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1 An individual based model for the eco-evolutionary emergence of  
2 bipartite interaction networks

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11 **Authors contribution**

12 OM, NL & HM conceived the study. OM wrote the simulation code and performed the analysis.  
13 OM, NL & HM wrote the manuscript.

14 **1 Data availability statement**

15 Data sharing not applicable to this article as no new data were generated during the current  
16 study. The functions for running the simulations are available in the Rpackage RPANDA ([Morlon  
17 et al., 2016](#)).

18 **2 Short running title**

19 Emergence of bipartite interaction networks

20 **3 Keywords**

21 ecological networks ; mutualism ; antagonism ; nestedness ; coevolution

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## 28 **Abstract**

29       How ecological interaction networks emerge on evolutionary time scales remains unclear. Here  
30 we build an individual-based eco-evolutionary model for the emergence of mutualistic, antagonis-  
31 tic and neutral bipartite interaction networks. Exploring networks evolved under these scenarios,  
32 we find three main results. First, antagonistic interactions tend to foster species and trait diver-  
33 sity, while mutualistic interactions reduce diversity. Second, antagonistic interactors evolve higher  
34 specialization, which results in networks that are often more modular than neutral ones; resource  
35 species in these networks often display phylogenetic conservatism in interaction partners. Third,  
36 mutualistic interactions lead to networks that are more nested than neutral ones, with low phylo-  
37 genetic conservatism in interaction partners. These results tend to match overall empirical trends,  
38 demonstrating that structures of empirical networks that have most often been explained by eco-  
39 logical processes can result from an evolutionary emergence. Our model contributes to the ongoing  
40 effort of better integrating ecological interactions and macroevolution.

## 41 **Introduction**

42       Species in ecological communities engage in a diverse set of antagonistic and mutualistic interac-  
43 tions such as predation, parasitism, pollination and seed dispersal. These interactions are thought  
44 to have important consequences for species and trait diversity (Ehrlich and Raven, 1964; Van Valen,  
45 1973; Hembry et al., 2014), as well as the structure of ecological networks (Bascompte and Jordano,  
46 2007; Thébault and Fontaine, 2010; Suweis et al., 2013; Dormann et al., 2017). In terms of diversity,  
47 empirical examples of very diverse communities seem more numerous in antagonistic (e.g. plant de-  
48 fense strategies, Futuyma and Agrawal, 2009) than mutualistic interactions (Hembry et al., 2014;  
49 Chomicki et al., 2019). Eco-evolutionary models have indeed found that antagonistic interactions  
50 foster, while mutualistic interactions impede, trait diversity (Yoder and Nuismer, 2010). If and how  
51 antagonistic and mutualistic interactions affect the generation and maintenance of species diversity  
52 is less clear (Weber et al., 2017).

53       In terms of the structure of ecological networks, empirical studies have repeatedly shown that

54 this structure is highly non-random (Fontaine et al., 2011). Two main patterns have been reported:  
55 modularity, with subsets of species interacting more strongly among each other than with the rest of  
56 the community (May, 1972; Krause et al., 2003), and nestedness, with specialist species preferentially  
57 interacting with generalists (Bascompte et al., 2003; Jordano et al., 2003; Lewinsohn et al., 2006;  
58 Bascompte and Jordano, 2007; Thébault and Fontaine, 2010; Rohr et al., 2014). While several  
59 factors play a role in explaining network structure, including intimacy (i.e. the degree of physical  
60 proximity or integration of partner taxa, (Fontaine et al., 2011)) and phylogenetic scale (Beckett  
61 and Williams, 2013), the nature of the interaction seems particularly important. In a comparison  
62 of 95 networks, Fontaine et al. (2011) showed that non-intimate antagonistic networks are often  
63 modular, while mutualistic networks are often nested, although there are clearly deviations from  
64 this general pattern (Olesen et al., 2007; Pilosof et al., 2014). Many studies have sought to explain  
65 the processes driving these non-random structures without reaching consensus.

66 One of the main hypotheses put forward for explaining non-random network structures is the  
67 stability hypothesis. Species rich communities are not stable when species interact at random  
68 (May, 1972; Krause et al., 2003; Jordano et al., 2003; Montoya et al., 2006); this instability is  
69 counteracted by nonrandom network structures that depend on the type of interaction (Fontaine  
70 et al., 2011). In particular, stable species coexistence is reached in modular networks in the case of  
71 antagonistic interactions, and in nested networks in the case of mutualistic interactions (Thébault  
72 and Fontaine, 2010). Nestedness reduces effective interspecific competition (Bastolla et al., 2009)  
73 and broadens the range of ecological conditions under which mutualistic species can coexist (Rohr  
74 et al., 2014; Saavedra et al., 2016; Grilli et al., 2017), especially in the presence of adaptive foraging  
75 (Valdovinos et al., 2016). Anti-modularity has a destabilizing effect in most ecological communities  
76 (Grilli et al., 2016). Nestedness in mutualist networks and modularity in antagonist networks also  
77 limit co-extinction cascades (May, 1972; Krause et al., 2003; Memmott et al., 2004; Stouffer and  
78 Bascompte, 2011).

79 A second family of hypotheses to explain nonrandom, interaction-dependent structures, relies on  
80 trait-dependent interactions. For example, Santamaría and Rodríguez-Gironés (2007) and Rezende  
81 et al. (2007a) showed that interactions determined by either phenotypic difference or phenotypic

82 similarity can generate nested networks, in particular when several traits are involved and when  
83 there is a phylogenetic signal in trait values. [de Andreazzi et al. \(2019\)](#) also recently showed  
84 that a strong effect of species trait values on the probability for two species to interact helps in  
85 explaining network structure, and in particular that trait matching fosters trait coevolution and  
86 helps in explaining the structure of antagonistic networks. Related to the trait-based hypothesis is  
87 the observation that the non-random structure of networks can emerge without being selected for  
88 when interaction strength is inherited from the parent species (the “network spandrel” hypothesis  
89 [Maynard et al., 2018](#); [Valverde et al., 2018](#)).

90 Finally, differences in abundances across species can on their own generate non-random struc-  
91 tures. In a neutral world where individuals encounter and interact at random with one another,  
92 individuals from rare specialist species are more likely to interact with individuals from abundant  
93 generalists. As species abundance distributions are generally imbalanced, with many rare species  
94 and a few abundant ones, this leads to nested networks ([Vázquez, 2005](#); [Vázquez et al., 2009](#); [San-  
95 tamaría and Rodríguez-Gironés, 2007](#); [Krishna et al., 2008](#); [Staniczenko et al., 2013](#); [Coelho and  
96 Rangel, 2018](#)). Hence, while the often-observed modularity of antagonistic networks cannot be ex-  
97 plained by neutral processes alone, the frequent nestedness of mutualistic networks can be a pure  
98 result of neutral encounters.

