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1 **Phenological traits foster persistence of mutualistic networks by promoting**  
2 **facilitation**

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13

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24 FD, CF, ETe and ETh designed the study. FD performed all the simulations and statistical analyses.

25 FD wrote the paper with contributions from all authors.

26 **Data availability statement:**

27 All scripts are available here: [https://github.com/f-duchenne/Phenology-favors-persistence-of-](https://github.com/f-duchenne/Phenology-favors-persistence-of-mutualistic-communities)  
28 [mutualistic-communities](https://github.com/f-duchenne/Phenology-favors-persistence-of-mutualistic-communities). There is no data in this study.

29

30

31        **Abstract**

32        Morphological and phenological traits are key determinants of the structure of mutualistic  
33 networks. They both create forbidden links, but phenological traits can also decouple interaction in  
34 time. While such difference likely affects the indirect effects among species and consequently network  
35 persistence, it remains overlooked. Here, using a dynamic model, we show that networks structured by  
36 phenology favor facilitation over competition within guilds of pollinators and plants, thereby  
37 increasing network persistence, while the contrary holds for networks structured by morphology. We  
38 further show that such buffering of competition by phenological traits mostly beneficiate to specialists,  
39 the most vulnerable species otherwise, which propagate the most positive effects within guilds and  
40 which promote nestedness. Our results indicate that beyond trophic mismatch, phenological shifts such  
41 as those induced by climate change are likely to affect indirect effects within mutualistic assemblages,  
42 with consequences for biodiversity.

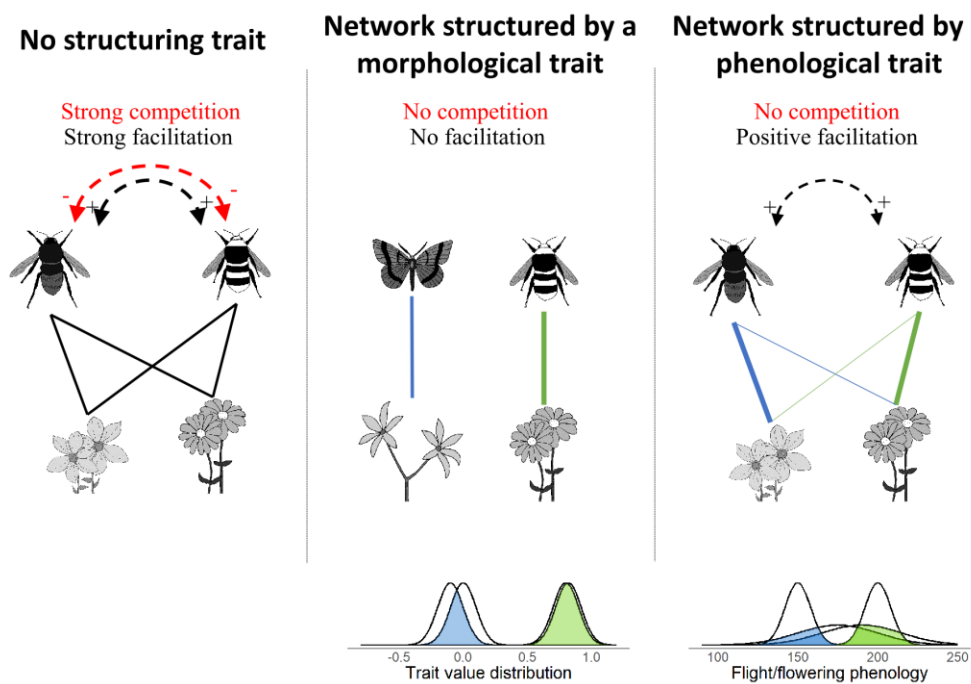
43        **Introduction**

44        For a century, the mechanisms that promote species coexistence in nature have fascinated the  
45 biologists, as the pervasive competitive interactions among species are expected to drive species  
46 exclusion and to limit coexistence (Volterra 1928; Gause 1934). This question becomes even more  
47 intriguing when dealing with complex systems because theoretical works have shown that the stability  
48 of a natural community should decrease with the number of species it contains and with the number of  
49 interactions among them (Gardner & Ashby 1970; May 1972). So far, this historical issue has been  
50 addressed by studying how the structure of ecological networks, either food webs or mutualistic  
51 networks, determine species coexistence and community stability (Neutel *et al.* 2002, 2007; Montoya  
52 *et al.* 2006; Otto *et al.* 2007; Okuyama & Holland 2008; Bastolla *et al.* 2009; Thébault & Fontaine  
53 2010). However the consequences of the species traits that shape the structure of these networks have  
54 been seldom considered in this context, despite the growing empirical evidence that traits, such as  
55 species phenology, are key for understanding the temporal dynamics of networks (CaraDonna *et al.*  
56 2021).

