, we used the interaction similarity of insect pairs, as the probability each insect in the pair
216 had of mimicking the interactions of the other (Fig. 2a). With increasing similarity, mimicking
217 probability increases, but the number of interactions to be mimicked - not shared by both
218 species - decreases. Given the higher level of specialisation in herbivory compared to
219 pollination networks, we expect a lower interaction overlap in herbivory networks, thus
220 reducing the probability of interaction mimicking (Fig. 2a). Therefore, \mathbf{R} incorporates the
221 differences in generalisation between pollination and herbivory networks.

222 Rewiring occurs as a two-step process (Ramos-Jiliberto et al., 2012): step 1 determines
223 which of the insects that lost a resource will rewire and step 2 determines to which plant species
224 each insect will rewire. The rewiring probability of insect species i (Step 1, Fig. 2b) was
225 calculated as $P_i = 1 - n_i$, where n_i is the abundance of i 's resources. Insects' resource
226 abundances were normalised to range between 0 and 1. As a result, rewiring probability was
227 inversely proportional to each insect's resource abundance: insects with the highest resource
228 abundance never rewire ($P_i = 1 - 1 = 0$), insects which lost their last resource ($P_i = 1 - 0 = 1$)
229 always rewire, and insects with intermediate resource abundances have an intermediate

230 probability of rewiring. Selected insects rewire to a new plant species (Step 2) in proportion to
231 plants' abundances and respecting **R**.

232

233 *Network datasets*

234 We compiled pollination networks from the Interaction Web Database and the Web of
235 Life. Herbivory networks were compiled from previous studies (Fontaine et al., 2009; Fontaine
236 & Thébault, 2015; Pires & Guimarães, 2013), and networks of both interaction types were
237 obtained from original papers. We excluded networks: i) in which animal species were not
238 insects, as we focus on plant-insect systems, ii) that were from the same interaction type and
239 author, to use independent networks, and iii) which were collected over more than two years
240 or across large spatial scales (*e.g.* the whole country), so that our networks represent observable
241 ecological communities in which co-occurrence between species is likely and our rewiring
242 assumptions valid. This resulted in 26 pollination and 19 herbivory networks (Table S1). We
243 used binary interaction data as we are comparing systems which are likely to vary in species
244 abundances, detectability and data collection methods (Dáttilo et al., 2016). We characterised
245 four network-level structural attributes of empirical networks: i) species richness; ii)
246 connectance,; iii) nestedness; and iv) modularity (see Appendix S1.1 for details).

247 We created two additional network collections as references, to which we refer as *null*
248 and *theoretical* datasets. These distinct datasets provide complementary references for the
249 effect of network structure, and for its interaction with population feedbacks and rewiring, on
250 resilience. Null networks serve as a specific reference for our empirical dataset, by keeping the
251 variation in network size, proportion of species in both interacting sets and connectance of our
252 empirical dataset, while lacking its network-level structural patterns, such as nestedness and
253 modularity. We generated 100 null networks for each empirical network using a null model in
254 which interactions are distributed in proportion to species degree, *i.e.* number of interaction

255 partners (null model 2; Bascompte et al., 2003). The resulting null networks therefore, serve as
256 a “control” for the empirical dataset.

257 Complementarily, theoretical networks act as a broader reference on how network
258 structure affects resilience, providing a benchmark for the effects of network structure on
259 resilience for any type of ecological network regardless of its structural properties. Because in
260 empirical networks structural patterns such as nestedness and modularity may coexist (Fortuna,
261 Lewinsohn, Valverde), and empirical networks may present sampling issues, we created
262 theoretical networks using models which favour a single pattern: nestedness, modularity or
263 none of the two, hereafter called random networks. For each of these patterns we created a set
264 of *even* and *uneven* networks, *i.e.* with equal and differing numbers of “plant” and “insect”
265 nodes, resulting in six sets of theoretical networks’ with 100 networks each (see Appendix S1.2
266 for more information).

267

268 *Simulations scenarios*

269 To elucidate how population feedbacks, generalisation through rewiring opportunities and
270 network structure affect the resilience of pollination and herbivory networks, we ran twelve
271 simulation scenarios using the empirical and null datasets (Table 1). We ran simulations on
272 empirical networks in half of these scenarios (100 simulation runs per network per simulation
273 scenario), and on null networks in the remaining scenarios.

274 To investigate how differences in network structure between pollination and herbivory
275 networks affect their resilience (Objective 1), we compare scenarios using empirical networks
276 with scenarios using null networks (S1 to S4, Table 1), in all of which insects did not rewire.
277 To investigate the effect of population feedbacks (Objective 2), we compare the first four
278 scenarios with four new scenarios (S5 to S8, Table 1): equivalent to the first four but in which
279 population feedbacks were switched between the two interaction types, *i.e.* pollination

280 networks were treated as antagonistic, and herbivory networks as mutualistic. To explore the
281 effect of generalisation on rewiring opportunities (Objective 3), the last four scenarios were
282 equivalent to the first four, but insects were allowed to rewire (S9 to S12, Table 1).
283 Additionally, we ran a total of 24 theoretical scenarios: for each of the six sets of theoretical
284 networks we ran four scenarios - two mutualistic and two antagonistic, with and without
285 rewiring.