99 Studies seeking to explain the non-random structure of species interaction networks have rarely  
100 focused on their emergence over evolutionary time scales, despite empirical evidence that there are  
101 evolutionary (phylogenetic) constraints to who interacts with whom ([Rezende et al., 2007b](#); [Elias  
102 et al., 2013](#)). They have instead often fixed the ecological context, for example by assuming an initial  
103 network is subject to local extinctions ([Thébaud and Fontaine, 2010](#)), or fixing the number of species  
104 and either the species abundance distribution ([Nuismer et al., 2013](#)) or the species trait distribution  
105 ([Santamaría and Rodríguez-Gironés, 2007](#)). There are notable exceptions though. [Minoarivelo and  
106 Hui \(2016\)](#) used an adaptive dynamics framework to show that coevolution can lead to both nested  
107 and modular networks for mutualistic interactions. In [de Andreazzi et al. \(2019\)](#), the authors  
108 investigated the effect of trait coevolution on network structure, but with the number of both  
109 species and interactions fixed according to empirical networks. In [Poisot and Stouffer \(2016\)](#), the

110 authors fitted to empirical networks a macroevolutionary model formalizing the evolution of species  
111 interactions, and surprisingly did not detect major differences between antagonistic and mutualistic  
112 networks. A recent study showed that neutral networks can evolve nested structures, probably as a  
113 result of asymmetric abundances, but did not investigate the effect of mutualistic and antagonistic  
114 interactions (Coelho and Rangel, 2018). Finally, Maynard et al. (2018) and Valverde et al. (2018)  
115 showed that nestedness and modularity may emerge from speciation divergence dynamics within  
116 antagonistic networks. The lack of a unified model mimicking the evolutionary emergence of species  
117 interaction networks as species diversify clearly limits our understanding of the macroevolutionary  
118 dynamics and consequences of inter-species interactions (Weber et al., 2017; Harmon et al., 2019).

119 Here we investigate the emergence of ecological networks as species coevolve, when individu-  
120 als engage into mutualistic, antagonistic or neutral interactions. We develop an individual-based,  
121 stochastic eco-evolutionary model (BipartiteEvol) that allows us to assess the effect of interaction  
122 type on species and trait diversity, network structure, and phylogenetic signal in interaction part-  
123 ners. We discuss results obtained when simulating the model in light of previous literature and  
124 empirical observations.

## 125 **Methods**

### 126 **An individual-based model for the eco-evolutionary emergence of bipartite in-** 127 **teraction networks**

128 We develop an individual-based, stochastic model, with discrete time steps and fixed population  
129 size, described in detail in our Supplementary Information. This model can be seen as an extension,  
130 in two main directions, of the spatially explicit neutral model of biodiversity where dynamics are  
131 modeled on a grid of  $N$  cells (Chave and Leigh Jr, 2002). As in the metacommunity version  
132 of this model, our model best represents evolutionary outcomes in a closed community without  
133 immigration. The first extension is that here each cell is occupied by two individuals, one from each  
134 of two interaction guilds (guild  $A$  and  $B$ ), and this co-occurrence determines interaction (Canard  
135 et al., 2014). The second extension is that each individual is characterized by its (potentially

136 multidimensional) trait value, and has fitness determined by both its trait value and that of the  
137 individual from the other guild occupying the cell. Offspring experience mutations that induce  
138 genetic differentiation and small trait deviations from their parents (Loeuille and Leibold, 2014).  
139 Genetic differentiation eventually leads to speciation (Manceau et al., 2015; Rosindell et al., 2015).  
140 The nature of the interactions can affect evolutionary outcomes in an eco-evolutionary feedback  
141 loop between who interacts with whom, the resulting adaptive pressures, and the gain or loss of  
142 interactions linked to adaptations to these pressures. At each time step, we track the trait values  
143 of each individual, their genealogical relationship, whether they experienced a mutation, and who  
144 they interact with. At the end of the simulations, we construct the resulting species phylogenies  
145 and species interaction networks.

146 *Eco-evolutionary dynamics* We start the simulations with a monomorphic population in each  
147 guild, all descending from a unique parent. At each time step we update the grid as follows:

- 148 • We select one individual from guild  $A$  at random and kill this individual. We record the trait  
149 value  $x_B$  of the individual of guild  $B$  present on this cell.
- 150 • We compute the fitness of all individuals of guild  $A$  present in the grid, should it interact with  
151 an individual of trait  $x_B$ .
- 152 • We select an individual from guild  $A$  to be the parent of the individual that replaces the killed  
153 one with probabilities proportional to each individual fitness. Hence, the filiation of the new  
154 individual depends on trait values and chance. We do not introduce dispersal limitation here,  
155 but this could be done in future work by selecting the parent with a probability proportional  
156 to its fitness times a dispersion kernel.
- 157 • The new individual from guild  $A$  has a probability  $\mu_A$  to experience a mutation, in which  
158 case its new trait is drawn independently in each dimension in a normal distribution centered  
159 on the parental trait with standard deviation  $\sigma$ . If no mutation occurs, the new individual  
160 inherits the trait value of its parent.
- 161 • We repeat the four previous steps for guild  $B$ .

162 • We record the genealogy obtained in each of the two guilds, as well as the mutations that  
163 occurred on this genealogy.

164 *Modeling the effect of trait-specific interactions on fitness* Each individual is characterized by  
165 its trait value  $x$ , which can have any dimension  $d$ . The distance in trait space of two interacting  
166 individuals determines the effect of the interaction on their fitness. Classical traits with fitness  
167 effects include proboscis and floral tube length, color preferences, and organism sizes or phenology  
168 in mutualist partners such as plants and their pollinators, or the presence of metabolic compounds  
169 and the ability to metabolize these compounds in antagonist partners such as plants and their  
170 herbivores. For example, a mismatch in phenology between a plant and its pollinator would induce  
171 a cost in reproductive success for the plant and in the ability to feed for the pollinator. We use a  
172 classical trait matching expression given by a Gaussian function, with maximal fitness effect when  
173 the traits of two interacting individuals are similar (Fig. S1, [Loeuille and Loreau \(2005\)](#); [Yoder  
174 and Nuismer \(2010\)](#)). The fitness function is parametrized by  $\alpha$ , which measures the specificity of  
175 the trait matching: high  $\alpha$  values correspond to scenarios where fitness effects are preponderant in  
176 interactors with very similar trait values (i.e. highly specialized interactions), while low  $\alpha$  values  
177 correspond to more neutral scenarios. Thereafter for simplicity we refer to  $\frac{1}{\alpha}$  as “niche width”. The  
178 fitness function is further parametrized by a parameter  $r$ , the ratio between the maximum and  
179 minimum fitness, that measures the overall effect of trait differences.