57        Recent findings have highlighted that ecological networks are structured by multiple species  
58 traits, such as, for pollination webs, flower shape and the length of the feeding apparatus of pollinators  
59 (Stang *et al.* 2006; Junker *et al.* 2013), flowering and flying phenology (Junker *et al.* 2013; Gonzalez  
60 & Loisele 2016), floral height (Junker *et al.* 2013) or floral scent (Schiestl 2010). Even if all these  
61 traits can play a similar structural role on overall network structure, for instance by promoting  
62 nestedness (Santamaría & Rodríguez-Gironés 2007; Encinas-Viso *et al.* 2012; Junker *et al.* 2013), they  
63 do not structure interactions with the same mechanisms, potentially affecting species coexistence.  
64 While some species traits, such as morphological traits, decrease competition only by defining  
65 forbidden interactions among species with different traits, other kinds of species traits, such as  
66 phenological traits, can also decrease competition by decoupling interactions in time. This  
67 fundamental difference between the two types of traits implies that the latter trait type can allow  
68 species from the same guild with distinctive trait values to interact indirectly, as they can share  
69 interaction partners at different times, whereas the former type of trait does not allow species to share  
70 interaction partners as soon as they differ in their traits. Such a difference for indirect interactions  
71 between morphological and phenological traits is likely to have important consequences as indirect  
72 effects are known to play a fundamental ecological and evolutionary role, as shown in food webs  
73 (Montoya *et al.* 2009; Salas & Borrett 2011) and mutualistic networks (Guimarães *et al.* 2017; Pires *et al.*  
74 2020). However, whether indirect effects among species depend on the type of traits that shape  
75 interaction networks remains unexplored and so does the consequences for species coexistence.

76        Contrasting effects of morphological and phenological traits might be especially important in  
77 pollination networks because the coexistence of mutualistic networks is expected to strongly depend  
78 on the relative importance of indirect competition and indirect facilitation within guilds, either plant or

79 pollinator. Indeed Bastolla et al. (2009) showed that the nestedness of mutualistic networks increases  
 80 network persistence by minimizing competition while preserving facilitation. In the case of  
 81 interactions structured by morphological traits, the absence of competition between two pollinators, or  
 82 plants, is expected to be coupled with the absence of indirect facilitation between these pollinators, or  
 83 plants, because the species involved do not share mutualistic partners (Fig. 1). In contrast, when  
 84 interactions are structured by phenological traits, they can be decoupled in time thus removing  
 85 competition but maintaining facilitation between the two pollinators, as they can still share the same  
 86 mutualistic partners (Fig. 1). From the schematic example presented in Figure 1, we expect that a  
 87 network mainly structured by phenological traits buffers competition but maintains facilitation within  
 88 plant and pollinator guilds, contrary to a network structured by morphological traits. We thus  
 89 hypothesize that in plant-pollinator networks, differences in phenological traits among species might



90 promote greater coexistence than species differences in morphological traits because phenology  
 91 differences might increase the relative importance of facilitation over competition among plants and  
 92 among pollinators.

93 **Fig. 1:** Schematic pollination networks with no structuring trait (left), structured by a  
 94 morphological trait (center) or by a phenological trait (right). Links between pollinators and plants  
 95 represent mutualistic interactions (+/+) whereas indirect effects within the pollinator guild are  
 96 represented by dashed arrows. Gaussians represent the distributions of the values of the  
 97 morphological trait or the flowering/flight periods for plants and pollinators, and the overlap among  
 98 them (colored area) represents the interaction strength.

99

100 Here we test this hypothesis and quantify how phenological and morphological traits affect the  
101 relative strength of competition and facilitation and the persistence of plant-pollinator networks. To do  
102 so we develop a dynamic model of pollination networks including intra-guild competition for access to  
103 mutualistic partners and measure direct and indirect effects among species over all possible paths in  
104 the networks. Our results reveal that niche partitioning due to the phenological and morphological  
105 traits, henceforth phenological and morphological forcing respectively, strongly differ in their  
106 consequences on pollination network structure and persistence when there is intra-guild competition.