286 For all simulation scenarios, we calculated the network robustness, a measure of
287 structural resilience, using the *bipartite* R package (Dormann et al., 2008; R Core Team, 2017).
288 The robustness metric is based on the attack tolerance curve, which describes the percentage
289 of species remaining in the network following sequential primary extinctions. We calculated
290 additional resilience measures for empirical scenarios S1 to S8: (i) the probability of
291 abundance-related secondary extinctions, *i.e.* the number of abundance-related secondary
292 extinctions as a proportion of all secondary extinctions; (ii) the average length of coextinction
293 cascades; (iii) the probability of coextinction cascades, *i.e.* a primary extinction leading to at
294 least one secondary extinction; and (iv) the probability of a long coextinction cascade, *i.e.* a
295 primary extinction leading to at a cascade of length three or more. The loss of plant species is
296 likely to lead to coextinctions of insects (cascades of length two) in networks of both interaction
297 types, while further coextinctions (length three or more) reveal whether cascades continue to
298 propagate across both trophic levels. We expect long cascades to be more common in
299 pollination than in herbivory networks.

300

301 *Statistical analysis*

302 We investigated the effect of network structure on robustness using simulation results of S1 to
303 S4 (Table 1) and a linear mixed-effects model (LMM), with robustness as the response
304 variable, and structure (empirical vs null), interaction type (pollination vs herbivory) and their

305 interaction as fixed effects. We then tested whether species richness, connectance, nestedness
306 and modularity were associated with network robustness. These linear models had the
307 robustness ratio between empirical and null networks as the response variable, and network
308 metric, interaction type, and their interaction as explanatory variables. The robustness ratio
309 should reveal if a particular network structure is associated with increases (ratio > 1) or
310 decreases (ratio < 1) in robustness.

311 Using S1 to S8 we investigated the effect of population feedbacks, and its interaction
312 with network structure, on network robustness. With LMMs, we compared the robustness of
313 empirical and null networks of both interaction types (S1-S4) with their robustness when
314 pollination networks were treated as antagonistic, and herbivory as mutualistic (S5-S8). Since
315 we expect the reciprocally positive population feedbacks of mutualisms to cause longer and
316 frequent coextinction cascades, we expect the robustness of pollination networks to increase
317 with reversed feedbacks, and the robustness of herbivory networks to decrease. The two models
318 (one per interaction type) had robustness as response variable, and structure (empirical vs null),
319 population feedbacks (original or reversed), and their interaction as fixed effects. We also
320 looked at the (i) probability of abundance-related secondary extinctions, and the (ii) length and
321 (iii and iv) probability of coextinction cascades. The eight LMMs (four response variables, two
322 interaction types) had structure (empirical or null), population feedbacks (original or reversed),
323 and their interaction as fixed effects. The (i) probability of abundance-related secondary
324 extinctions and (iii) of coextinction cascades was logit transformed.

325 To understand how differences in generalisation and rewiring opportunities interact
326 with network structure to affect network robustness, we used one LMM. The response variable
327 was the ratio between robustness in scenarios with (S9-S12) and without (S1-S4) rewiring.
328 Ratios larger than one indicate that robustness increased with rewiring. Network structure

329 (empirical or null), interaction type (pollination or herbivory), and their interaction were the
330 fixed effects.

331 In all analyses, we used the Akaike Information Criteria (AIC) to select between (i) no
332 random structure and (ii) network identity as a random effect (following Zuur et al., 2009), and
333 the *emmeans* R package (Lenth, 2018) to perform *a posteriori* Tukey tests. For theoretical
334 scenarios, we followed a similar statistical approach (see Appendix S1.3 for details).

335

336 **Results**

337 Pollination networks had 136 species on average (min = 18, max = 451, median = 78), while
338 herbivory networks had 98.5 (min = 17, max = 655, median = 58; Table S1). Species richness
339 ($t=0.93$, $df=36.9$, $p=0.36$) and connectance ($t=0.37$, $df=32.4$, $p=0.71$) were not significantly
340 different in pollination and herbivory networks (Figs S2a-b). Nestedness was more common
341 than modularity in both network types, as 15.8% (3 out of 19) of herbivory and 11.5% (3 out
342 of 26) of pollination networks were significantly modular, while 68.4% (13 out of 19) of
343 herbivory and all pollination networks were significantly nested. Pollination networks were
344 more nested than herbivory networks ($t=2.99$, $df=42.8$, $p<0.01$), while both network types had
345 similar modularity (Figs S2c-d; $t=1.31$, $df=31.1$, $p=0.2$).

346 The structure of empirical networks had a negative effect on their robustness (Fig. 3;
347 $t=4.35$, $df=43$, $p<0.001$) as null networks had higher robustness than their empirical
348 counterparts. The final model included network identity as a random effect. The negative effect
349 of network structure on robustness, however, was only statistically significant for pollination
350 networks (Fig. 3a; $p<0.001$). The negative effect of empirical network structure on robustness
351 seems to be mainly associated with nestedness (Fig. S3) since with increasing nestedness (z -
352 scored) networks were less robust ($F_{(3,41)}=34.63$, $p<0.001$), especially pollination networks
353 (Fig. S3c; $t=3.78$, $p<0.001$). Nestedness decreased during network collapse similarly across

354 scenarios (Fig. S4), while network fragmentation in components remained constant (Fig. S5).
355 Simulations with theoretical networks reinforced the findings of empirical networks: nested
356 networks always had lower robustness than random or modular networks (Fig. 4a). The
357 interaction between network structure (random, nested or modular) and population feedbacks
358 (mutualistic and antagonistic) was statistically significant (even: L-ratio=815.8, $p<0.001$;
359 uneven: L-ratio=604.9, $p<0.001$; Fig. 4a). Nestedness had a negative effect on the robustness
360 of even and uneven networks with mutualistic and antagonistic population feedbacks ($p<0.001$
361 in every comparison). Modularity often had a small positive effect on network robustness, for
362 mutualistic ($p<0.001$ for all comparisons) and antagonistic networks ($p<0.001$ for most
363 comparisons).