180 In mutualistic interactions, individuals from both guilds have higher fitness ( $W_A$  and  $W_B$ ) when  
181 they have similar trait values:

$$\begin{aligned} W_A(x_A, x_B) &= \frac{1}{r_A - 1} + e^{-\|x_A - x_B\|^2 \times (\alpha_A^2/2)} \\ W_B(x_A, x_B) &= \frac{1}{r_B - 1} + e^{-\|x_A - x_B\|^2 \times (\alpha_B^2/2)} \end{aligned} \tag{1}$$

182 In antagonistic interactions, individuals from the consumer clade (B) have higher, and those  
183 from the resource clade (A) lower, fitness when they have similar trait values, so the fitness differs  
184 from the mutualistic scenarios only for clade A:



$$\begin{aligned}
W_A(x_A, x_B) &= \frac{1}{r_A - 1} + 1 - e^{-\|x_A - x_B\|^2 \times (\alpha_A^2/2)} \\
W_B(x_A, x_B) &= \frac{1}{r_B - 1} + e^{-\|x_A - x_B\|^2 \times (\alpha_B^2/2)}
\end{aligned}
\tag{2}$$

185 We obtained the neutral case by taking  $\alpha = 0$  in the expression for mutualistic fitness (taking  
186  $\alpha = 0$  in the antagonistic version would yield identical simulations).

187 *Defining species and phylogenies* Based on the resulting genealogies with mutations, we define  
188 species following the model of Speciation by Genetic Differentiation (Manceau et al., 2015), except  
189 that we allow  $s$ , the number of mutations needed to belong to different species, to vary (similarly  
190 to what is done in Rosindell et al. (2015)). Species are thus the smallest monophyletic group of  
191 individuals from the genealogy such that two individuals separated by less than  $s$  mutations belong  
192 to the same species. This is a protracted mode of speciation, and the time needed for speciation  
193 to complete increases with parameter  $s$ . This species definition allows for polymorphic species.  
194 We compute the resulting species-level phylogenies from the genealogy with mutation positions  
195 (Manceau et al., 2015). Speciation occurs as the result of accumulating mutations, whatever their  
196 effect on the phenotype. It can thus merely result from drift, and we expect species diversity to  
197 build up under neutral dynamics. However, if trait diversity is favored – as would be the case if the  
198 presence of predators generates disruptive selection – we expect to see an increased species diversity  
199 as more mutations are likely to get fixed.

200 *From individuals' interaction to species interaction networks* The interaction network is defined  
201 at the scale of the entire grid and is based on individuals' co-occurrence: we consider that two  
202 individuals interact if they co-occur in the same cell. Next, at the species level, we consider both  
203 a quantitative and a binary network. For the quantitative network, we take the strength of the  
204 interaction between two species to be the number of pairs of individuals of these species interacting  
205 together. For the binary network, we consider that two species interact if at least one pair of  
206 individuals of these species interact (that is if their interaction strength in the quantitative network  
207 is nonzero). While interactions in our networks are constructed based on only co-occurrence, they  
208 depend on trait values through the effect of traits on invasion probabilities. An interaction network

209 in our model thus results from the cumulative effects of smaller scale interaction events (as for  
210 example in [Pillai et al., 2011](#)).

211 We provide codes for running simulations of BipartiteEvol in RPANDA ([Morlon et al., 2016](#),  
212 function `sim.BipartiteEvol`).

### 213 **Analyzing emerging patterns**

214 In order to explore emerging patterns, we performed a series of simulations under neutral,  
215 mutualistic and antagonistic scenarios. We followed the evolution of a (closed) community made of  
216  $N = 4000$  individuals in each guild during  $8e7$  death events. This simulation duration was enough  
217 for most of the simulations to have reached stationary state, at least for the summary statistics we  
218 followed (Fig. S2-S3). We ran most of our simulations with a trait dimension  $d = 3$ , as ecological  
219 networks are thought to be best described by traits with several yet few dimensions ([Eklöf et al.,](#)  
220 [2013](#)). To check the robustness of our result to trait dimensionality, we also ran simulations for  
221  $d = 1$  and  $d = 10$  for a selected parameter set (Fig S28-S34). We chose initial trait values 2 and 0  
222 for guild  $A$  and  $B$  in all trait dimensions. We also chose a standard deviation  $\sigma = 1$ ; considering a  
223 different  $\sigma$  would be equivalent to dividing  $\alpha_A$  and  $\alpha_B$  by  $\sigma$ . We held the mutation probabilities  $\mu_A$   
224 and  $\mu_B$  constant at 0.05. We fixed  $r_A$  at 10 and  $r_B$  at  $+\infty$ . In the case of mutualistic interactions,  
225 this renders species from guild B obligate mutualists (their fitness is zero if they do not interact  
226 with species from guild A, e.g. pollinators that entirely depend on a specific clade of plants) while  
227 species from guild A are facultative mutualists (e.g. plants that can be pollinated by pollinators not  
228 represented in B). In the case of antagonistic interactions,  $r_B = +\infty$  means that consumer species  
229 entirely depend on interaction with their resources. Besides the neutral case ( $\alpha_A = \alpha_B = 0$ ), we  
230 simulated all the combinations of  $\alpha_A$  and  $\alpha_B$  in 0.01, 0.02, 0.05, 0.1, 0.2, 0.5, 1, 10 for both mutualistic  
231 and antagonistic interactions. We performed 10 simulations for each scenario and each parameter  
232 set (20 in the neutral case).