## 107 **Methods**

108 We developed a dynamic model describing the interactions between two guilds, pollinators ( $P$ ) and  
109 plants ( $F$ , flowers). This model extends a classical model of mutualistic networks (Bastolla *et al.* 2009;  
110 Rohr *et al.* 2014; Pascual-García & Bastolla 2017) by modeling competition as a function of plant-  
111 pollinator interactions, i.e. in the functional response of mutualistic interactions, which is key for  
112 studying the dynamics of mutualistic networks (Valdovinos 2019). Our model assumes that species  
113 belonging to the same guild compete with each other for partners, and species from distinct guilds  
114 interact mutualistically. Mutualistic interactions are obligate and defined by both phenological and  
115 morphological matching between plants and pollinators. This model is detailed below, and some  
116 complementary details about modelling choices are given in Supplementary Methods.

### 117 *Phenological and morphological traits structure the networks*

118 Each species was characterized by a phenological and a morphological distribution, both modeled  
119 by Gaussian curves. A Gaussian allows to represent a bell shape that often fits well the phenologies of  
120 flowering and pollinator activity (Rabinowitz *et al.* 1981; Malo 2002; Stewart *et al.* 2020) or  
121 morphological trait distributions (Sletvold *et al.* 2016). Gaussian parameters have direct biological  
122 meaning: the mean corresponds to the phenology peak or average morphological trait value and the  
123 variance to the phenology duration or morphological variation within species. For phenology, we used  
124 circular wrapped Gaussian distributions to account for the fact that seasonal dynamics are circulars  
125 and that two species can have overlapping phenologies in winter. For morphology, we used a one  
126 dimension niche, which is not circular, following classical assumptions of models based on  
127 morphological traits (Santamaría & Rodríguez-Gironés 2007). The mean flowering date and the mean  
128 flight date of the phenologies, i.e. the mean of the corresponding Gaussians, were sampled from a  
129 normal distribution  $N(190,70)$ , representing the pollination season in day of the year. Other trait values  
130 were sampled from uniform laws detailed in Table 1. While using a circular-wrapped distribution for  
131 phenology and not for morphology increases realism, it also introduces a difference of distribution  
132 between the two trait types that could influence our results. We checked this potential effect by  
133 performing the analysis using circular wrapped distribution for both trait types, and our results  
134 remained unchanged (*cf.* Supplementary Methods and Figure S7).

135 The network interactions between plants and pollinators were defined as a function of the matches  
 136 among the species phenologies and among the species morphologies. These matches are measured as  
 137 the overlapping area of the Gaussians, modeling either the phenological or the morphological trait  
 138 values of plants and pollinators, which is the area under the curve determined by the minimum density  
 139 of both Gaussians at each point. These matches were stored in two matrices of dimension  $n_f \times n_p$ , the  
 140 number of plant and pollinator species respectively, one containing phenological matches ( $Phe$ ) and  
 141 one containing the morphological matches ( $M$ ). To modulate the structuring effects of phenological  
 142 and morphological traits, we elevated the terms of the matrices to a power ranging from 0 to 1, with  
 143  $PF$  (phenological forcing parameter) and  $MF$  (morphological forcing parameter) the exponents for  
 144 phenologies and morphologies respectively. A higher exponent corresponds to a higher forcing (*i.e.*  
 145 structuring effect of the given trait), 0 meaning that the corresponding trait does not constrain species  
 146 interactions (*i.e.* no forcing, or structuring effect). Finally, the interaction matrix, called  $I$  and of  
 147 dimension  $n_f \times n_p$ , was built by doing the Hadamard product (term to term) between the two  
 148 matrices:

$$149 \quad I = Phe^{PF} \circ M^{MF} \quad (1)$$

150  $I_{ij}$  represents the interaction strength between the plant  $i$  and the pollinator  $j$ .