364 Switching population feedbacks of empirical networks, significantly increased the
365 robustness of pollination networks (Fig. 3a; $t=3.29$, $df=75$, $p=0.001$), of both empirical
366 ($p<0.001$) and null networks ($p=0.03$). Accordingly, treating herbivory networks as mutualistic
367 had a negative effect on network robustness (Fig. 3b; $t=4.3$, $p<0.001$), similar for empirical and
368 null networks ($p<0.001$). Network identity was selected as a random effect only on the
369 pollination model. Theoretical scenarios support our empirical results, showing that even and
370 uneven networks with antagonistic population feedbacks are more robust than mutualistic
371 networks of any structure ($p<0.001$; Fig 4a).

372 Extinction cascades in empirical networks highly depended on population feedbacks
373 (Table S2, Fig. S6), since abundance-related extinctions were more common in pollination
374 networks treated as mutualistic (P-M) than in pollination networks treated as antagonistic (P-
375 A; Fig. S6a). Coextinctions cascades were also longer in P-M than in P-A (Fig. S6c), and long
376 cascades were also much more likely in P-M than P-A (Fig. S6g). Similarly, for herbivory
377 networks, cascades were longer when networks were treated as mutualistic (H-M) than when
378 treated as antagonistic (HA; Fig. S6d), and the probability of coextinction cascades of any

379 length was higher in H-M than H-A (Figs S6f, h). Coextinction cascades continued to be longer
380 in mutualistic networks even when competition for resources - to balance potential competitive
381 effects between herbivore insects - is included in pollination systems (Appendix S2).

382 Allowing insects to rewire, increased the robustness of empirical and null networks of
383 both interaction types (Fig. 5; $t=2.95$, $df=43$, $p<0.01$). The largest observed increase was for
384 empirical pollination networks ($27\% \pm 20$, mean \pm SD, $min=4\%$, $max=74\%$), followed by null
385 pollination networks ($13\% \pm 5$, mean \pm SD, $min=7\%$, $max=28\%$), and herbivory networks
386 (empirical: $4\% \pm 4$, mean \pm SD, $min=-4\%$, $max=11\%$, null: $2\% \pm 4$, mean \pm SD, $min=-11\%$,
387 $max=6\%$). Network structure had a significant effect on pollination networks, since empirical
388 networks benefited more from rewiring than null networks ($p<0.001$), but it had no effect on
389 herbivory networks ($p=0.88$). Empirical pollination networks also benefited more from
390 rewiring opportunities than empirical herbivory networks ($p<0.001$). Only one empirical and
391 two null herbivory networks had lower robustness when herbivores were allowed to rewire.

392 The effect of adding rewiring to theoretical networks depended on the interaction
393 between network structure and interaction type (even: L-ratio=661.19, $p<0.001$; uneven: L-
394 ratio=563.33, $p<0.001$). Interaction rewiring homogenised robustness across network structure
395 and interaction type scenarios (Fig. 4b), strongly benefiting mutualistic networks (Fig. 6),
396 especially with nested structures ($p<0.001$ for all comparisons). On the other hand, interaction
397 rewiring consistently had a small negative effect on antagonistic networks (Fig. 6). Rewiring
398 slightly decreased the robustness of 89.7% of antagonistic networks: the only 62 antagonistic
399 networks (out of 600) which benefited from rewiring were mostly nested (32 even, 14 uneven),
400 followed by random (7 even, 2 uneven) and modular (4 even, 3 uneven). Tukey results suggest
401 that the effect of network structure on the robustness of antagonistic networks was small: with
402 the exception of nested networks which had higher ratios than modular ($p<0.01$) and random

403 networks ($p < 0.05$) in even scenarios, there was no difference between random and modular
404 even networks ($p = 0.99$), or between uneven networks with any structure (all $p > 0.05$).

405

406 **Discussion**

407 We presented a link between the natural history of two plant-insect systems and the processes
408 that shape their network resilience. We combined the ecological resilience concept (Holling,
409 1973, 1996; Walker et al., 2004) with adaptive network models, to investigate three potential
410 drivers of community resilience to species extinctions. We did this while systematically
411 controlling for the effects of network structure and the type of demographic feedbacks on
412 robustness, a proxy for resilience to extinctions. When species are not allowed to rewire
413 interactions, network structure negatively affects robustness. The higher levels of nestedness
414 observed in our pollination dataset could be a key determinant of their lower resilience,
415 challenging previous results showing that nestedness facilitates biodiversity persistence
416 (Bastolla et al., 2009; Memmott et al., 2004; Rohr et al., 2014; Thébault & Fontaine, 2010).
417 Further, we found that the demographic effects of mutualisms also reduce the resilience of
418 pollination networks, which undergo longer and more frequent extinction cascades. Finally,
419 interaction rewiring enhances network resilience, especially in pollination systems, suggesting
420 that the extent of a system's interaction flexibility is another key determinant of its resilience
421 to extinctions. Our analyses were strengthened by the use of theoretical networks with
422 controlled structures, which indicate the generality of our findings, but also presented new
423 insights.