233 At the end of each simulation, we built the resulting phylogenies and interaction networks using  
234 three different species definition thresholds  $s$  ( $s = 1, 10$  and  $50$ ). We computed species richness, as  
235 well as trait diversity on each trait dimension as the variance in trait values across all individuals. In

236 addition, in order to investigate under which conditions trait coevolution between species on the two  
237 sides of the network occurs, we measured the correlation in trait values of co-occurring individuals.  
238 We computed nestedness and modularity using the R-package bipartite (Almeida-Neto and Ulrich,  
239 2011; Dormann et al., 2008)). Nestedness was measured with the NODF metric using the func-  
240 tion `nested`, with `method = "weighted NODF"` for quantitative networks and `method = "NODF2"`  
241 for binary networks. Modularity was computed for quantitative networks only, using the function  
242 `computeModules` (the corresponding `quanBiMo` algorithm is not adapted to binary networks (Dor-  
243 mann and Strauss, 2014)). We compared the binary nestedness values to the distribution of values  
244 obtained for two null models. In the first, thereafter called NM1, the network connectance is kept  
245 constant (`method "shuffle.web"` in the function `nullModel`). In the second, thereafter called NM2,  
246 row and column sums of the interaction matrix are kept constant (`method "r2d"`). This is equivalent  
247 to randomly reassigning a position on the grid for all individuals regardless of their trait values,  
248 which is also how we generate interactions in our neutral simulations and provides a way to cor-  
249 rect for species abundances. We also compared the quantitative nestedness and modularity values  
250 to the distribution of values obtained for NM2 (NM1 is applicable to only binary networks). We  
251 computed Z-scores, defined as  $\frac{x-\mu}{\sigma}$ , where for a given metric  $x$  is the value outputted by our simu-  
252 lation and  $\mu$  and  $\sigma$  are the mean and standard deviation of the values under the null model. While  
253 Z-scores are not appropriate for comparing nestedness values between networks of different sizes  
254 (Song et al., 2017), they are a good way of assessing the significance of nestedness values against  
255 a null model. Finally, we computed the phylogenetic signal of interaction partners using a Mantel  
256 test that assesses the significance of the correlation between the phylogenetic distance of two species  
257 and the dissimilarity of their interaction partners. In order to limit the effect of species definition  
258 on our results, we used a phylogenetic metric to quantify this dissimilarity. We used the (weighted)  
259 fraction of unshared phylogenetic branch length between the two sets of interaction partners (com-  
260 puted using quantitative `uniFrac` (Lozupone et al., 2007), `"d_1"` in the function `GUniFrac` from  
261 the R package `GUniFrac` (Chen, 2012)). We also performed the analyses with a non-phylogenetic  
262 metric, the Jaccard dissimilarity index – computed with the function `cluster_similarity` from  
263 the R-package `clusteval` – for comparison.

## 264 **Results**

265 Figure 1 shows two typical simulations, one mutualistic and the other antagonistic, that illustrate  
266 general results concerning the evolution of trait values and species interaction networks. Other  
267 figures in the main text show emergent properties of mutualistic, antagonistic and neutral networks  
268 when the niche width of species from guild A (i.e. resources in antagonistic networks and facultative  
269 mutualists in mutualistic networks) varies and that of guild B (i.e. consumers in antagonistic  
270 networks and obligate mutualists in mutualistic networks) is fixed, and for three-dimensional traits.  
271 Figures in the Supplementary Material report results for other parameter sets, including results  
272 when the niche width of species from guild B varies and that of guild A is fixed, and for trait  
273 dimension  $d = 1$  and  $d = 10$ . Results for these trait dimensions were qualitatively similar (Fig  
274 S28-S34).

### 275 **Trait diversity**

276 In mutualistic scenarios, trait values stay fairly constant through time (Fig. 1A) and trait  
277 diversity is lower than in neutral scenarios (Fig. 2A & Fig. S4). Trait matching in mutualistic  
278 networks results in stabilizing selection that constrains trait evolution on both sides of the network.  
279 Trait diversity within a guild is generally constrained by niche width in this guild, but not by niche  
280 width in the interacting guild, even if exceptions occur in extreme cases when niche width in one of  
281 the two guilds is smaller than, or comparable to, the effect size of mutations (here fixed to  $\sigma = 1$ ,  
282 Fig. 2A & Fig. S4). The correlation between the traits of interacting individuals is slightly positive  
283 but stays very low (Fig. 2B & Fig. S5).

284 Patterns are strikingly different in antagonistic scenarios, where clusters of traits progressively  
285 emerge from co-evolutionary dynamics (Fig. 1B). Disrupting selection acting on resource species  
286 typically increases trait diversity compared to neutral scenarios for both consumers and resources,  
287 with similar levels of diversity in the two guilds (Fig. 2A & Fig. S4). Trait diversity increases  
288 with the niche widths of both resource and consumer species, but collapses when consumers have a  
289 larger niche than resources (Fig. 2A & Fig. S4). The traits of interacting individuals are positively  
290 correlated, suggesting strong trait coevolution (Fig. 2B & Fig. S5).

## 291 Species richness

292 Consistent with temporal dynamics of trait diversity, species diversification is lower in mutu-  
293 alistic than antagonistic networks (Fig. 1A versus B). Species richness is systematically larger in  
294 antagonistic than in mutualistic networks, regardless of niche width and species definition (Fig.  
295 2C,D & Fig. S6-S9).

296 In mutualistic scenarios, species richness tends to be lower than in neutral scenarios (Fig. 2C,D  
297 & Fig. S6-S9). Species richness is comparable to what is obtained in the neutral case when species'  
298 niches are so large that individuals have approximately the same fitness regardless of who they  
299 interact with. But for narrower niches, trait matching is more influential and stabilizing selection  
300 inhibits speciation. Species richness within a guild thus decreases when niches in that guild become  
301 narrower (Fig. 2C,D & Fig. S6-S9).

302 In antagonistic scenarios, species richness is in general higher for resource than for consumer  
303 species (Fig. 2C,D & S7-S9). The effect of niche width on species richness depends on the species  
304 definition threshold  $s$ . For a low  $s$ , resource species richness is similar to what is obtained in neutral  
305 simulations and unaffected by niche width of either resource or consumer species (Fig. 2C & S7).  
306 Consumer species richness tends to be lower than in neutral simulations (Fig. 2C & S7). It is not  
307 affected by the niche width of resource species (Fig. 2C) but decreases when the niches of consumer  
308 species become narrower, as long as it remains larger than the effect size of mutations. For a higher  
309  $s$  (around 50, Fig. 2D & S9), species richness is affected by niche width in a similar way for resource  
310 and consumer species, and can be either higher or lower than in neutral simulations. Cases when  
311 species richness is higher than in neutral simulations correspond to scenarios with intermediate  
312 resource niche width, and narrower niche widths for consumer than resource species (Fig. 2D, S9).