### 151 *Dynamic model*

152 We modelled the dynamics of the abundance of each pollinator and each plant using the following  
 153 equations and parameters (Table 1):

$$154 \quad \frac{dP_j}{dt} = P_j \left( -\frac{P_j}{K_j} - m_j + \frac{\alpha_j \sum_{k=1}^{n_f} I_{kj} \times F_k}{1 + \beta \sum_{k=1}^{n_f} I_{kj} \times F_k + c \sum_{k=1}^{n_p} \omega_{kj} \times P_k} \right) \quad (2)$$

$$155 \quad \frac{dF_i}{dt} = F_i \left( -\frac{F_i}{K_i} - m_i + \frac{\alpha_i \sum_{k=1}^{n_p} I_{ik} \times P_k}{1 + \beta \sum_{k=1}^{n_p} I_{ik} \times P_k + c \sum_{k=1}^{n_f} \theta_{ki} \times F_k} \right) \quad (3)$$

156  $P_j$  corresponds to the abundance of pollinator species  $j$  and  $F_i$  to the abundance of plant species  $i$ .  
 157  $K_j$  is the carrying capacity of the species  $j$  (either a pollinator or a plant) and  $m_j$  its mortality rate. The  
 158 benefits of mutualism on the growth of plant and pollinator species are represented by a functional  
 159 response which depends both on the abundance of the mutualistic partners and on the abundance of the  
 160 within-guild competitors. First, the mutualism benefit for species  $j$  increases with  $\alpha_j$ , which combines  
 161 together the conversion efficiency and the search rate or the attractiveness rate for pollinators and  
 162 plants respectively, and with the interaction strength with its mutualistic partners ( $I_{ij}$ ). Second, the  
 163 benefit saturates with the abundance of the mutualistic partners depending on the handling time  
 164 parameter  $\beta$ . Third, it decreases with the abundance of within-guild competitors depending on the  
 165 maximum competition strength  $c$  and on the intensity of competition on species  $j$  from competitor  
 166 species  $k$ , which is  $\omega_{kj}$  for pollinators and  $\theta_{ki}$  for plants.  $\omega_{kj}$  is defined as:

167 
$$\omega_{kj} = \frac{1}{\sum_{i=1}^{n_f} I_{ij} \times F_i} \times D_{kj}^{PF} \times \sum_{i=1}^{n_f} F_i \times I_{ik} \times I_{ij} \quad (4)$$

168  $\omega$  is a matrix of dimensions  $n_p \times n_p$ , containing intra and inter-specific competition terms among  
 169 pollinators.  $\omega_{kj}$  depends on  $D_{kj}^{PF}$ , which is the intra-guild phenological overlap between the pollinator  $j$   
 170 and the pollinator  $k$  elevated at power  $PF$  (phenological forcing), as well as on the strengths of the  
 171 interactions between pollinator  $k$  and the different plants visited by pollinator  $j$  and on the relative  
 172 dependence of pollinator  $j$  on these plants. Competition intensity on pollinator species  $j$  thus increases  
 173 if other pollinators co-occur at the same time (i.e. high phenological overlap) and interact with the  
 174 plant species on which pollinator  $j$  depends. More specifically, competition strength received by  
 175 pollinator  $j$  from pollinator  $k$  through plant  $i$  is proportional to abundance of pollinator  $k$  ( $P_k$ ) and to  
 176 the amount of interactions that represents plant  $i$  ( $I_{ij} \times F_i$ ) relatively to all interactions maintained by  
 177 pollinator  $j$  ( $\sum_{i=1}^{n_f} I_{ij} \times F_i$ ). So, if a plant becomes extinct it does not promote competition among  
 178 pollinators anymore, and reciprocally. Note that in our model no phenological overlap ( $D_{kj}^{PF} = 0$ )  
 179 means no competition, assuming that there is no resource depletion by earlier species that affects later  
 180 ones (see Supplementary Methods). An analog matrix called  $\theta$  is built for plants, meaning that plants  
 181 also compete for pollinators in the same way.

182 Overall,  $\omega$  and  $\theta$  introduce the fundamental difference between phenology and morphology traits  
 183 in our model. Indeed, there is no competition between plants  $k$  and  $j$  or between pollinators  $k$  and  $j$  if  
 184 their phenologies do not overlap ( $D_{kj}^{PF} = 0$ ) even if they can still share some mutualistic partners  $i$  (i.e.  
 185  $I_{ik} \times I_{ij} > 0$ ). However, morphological traits can only prevent competition if species  $k$  and  $j$  do not  
 186 share any mutualistic partner (i.e.  $\forall i I_{ik} \times I_{ij} = 0$ ).