424 Our results on theoretical networks support our empirical finding that highly nested
425 networks are less robust than networks with alternative structures. Besides challenging the
426 notion that nestedness promotes biodiversity persistence (Bastolla et al., 2009; Memmott et al.,
427 2004; Rohr et al., 2014; Thébault & Fontaine, 2010; but see Santamaría et al., 2016), our results

428 contribute to the pivotal debate on the relationship between network structure and dynamics
429 (Landi et al., 2018), reinforcing the idea that the positive effect of nestedness on robustness
430 only holds under specific extinction scenarios (Burgos et al., 2007). The diverse set of
431 resilience concepts and their corresponding operational proxies used in ecology could explain
432 the contrasting results presented by studies using network robustness and alternative measures.
433 Nested networks are very sensitive to attacks on generalists (Burgos et al., 2007) and, in
434 robustness analysis, even when randomly targeting species to suffer extinctions, generalists are
435 indirectly affected due to the high level of interaction asymmetry of nested networks (Silva et
436 al., 2007). Therefore, in a scenario of species extinctions and of static topology, nestedness
437 facilitates network collapse, especially of mutualistic networks.

438 Incorporating interaction rewiring led to a higher increase in the robustness of
439 pollination when compared to herbivory networks, as expected from the high level of
440 generalisation – and hence flexibility - of pollination systems (Fontaine et al., 2009; Waser,
441 1986). When species switched interactions, the robustness of pollination networks approached
442 those of herbivory networks. Our empirical results support the notion that interaction rewiring
443 generally has positive effects on network persistence (Gilljam et al., 2015; Ramos-Jiliberto et
444 al., 2012; Valdovinos et al., 2013, 2016). The strong positive effect of rewiring on the resilience
445 of pollination networks likely arises from its positive fitness consequences for mutualist
446 species, which without further adaptations can often rapidly readjust to the most abundant
447 partners (Janzen, 1985). The higher increase in robustness in pollination networks stems from
448 their high generalisation level as well from their high nestedness, as the increase was larger in
449 empirical than in null pollination networks. The structure of nested networks – an interaction
450 core held by generalists working as an umbrella for specialists' interactions - provides the
451 conditions for the continuous adaptive switching of interactions. Importantly, the positive
452 effect of rewiring on robustness also holds for mutualistic theoretical networks especially with

453 nested structures, but not for theoretical antagonistic networks of any structure. This interesting
454 result suggests that the combination of different structural patterns within herbivory networks
455 may act as a buffer to extinctions. This insight could only have arisen from our combined use
456 of empirical and theoretical networks, a combination which should be carefully considered in
457 future network modelling studies.

458 Switching population feedbacks – i.e., treating pollination as antagonistic and vice-
459 versa – increased the robustness of pollination networks and decreased the robustness of
460 herbivory networks. Theoretical networks support this result, since antagonistic networks were
461 consistently more robust than mutualistic, regardless of network structure. Although this result
462 leads to the conclusion that mutualisms have a negative effect on resilience, in nature, the
463 negative effect of such cascading events may be counterbalanced by other interaction types
464 that influence the demographic dynamics at the community scale (Dáttilo et al., 2016; Sauve
465 et al., 2014). Our results on the frequency and length of extinction cascades reveal that the
466 robustness of systems treated as mutualistic decreases due to the presence of longer extinction
467 cascades, which ricochet between trophic levels. An important question is whether our results
468 are robust to other functional responses. At this point, we can say that assuming a Type I
469 functional response, pollination networks collapse faster due to frequent and longer and
470 extinction cascades than herbivory networks. Most studies looking at network robustness focus
471 on how species in one set (*e.g.* insects) respond to the loss of species on the other set (*e.g.*
472 plants; Traveset et al., 2017; Vieira & Almeida-Neto, 2015). By constraining coextinctions in
473 our modelling frameworks we may be missing these realistic scenarios of horizontal extinction
474 cascades (Sanders et al., 2013).

475 Adaptive network models can promote theoretical integration by accounting for
476 dynamics at population and community levels, and the structuring feedbacks between species
477 abundances, traits and interactions (Gross & Sayama, 2009; Poisot et al., 2015; Raimundo et

478 al., 2018). We chose a resilience concept - the persistence of community structure and its
479 structuring feedbacks (Holling, 1973; Walker et al., 2004) - that fits the ANM rationale and
480 allows the use of network robustness to describe how ecological resilience is affected by
481 extinctions. To date, ANMs and the effect of interaction rewiring on the dynamics and
482 robustness of networks have been mostly applied to pollination systems (CaraDonna et al.,
483 2017; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2016) or to generalised antagonistic
484 systems such as food webs (Curtisdotter et al., 2011; Gilljam et al., 2015). Importantly,
485 interaction rewiring is pervasive in nature and is not restricted to species that lose interaction
486 partners (CaraDonna et al., 2017; MacLeod et al., 2016). Instead, it happens by a variety of
487 mechanisms, and can be more or less phylogenetically constrained across biological systems
488 (Raimundo et al., 2018). Different mechanisms and timescales of interaction rewiring should
489 be included in future resilience studies.