## 313 Network structure

314 Mutualistic interactions typically lead to the progressive emergence of nested networks (Figure  
315 1A), while antagonistic interactions lead to modular networks (Figure 1B). When we look at network  
316 metrics without any comparison to a null model, most networks that have higher nestedness values  
317 than those in the neutral case were generated in mutualistic scenarios, while most of those that have

318 higher modularity values than those in the neutral case were generated in antagonistic scenarios  
319 (Fig. 3A, Fig S10 & S15).

320 When compared to the null model that corrects for only connectance (NM1), all networks show  
321 up as significantly nested, including neutral ones (Fig. 3B, S12-S13 & S17-S18). Z-values are very  
322 high and mostly depend on the diversity of the community, with higher Z-values obtained for more  
323 diverse communities (Fig. S14).

324 When compared to the null model that corrects for abundance (NM2), neutral models are neither  
325 nested nor anti-nested, and they are not modular either (Fig. 3C,D & Fig. S19-S20, S22-S23).  
326 Mutualistic networks are similar to neutral ones. The only deviation occurs when the facultative  
327 mutualists have an intermediate niche width that is larger than that of the obligate mutualists;  
328 in this case, mutualistic networks are slightly anti-nested and modular (Fig. S19-S20, S22-S23).  
329 Antagonistic networks deviate sharply from neutral ones; they most often exhibit a modular, anti-  
330 nested structure that peaks at intermediate resource niche width (Fig. 3C,D) and small consumer  
331 niche width (Fig. S19, S22). The results stay qualitatively similar for  $s = 10$  (Fig. S20, S23).

### 332 **Phylogenetic signal**

333 While modules in antagonistic networks seem strongly constrained by phylogenetic history (Fig.  
334 1B), interactions in mutualistic networks seem rather independent from this history (Fig. 1A).  
335 Indeed, the Mantel correlation between phylogenetic distance and similarity in interaction partners  
336 is generally weak and non-significant on both sides of mutualistic networks, comparable to what is  
337 found for neutral networks (Fig. 4A & B). The correlation is stronger in antagonistic networks, and  
338 significant in many simulations (Fig. 4A,B). This phylogenetic signal is often stronger for resource  
339 than for consumer species and higher for an intermediate consumer niche width and/or wider re-  
340 source niche width (Fig. 4B, Fig. S26). Results are qualitatively similar across species definition  
341 thresholds and dissimilarity metrics, although fewer networks display significant correlation values  
342 for  $s = 1$  than for  $s = 10$  and for the Jaccard than for the Unifrac metric (Fig. S24-S27).

## 343 Discussion

344 Our model allows a direct comparison of the effect of antagonistic, mutualistic, and neutral  
345 interactions on the dynamics of trait and species diversity as well as on the structure of the interac-  
346 tion network. We find that antagonistic interactions enhance both trait and species diversity, and  
347 result in modular interaction networks with phylogenetic signal in interaction partners. Mutualistic  
348 interactions instead limit trait and species diversity, and result in interaction networks that oth-  
349 erwise resemble neutral networks, with a tendency for nestedness rather than modularity, and low  
350 phylogenetic signal in interacting partners.

351 We discuss these results in light of empirical observations, keeping in mind that our model  
352 best mimics eco-evolutionary dynamics in a closed metacommunity, where diversity is the result  
353 of speciation-extinction dynamics, while most empirical networks are built at the community level,  
354 where diversity can also be introduced through immigration, which can change qualitative patterns  
355 (as in [Maynard et al., 2018](#)). Similar to what has been done in developments of the neutral bio-  
356 diversity model, our model could be developed to include dispersal limitation and to sample local  
357 communities at different spatial scales, or as a continent-island model, where the local community  
358 receives immigrants from the metacommunity. This would also help understand how local networks  
359 assemble from ‘meta-networks’ ([Gravel et al., 2011](#); [Morlon et al., 2014](#)). Other limitations of our  
360 model include the ‘zero-sum’ assumption that total population size remains constant, not account-  
361 ing for sexual reproduction, and not varying the degree of intimacy, which can all affect network  
362 structure.

363 Our result that antagonistic interactions tend to enhance, while mutualistic ones impede, trait  
364 and species diversity, is generally consistent with previous empirical and theoretical studies ([Ehrlich  
365 and Raven, 1964](#); [Yoder and Nuismer, 2010](#); [Janz, 2011](#); [Hembry et al., 2014](#)). For example, previous  
366 studies suggest that investment in defense traits results in higher diversification rates in North  
367 American milkweeds ([Agrawal et al., 2009](#)), while specialized pollination in Yucca-moth interactions  
368 does not increase Yucca diversification ([Smith et al., 2008](#)). Consistently, [Armbruster and Muchhala  
369 \(2009\)](#) showed that in several groups of angiosperms, diversity promotes floral specialization –  
370 through character displacement – rather than the reverse. Still, we do not exclude the possibility

371 that in some systems mutualism has a positive impact on diversification, as has been suggested by  
372 other studies, such as in the case of fig-wasp interactions (Cruaud et al., 2012). Indeed our model  
373 may output different results regarding the effect of mutualism if we allowed total population sizes  
374 to vary and/or if we accounted for dispersal limitation and/or sexual reproduction. Mutualistic  
375 interactions may indeed increase the density of individuals a community can sustain, either through  
376 more efficient feeding and reproduction or by opening new adaptive zones. This could in turn allow  
377 the maintenance of more diverse communities (Rosenzweig et al., 1995; Emerson and Kolm, 2005;  
378 Joy, 2013). It has also been proposed that geographical isolation is necessary for mutualism to  
379 promote speciation, and our non-spatial model cannot account for this potential effect (Thompson  
380 and Cunningham, 2002; Kay and Sargent, 2009). In the case of pollination, mutualistic interactions  
381 can also facilitate reproductive isolation, which cannot be modeled by our asexual model (van der  
382 Niet and Johnson, 2012). Our results suggest that mutualism on its own, in the absence of such  
383 mechanisms, is unlikely to promote diversity.