### 187 *Simulations*

188 Parameter values used for the simulations are described in Table 1. All phenological and  
 189 morphological traits as well as functional response parameters exhibit inter-specific heterogeneity,  
 190 except for handling times ( $\beta$ ) that we kept constant to save computing time, as systems reached the  
 191 equilibrium much faster when species functional responses differed only on the  $\alpha$  parameter.

192 We generated 1000 initial networks varying in the above-mentioned parameters (Table 1). For each  
 193 of these networks, we performed simulations with five values of  $MF$ , five values of  $PF$  and with four  
 194 values of intra-guild competition strength ( $c$ ), leading to a total of 100 000 simulations (1000×5×5×4).  
 195 We solved the equations numerically using the *lsoda* solver implemented in the R package *deSolve*  
 196 (Soetaert *et al.* 2010). We stopped the simulation when the variance of species abundance over the last  
 197 10 time-steps was lower than  $10^{-9}$ , which was enough to reach the equilibrium (i.e. negative real part  
 198 of eigenvalues of the Jacobian matrix).



200 We quantified two indices at the network level: the network persistence, which is the percentage of  
 201 species with an abundance  $>10^{-5}$  at equilibrium and the nestedness of the interaction matrix, calculated  
 202 as the weighted NODF (Galeano *et al.* 2009) of the interaction matrix  $I$  at equilibrium, after we  
 203 removed extinct species and rounded the interaction strengths  $I_{ij}$  to the 5<sup>th</sup> digit to avoid numerical  
 204 issues. We also calculated the network viability over the 1000 networks of each parameter  
 205 combination, which is the proportion of simulated networks containing at least one plant and one  
 206 pollinator at equilibrium.

207 **Table 1: Parameter values of the dynamic model.** Parameter combinations correspond to the  
 208 different combinations of intra-guild competition, morphological forcing and phenological forcing,  
 209 which are the parameters of interest here. Other important parameters vary among the 1,000 initial  
 210 networks in order to explore a wide set of possible pollination networks.

Parameter abbreviation	Meaning	Value	Variation among		
			species	1000 initial networks	Parameter combinations
<b>n<sub>r</sub></b>	Initial number of plant species	75	-	No	No
<b>n<sub>p</sub></b>	Initial number of pollinator species	75	-	No	No
<b>K</b>	Plant ( $K_i$ ) or pollinator ( $K_j$ ) carrying capacity	$K_i \sim U(10,600)$ $K_j \sim U(1,60)$	Yes	Yes	No
<b>m</b>	Plant ( $m_i$ ) or pollinator ( $m_j$ ) mortality rate	$m_i \sim U(0.2,0.4)$ $m_j \sim U(0.8,1)$	Yes	Yes	No
<b>α</b>	Plant ( $\alpha_i$ ) or pollinator ( $\alpha_j$ ) attractiveness rate	$\sim U(0.8,1)$	Yes	Yes	No
<b>β</b>	Plant or pollinator saturation term (handling time)	0.9	No	No	No
<b>c</b>	Intra-guild maximum competition strength	0/0.25/0.5/0.75	No	No	Yes
<b>MFD</b>	Mean Flowering ( $MFD_i$ ) or Flight ( $MFD_j$ ) date	$\sim N(190,70)$	Yes	Yes	No
<b>SD</b>	Flowering ( $SD_i$ ) or Flight ( $SD_j$ ) period duration (standard deviation)	$\sim U(5,40)$	Yes	Yes	No
<b>TM</b>	Plant ( $TM_i$ ) or pollinator ( $TM_j$ ) morphological niche center	$\sim U(-1.5,1.5)$	Yes	Yes	No
<b>G</b>	Width of plant ( $G_i$ ) or pollinator ( $G_j$ ) morphological niche (standard deviation)	$\sim U(0.1,0.9)$	Yes	Yes	No
<b>MF</b>	Morphological forcing parameter	0/0.25/0.5/0.75 /1	-	No	Yes
<b>PF</b>	Phenological forcing parameter	0/0.25/0.5/0.75 /1	-	No	Yes