490 Ecological theory posits that topology, interaction type, specialisation of target species,
491 and interaction rewiring affect the resilience of ecological networks (Mariani et al., 2019), but
492 simulation studies that systematically control for the effects of each mechanism remain scarce.
493 We sought to untangle the effect of three different interaction attributes on the robustness of
494 ecological networks. Combining natural history information on plant-insect systems with
495 adaptive network models, will help ecologists to apply community ecology theory to
496 conservation and restoration in predictive ways (Raimundo et al., 2018).

497

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503

504 **Authors' Contributions**

505 KPM and RLGR conceived the study; KPM, RLGR and FMDM developed and/or checked the
506 code; KPM and IPV analysed the data; KPM, JM and RLGR led the writing of the manuscript.

507 All authors contributed critically to the drafts and gave final approval for publication.

508

509 **Data Availability Statement**

510 Networks, listed at the Supporting Information, are available at the Interaction Web Database
511 (<https://www.nceas.ucsb.edu/interactionweb/>) and the Web of Life ([http://www.web-of-](http://www.web-of-life.es/)
512 [life.es/](http://www.web-of-life.es/)). EK Del-Val kindly provided network H17 (Table S1).

513

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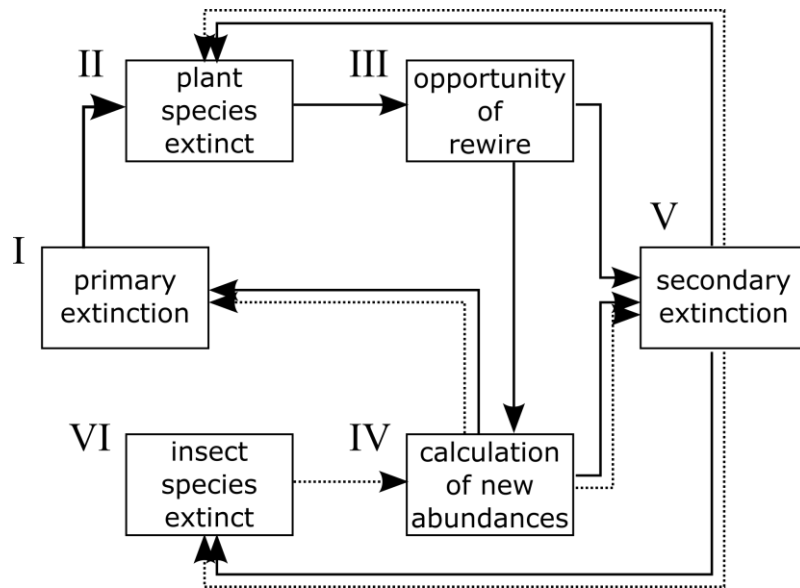
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720 **Tables and Figures**

721 **Table 1.** Simulation scenarios of empirical and null networks: network interaction type
 722 (pollination or herbivory), structure (empirical or null), population feedbacks (original or
 723 reversed), and interaction rewiring (on or off). Objectives for which scenarios were used (Ob1,
 724 Ob2 and Ob3) are marked with an X. For theoretical scenarios, refer to Supplementary
 725 Information.

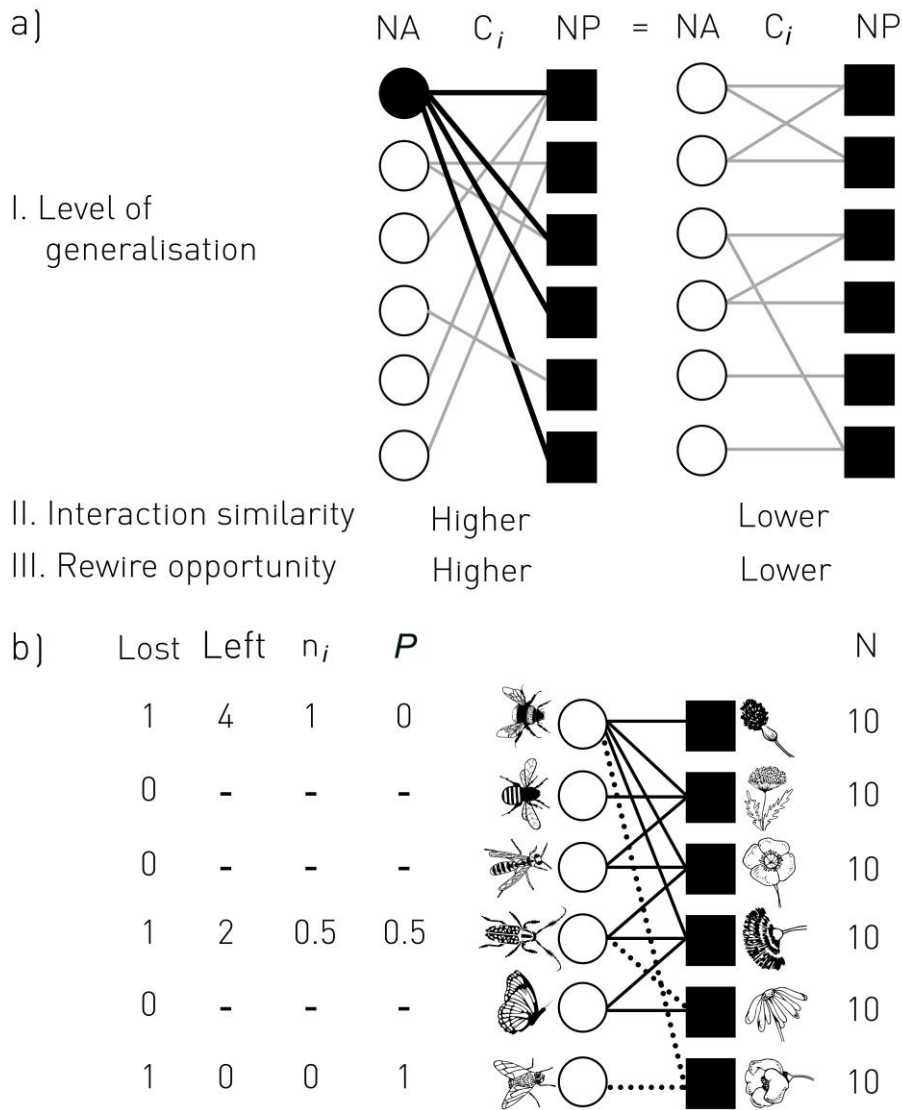
Scenario	Type	Structure	Feedback	Rewire	Ob1	Ob2	Ob3
S1	Pollination	Empirical	Original	Off	X	X	X
S2	Herbivory	Empirical	Original	Off	X	X	X
S3	Pollination	Null	Original	Off	X	X	X
S4	Herbivory	Null	Original	Off	X	X	X
S5	Pollination	Empirical	Reversed	Off		X	
S6	Herbivory	Empirical	Reversed	Off		X	
S7	Pollination	Null	Reversed	Off		X	
S8	Herbivory	Null	Reversed	Off		X	
S9	Pollination	Empirical	Original	On			X
S10	Herbivory	Empirical	Original	On			X
S11	Pollination	Null	Original	On			X
S12	Herbivory	Null	Original	On			X