384 Our model generates clear structural differences between antagonistic and mutualistic com-  
385 munities. We find that antagonist interactions generate modular networks, regardless of whether  
386 modularity values are corrected for abundance or not. This modularity emerges as a response to  
387 reciprocal specialization and coevolution between resources and consumers, as demonstrated by the  
388 positive correlation between the traits of interacting partners. Our results regarding nestedness are  
389 much more contingent on whether or not nestedness values are corrected for connectance and/or  
390 abundance. Raw nestedness values are higher in mutualistic than neutral (and antagonistic) com-  
391 munities, as observed in empirical networks (Thébault and Fontaine, 2010; Fontaine et al., 2011).  
392 When we do not correct for species abundances, all the networks, including neutral and antagonis-  
393 tic networks, are significantly nested. Finally, when we correct for species abundances, nestedness  
394 values are non-significant for neutral communities, and either non-significant or significantly lower  
395 than those obtained for the null model for antagonist (and a few mutualist) communities. These  
396 results are consistent with the literature, as most empirical or theoretical studies that found signif-  
397 icant nestedness in bipartite networks did not use a null model correcting for species abundances  
398 (Thébault and Fontaine, 2010; Lewinsohn et al., 2006; Bascompte et al., 2003), while those that



399 corrected for abundances did not find a clear nested pattern (Vázquez, 2005; Staniczenko et al.,  
400 2013; Canard et al., 2014). The nestedness signal observed in bipartite networks may thus well  
401 be linked to uneven species abundance distributions, in agreement with the neutral hypothesis  
402 (Vázquez, 2005; Vázquez et al., 2009; Santamaría and Rodríguez-Gironés, 2007; Krishna et al.,  
403 2008; Staniczenko et al., 2013; Coelho and Rangel, 2018). In this case, understanding differences in  
404 raw nestedness values between mutualist, neutral, and antagonist communities boils down to under-  
405 standing why communities are increasingly asymmetrical in abundances as we move from antagonist  
406 to neutral and finally mutualist communities. Under our model, the relatively low asymmetry of  
407 species abundances in antagonist networks could be linked to the coexistence of several abundant  
408 species facilitated by modular structures. The strong asymmetry of species abundances in mutualist  
409 networks could be linked to the transient nature of many rare species; we indeed often observed a  
410 single adaptive optimum in our simulated mutualist networks, suggesting that mutants could fre-  
411 quently be maladapted. In addition to this dominating effect of abundance, trait-based preferential  
412 interactions reduce nestedness in antagonist communities, while this effect is generally insignificant  
413 in mutualist communities in which trait values are quite constrained. The differences in network  
414 structure between antagonistic and mutualistic communities generated by our model are consis-  
415 tent with the classical dichotomy between antagonistic and mutualistic structures (Thébault and  
416 Fontaine, 2010; Fontaine et al., 2011). While many empirical examples show that this dichotomy is  
417 not as general as once thought (Pilosof et al., 2014; Olesen et al., 2007), our model shows that it can  
418 emerge from simple evolutionary rules at the individual level. Relaxing simplifying hypotheses of  
419 our model could provide a more nuanced view. For example, sexual reproduction, spatial structure,  
420 fluctuation in population sizes and intimacy could generate modular mutualistic communities, as is  
421 sometimes observed in empirical data (Olesen et al., 2007), by allowing trait diversification and the  
422 creation of clusters in trait space.

423 Our results regarding phylogenetic signal, which measures evolutionary conservatism in inter-  
424 action partners, are also consistent with empirical observations for antagonistic communities, in  
425 which resource species generally show a stronger phylogenetic signal than consumer species, once  
426 again in accordance to empirical observations (Krasnov et al., 2012; Elias et al., 2013; Fontaine and

427 [Thébault, 2015](#)). In plant-herbivore systems, the stronger conservatism in interaction partners seen  
428 in plants has sometimes been interpreted as the combination of factors acting on both sides of the  
429 network. Chemical defenses in plants are difficult and therefore slow to evolve and thus display a  
430 high phylogenetic conservatism. In herbivores on the contrary, resource shifts among close relatives  
431 to avoid enemies and/or reproductive interference are frequent, reducing phylogenetic conservatism  
432 ([Fontaine and Thébault, 2015](#)). However, in our simulations trait evolutionary rates, which are  
433 controlled by the mutation probability and the effect size of mutations, were symmetrical between  
434 resource and consumer species. We did not include enemies or reproductive interference either. We  
435 instead suggest that the difference in phylogenetic signal between resource and consumer species  
436 is linked to a difference in the nature of the selection pressure they experience. Resource species  
437 experience a selection pressure to avoid consumption, and they can evolve in almost any direction to  
438 escape consumers (only the few directions in trait space favorable to consumers must be avoided).  
439 Consumers instead experience a selection pressure to evolve specific traits adapted to consuming  
440 the existing resource species, and it is thus not uncommon to see resource shifts and convergence  
441 in traits, even between rather phylogenetically distant species, which weakens phylogenetic signal.  
442 In mutualistic communities, our model generally does not display a significant phylogenetic signal.  
443 While a tendency towards lower phylogenetic signal in mutualist compared to antagonistic commu-  
444 nities has been observed in empirical communities ([Fontaine and Thébault, 2015](#)), it is significant  
445 ([Rezende et al., 2007b](#)). This disconnect between our model and empirical networks is likely linked  
446 to the restricted evolved trait range produced by our mutualistic model, and the result could change  
447 if sexual reproduction, spatial structure and/or variable population size were accounted for.

448 The general qualitative patterns discussed above hold for a large range of parameter space with  
449 a noticeable effect of niche width – which in our model is closely related to selection pressures  
450 – on the values of the different metrics we measured. In antagonistic communities, we found the  
451 strongest patterns – for all observed metrics, including diversity, network structure and phylogenetic  
452 signal – when niche width is larger for resources than for consumers. This situation corresponds  
453 to the case when selection pressures promote the evolution of specialization to specific resources in  
454 consumers. As detailed above, this specialization leads to modular structures, and imposes a strong

455 disruptive selection pressure on resources that enhances diversity and strengthens phylogenetic signal  
456 by preventing trait convergence. In mutualistic scenarios, niche width in one guild impacts mostly  
457 trait and species diversity in that guild, but not in the interacting guild; small niche width indeed  
458 results in stronger stabilizing selection that constrains diversity, but does not affect the strength  
459 of stabilizing selection in the interacting guild. The only cases when niche width impacts network  
460 structure in mutualist networks occur when there is a very high asymmetry in niche width between  
461 the two guilds, in which case species from the small niche guild will evolve specialization in response  
462 to the high trait variability in the large niche guild, leading to the emergence of modular networks  
463 that resemble these seen in antagonistic scenarios, or some empirical mutualistic networks [Olesen](#)  
464 [et al. \(2007\)](#). The patterns were robust to trait dimensionality, which we did not expect considering  
465 previous literature ([Gilman et al., 2012](#); [Ispolatov et al., 2016](#)). Future work could investigate this  
466 aspect more thoroughly, along with adding limits to the trait space and/or a correlation between  
467 the traits. Trait correlations could produce interesting emerging behaviors, especially if they are  
468 asymmetrical between the two guilds.