211

212 *Partitioning of direct, indirect and total effects*

213 To study how the phenological and the morphological structures affect the propagations of indirect  
 214 effects, we calculated the direct effect, the indirect effect and the sum of both, i.e. the total effect,  
 215 among each species pair (Fig. 2). Since we were not interested in the equilibrium displacement  
 216 following a perturbation but in estimating the strength of links among species at equilibrium, we used  
 217 the analytic formulas demonstrated by Nakajima & Higashi (1995), which considers the net effect of a  
 218 sustained unit increase in species  $j$  on species  $i$  growth rate (“abundance to inflow” perturbation,

219 Nakajima & Higashi 1995). This method allowed us to estimate how a species was affected by an  
 220 increase of the abundance of another species at equilibrium. In this case, the jacobian matrix ( $A$ ),  
 221 estimated using persistent species only, represented the direct effects among pairs of species  
 222 (Nakajima & Higashi 1995). As the competition was implemented in a direct way (equations (2) and  
 223 (3)), it was considered as a direct effect. Total effects were estimated from the sensitivity matrix ( $S$ ),  
 224 which was defined by the inverse of the jacobian matrix:

$$225 \quad S = A^{-1} \quad (5)$$

226 Then, the total effect of a species  $j$  on a species  $i$  ( $T_{ij}$ ) was calculated from the coefficients of  $S$   
 227 using the following formula:

$$228 \quad T_{ij} = \frac{s_{ij}}{s_{ii}s_{jj} - s_{ij}s_{ji}} \quad (6)$$

229 Thus, the total effect  $T_{ij}$  was the effect of the disturbed species  $j$  on the focal species  $i$  by all the  
 230 paths, excepting paths that revisit one of the two species  $i$  and  $j$ . By doing so, we removed paths  
 231 looping on the disturbed (i.e. donor) or on the focal (i.e. receiver) species, allowing us to focus on  
 232 interspecific relationships. Then, the effect of the species  $j$  on the species  $i$  through indirect effects  
 233 ( $IE_{ij}$ ), was calculated as:

$$234 \quad IE_{ij} = T_{ij} - A_{ij} \quad (7)$$

235 We further categorized these direct, indirect and total effects into four types depending on the  
 236 guilds of the donor and the receiver species: effects within the pollinator guild, effects within the plant  
 237 guild, effects between guilds received by plants (from pollinators), and effects between guilds received  
 238 by pollinators (from plants).

#### 239 *Analysis of the indirect effect contributions*

240 We calculated the contributions of indirect effects to the total effects received by species within  
 241 ( $\overline{IEC_p}$  and  $\overline{IEC_f}$ ) and among ( $\overline{IEC_{pf}}$  and  $\overline{IEC_{fp}}$ ) guilds. The contributions were averaged over all pairs  
 242 of persisting species, as detailed in Supplementary Methods. The signs of these contributions  
 243 correspond to the sign of indirect effects while the absolute value of these contributions correspond to  
 244 their importance relatively to direct effects.

245 Diversity and nestedness have been shown to affect the importance of indirect effects in  
 246 ecological networks (Bastolla *et al.* 2009; Iles & Novak 2016). As phenological and morphological  
 247 forcing might affect network diversity and nestedness at equilibrium, we disentangled the effects  
 248 mediated by diversity and nestedness from the direct effects of phenological and morphological  
 249 forcing on the relative contribution of indirect effects to total effects among species within guilds  
 250 ( $\overline{IEC_p}$  or  $\overline{IEC_f}$ ), by performing a path-analysis for each guild. To do so, we used Structural Equation