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727

728 **Figure 1.** Diagram of extinction cascades. Full arrows indicate consequences of plant species
 729 losses and dashed arrows the consequences of animal species losses. Cascades start with the
 730 primary extinction of a plant (I and II). Insects interacting with that plant have the chance of
 731 rewiring (III). When rewiring is successful, abundances are recalculated (IV), and if new
 732 abundances are positive a new cascade begins (I and II). Species that become disconnected or
 733 whose abundance reach zero suffer secondary extinctions (V). Secondary plant extinctions lead
 734 to a similar sequence of events to primary extinctions. Secondary animal extinctions (VI) lead
 735 to the recalculation of abundances.



736

737 **Figure 2.** a) Differing levels of generalisation lead to different levels of interaction similarity

738 (niche overlap), resulting in different rewiring opportunities. Both networks have equal

739 connectance (C_i), number of animal (NA) and plant (NP) species, but the presence of a

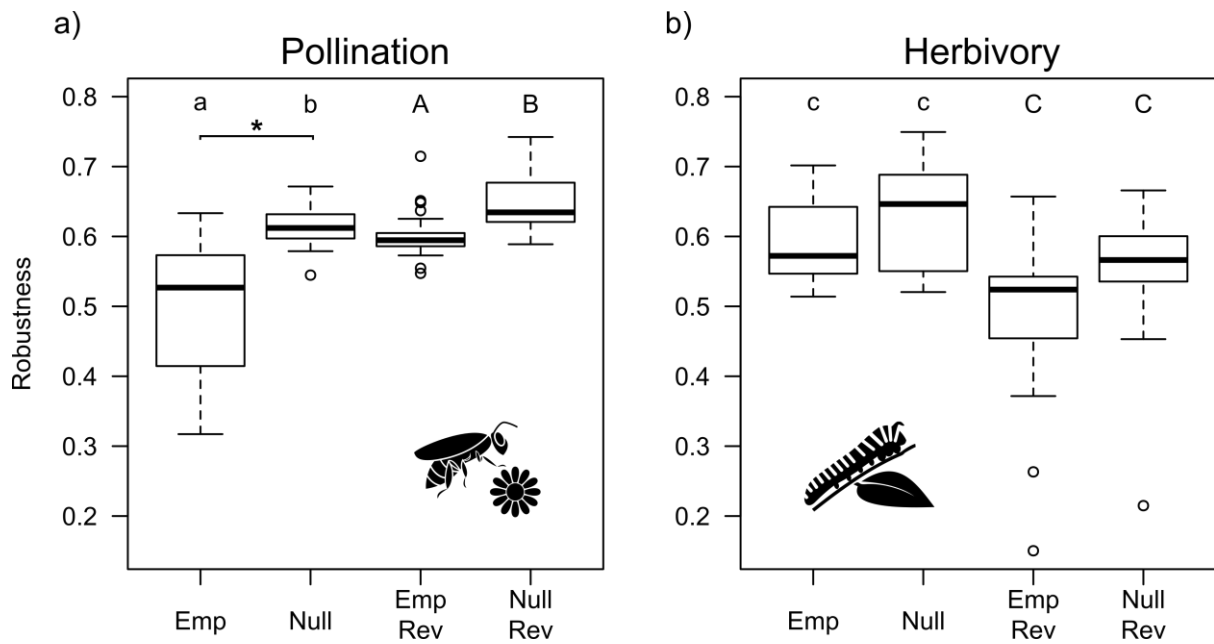
740 generalist species (black circle), leads to higher interaction similarity and rewiring