469 Our eco-evolutionary model allowed us to study the effect of different types of interactions  
470 on the emergence of ecological networks as species and traits diversify. Despite the simplicity of  
471 the processes involved, the model generated clear differences between mutualistic and antagonistic  
472 communities that are broadly consistent with empirical observations. There is a lot of room for  
473 future developments, such as accounting for geographical processes ([Thompson, 2005](#)), dispersal  
474 from meta- to local communities, and the simultaneous effects of different interaction types ([Fontaine](#)  
475 [et al., 2011](#); [Montesinos-Navarro et al., 2017](#)). Developing an inference tool associated to this model  
476 would also be an important step to quantify, for example, the actual effect of trait matching or trait  
477 differences on selection pressures and trait coevolution from empirical data ([Manceau et al., 2017](#))  
478 . Such efforts are required if we want to better understand the macroevolutionary consequences of  
479 species interactions ([Weber et al., 2017](#); [Harmon et al., 2019](#)).

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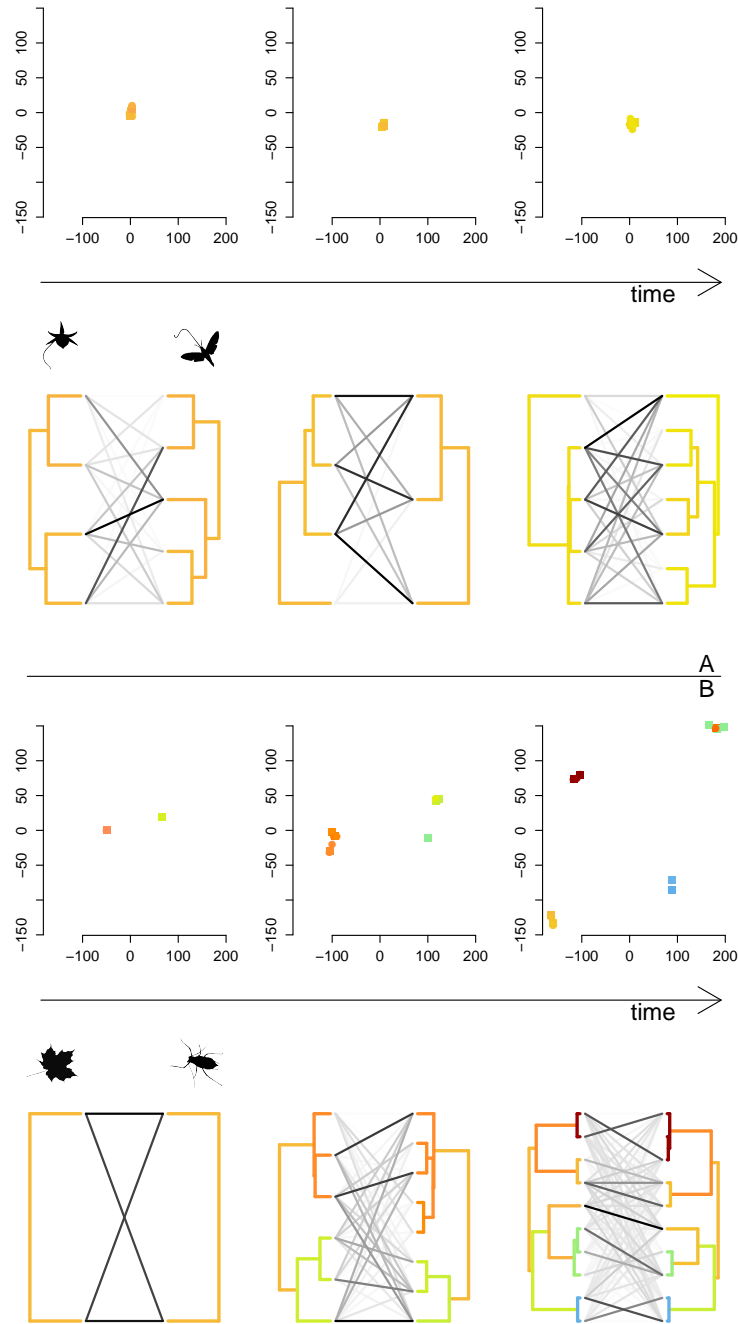


Figure 1: **Example outputs of the eco-evolutionary model for mutualistic (panel A) and antagonistic (panel B) interactions.** In each panel the upper row shows the evolution of trait values (in a three-dimensional trait space, point color representing the third trait dimension). The lower row shows the evolution of interaction networks and associated phylogenies. Darker links in the network correspond to interactions of higher strength; branches in the phylogenies are colored according to the value of the trait's third dimension so that it matches the colors of the corresponding dots in the upper row. Round dots correspond to species from guild A, square ones to species from guild B.