741 opportunities. b) The rewiring probability (P) of insects that lost interaction partners (dashed

742 lines) is inversely proportional to their resource abundance (n_i : normalised resource

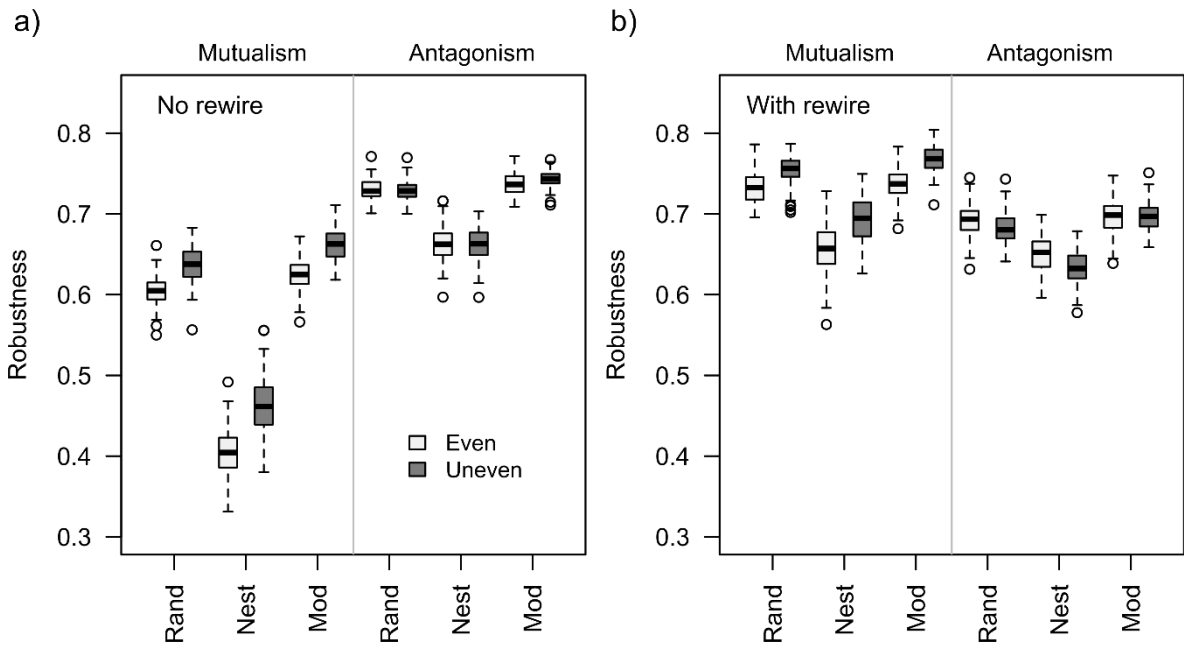
743 abundance of each insect). Number of resources “Lost” and “Left”. In this example, all

744 resources have abundance $N = 10$.



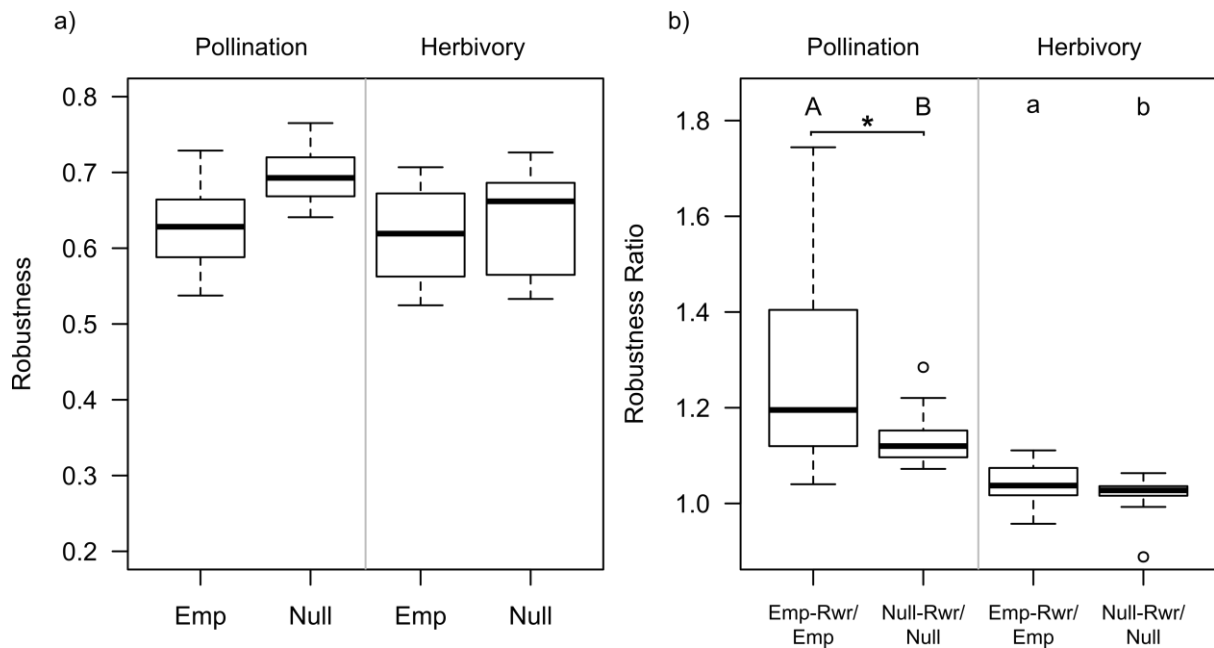
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746 **Figure 3.** Robustness of a) pollination and b) herbivory networks in the first eight simulation
 747 scenarios (Table 1): empirical and null networks, without (Emp and Null) and with (Emp-Rev
 748 and Null-Rev) reversed population feedbacks. Objective 1: comparisons between empirical and
 749 null networks with non-reversed population feedbacks - Emp vs Null - for pollination and
 750 herbivory networks are marked with an asterisk if statistically different ($p < 0.05$). Objective 2:
 751 comparisons between non-reversed (Emp and Null) and reversed (Emp-Rev and Null-Rev)
 752 population feedbacks scenarios of pollination and herbivory networks are represented by
 753 different letters (all c in herbivory as the interaction between network structure and population
 754 feedbacks was non-significant). Different letter cases (A vs a) represent $p < 0.05$.