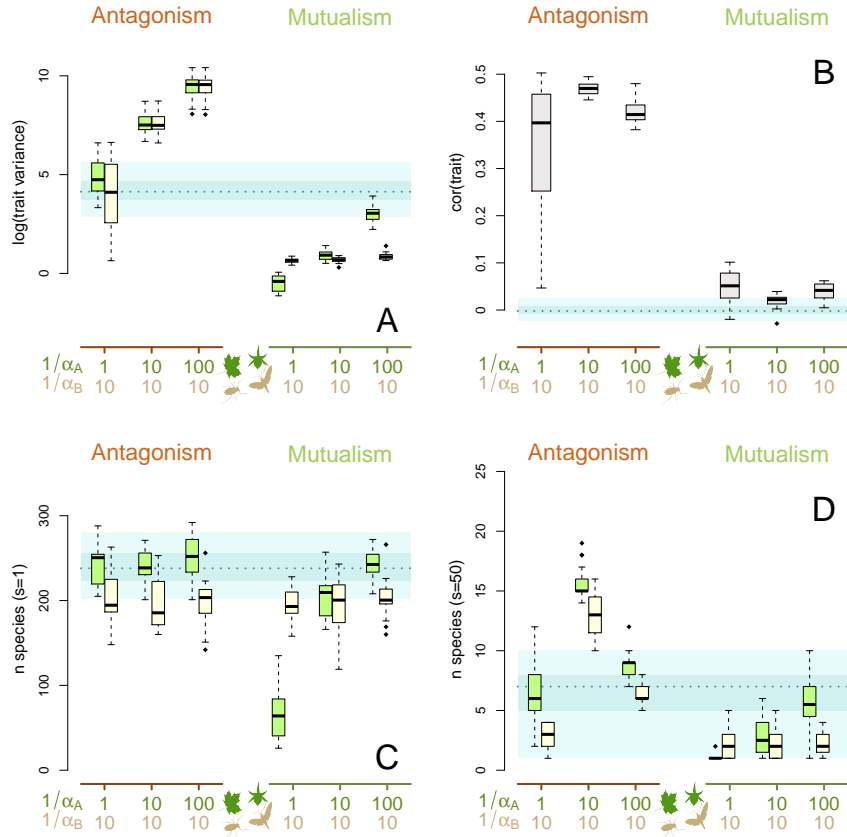


Figure 2: **Effect of interaction type on the emergence of trait and species diversity.** A : Logarithm of the variance of the first dimension of the species trait as a function of niche width for guild A (green boxplots) and B (white boxplots). The blue area shows values obtained for neutral simulations (range of values, quartiles and median). Antagonistic interactions commonly lead to higher, and mutualistic scenarios lower, trait diversity than in neutral simulations. Results for the other two trait dimensions are similar (results not shown). B : Correlation of the first dimension of the traits of the interacting individuals. Traits are consistently positively correlated in antagonistic scenarios, and correlation values stay pretty low in mutualistic ones. Results were similar for the other two trait dimensions (results not shown). C : Species richness in each guild for a species definition threshold  $s = 1$ . Diversity is higher in antagonistic scenarios than in mutualistic ones but always stays below that obtained for neutral scenarios. D : Species number in each guild for a species definition threshold  $s = 50$ . Diversity is higher in antagonistic scenarios than in mutualistic ones, and a few antagonistic scenarios display a diversity that is higher than in neutral simulations.

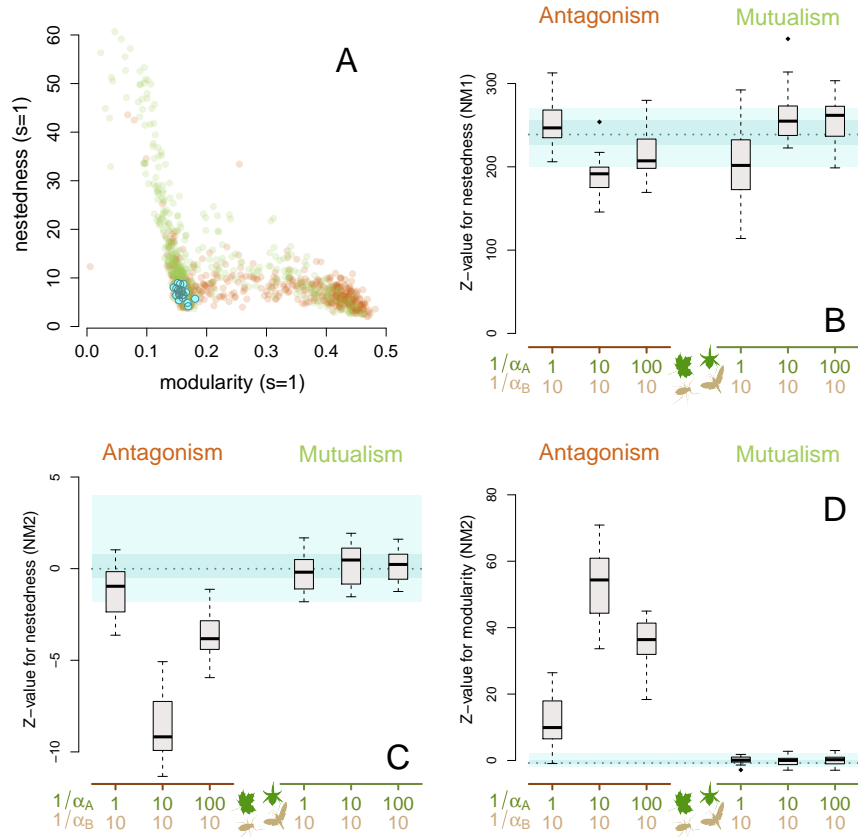


Figure 3: **Effect of interaction type on nestedness and modularity** A : Each point shows quantitative modularity and nestedness values for a single simulated network. The networks that have high nestedness values are mostly mutualistic ones (in green), while those with high modularity values are mostly antagonistic ones (in red). Blue points show the results for neutral simulations. B : Z-values for the binary NODF metric corrected by null model NM1 as a function of niche width. The blue area shows values obtained for neutral simulations (range of values, quartiles and median). All networks show up as significantly nested. C : Z-values for the quantitative NODF corrected by null model NM2. Mutualistic and neutral networks have similar levels of nestedness and are neither significantly nested nor anti-nested. A large proportion of antagonistic networks are significantly anti-nested. D : Z-values for the quantitative modularity metric corrected by null model NM2. Mutualistic and neutral networks have similar levels of modularity and are not significantly modular. Most of the antagonistic networks are significantly modular. Results are shown for a species definition threshold  $s = 1$ .

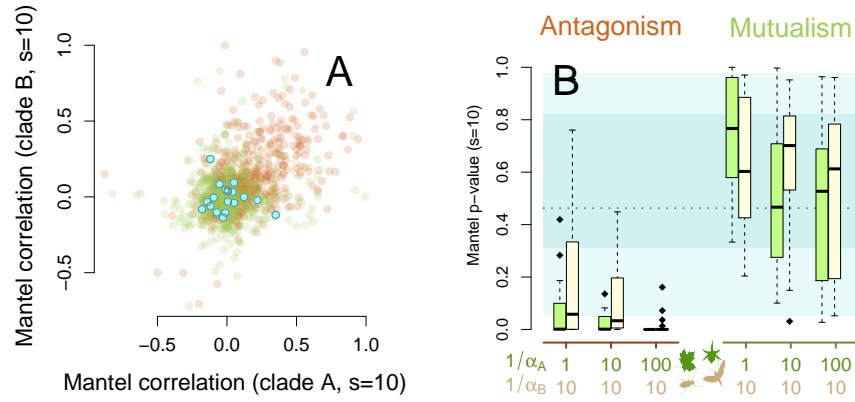


Figure 4: **Effect of interaction type on phylogenetic signal in interaction partners.** A : Each point shows, for a single simulation, the Mantel correlation between phylogenetic distance and dissimilarity in interaction partners on both side of the network. The correlation is higher for antagonistic (in red) than for mutualistic (in green) or neutral (in blue) networks. B : Mantel p-value as a function of niche width. The blue area shows values obtained for neutral simulations (range of values, quartiles and median). White boxplots show results for guild A and green boxplots for guild B. Results are shown for the Unifrac dissimilarity metric and a species definition threshold  $s = 1$ .