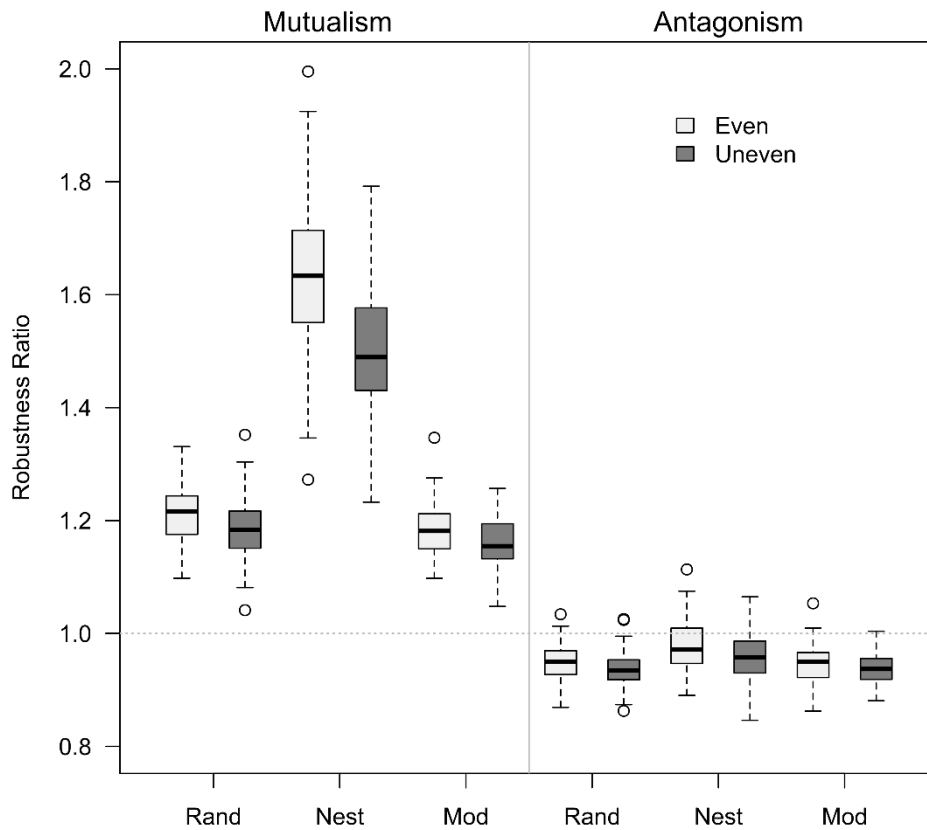
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756 **Figure 4.** Robustness of theoretical networks in scenarios a) without (12 scenarios) and b) with
 757 rewiring (12 scenarios). Light boxes represent scenarios with even networks and dark boxes
 758 scenarios with uneven networks. Rand = random structure, Nest = nested and Mod = modular
 759 networks.



760

761 **Figure 5.** a) Robustness of pollination and herbivory networks in simulation scenarios in which
 762 insect species are allowed to rewire (S9 to S12, Table 1) using empirical (Emp) and null (Null)
 763 networks. b) Effect of rewiring (Rwr) on network robustness was measured as the ratio between
 764 robustness on scenarios with (S9 to S12) and without (S1 to S4) rewiring (Table 1) - *e.g.* in
 765 pollination, “Emp-Rwr/Emp” corresponds to the robustness ratio between S9 (scenario with
 766 rewire) and S1 (scenario without rewire). Comparisons between empirical and null networks
 767 of the same interaction type (*e.g.* Emp-Rwr/Emp vs Null-Rwr/Null for pollination) are marked
 768 with an asterisk when $p < 0.05$. Comparisons between networks of different interaction types
 769 but with similar structure (*e.g.* Emp-Rwr/Emp for pollination vs Emp-Rwr/Emp for herbivory)
 770 are represented by different letters. Different letter cases (A vs a) represent $p < 0.05$.



771

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Figure 6. For theoretical networks, the effect of rewiring on network robustness was also

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measured as the ratio between robustness on the 12 scenarios with and 12 scenarios without

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rewiring. Light boxes represent scenarios with even and dark boxes scenarios with uneven

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networks. The horizontal dashed line marks the transition between positive and negative effects

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of interaction rewiring (ratio = 1). Rand = random structure, Nest = nested and Mod = modular

777

networks.