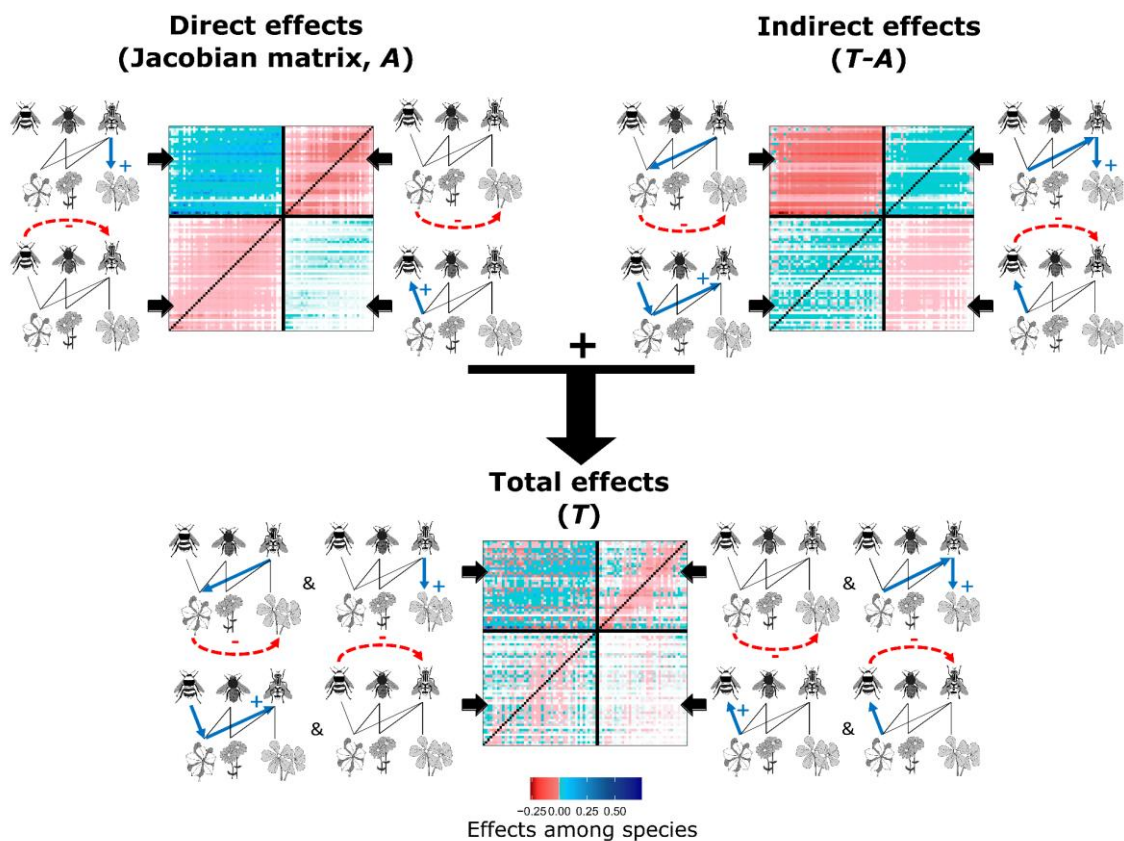
251 Modeling (SEM) following a previous study (Thébault & Fontaine 2010), as detailed in  
 252 Supplementary Methods.

253 *Indirect, direct and total effects at the species level*

254 To quantify the amount of direct, indirect and total effects generated by each species, we summed  
 255 all the effects of each species to every other species from the same guild, thereby obtaining the effect  
 256 of species  $j$  on the growth rate of the total abundance of its guild excepting species  $j$ . The direct effect  
 257 generated by pollinator species  $j$  to all other pollinators ( $PDE_{j(p)}$ ) is:

258 
$$PDE_{j(p)} = \sum_{i=1}^{n_{peq}} (i \neq j) A_{ij} \quad (8)$$

259 Where  $n_{peq}$  is the number of pollinator species persisting at equilibrium. We did the same for plants  
 260 and for indirect and total effects, using  $IE_{ij}$  and  $T_{ij}$  terms respectively instead of  $A_{ij}$ . We thus obtained  
 261 three values for each plant and pollinator species corresponding to generated direct, indirect and total  
 262 effects within guilds.



263 **Fig. 2: Example of matrices of direct, indirect and total effects at equilibrium.** Jacobian matrix (A,  
 264 top left), indirect effect matrix (top right, see methods) and total effect matrix (T, bottom) of a network  
 265 at equilibrium, for MF=0.5, PF=0.5 and c=0.5. Blue colors represent positive effects while red colors  
 266 represent negative effects among species. Matrix diagonals were uncolored to focus on inter-specific  
 267 relationships (see Methods). In the Jacobian matrix, blocks along the diagonal represent the  
 268 competition effects within guilds, while off-diagonal blocks represent plant-pollinator direct effects.  
 269 The total effect matrix (T) represents the sum of the direct and indirect effects among species, so the  
 270 term to term difference between both matrices (T – A) gives the indirect effects only. Schematic  
 271

272 *networks represent examples of short path indirect effects but in our method we integrated indirect*  
273 *effects over all possible paths.*

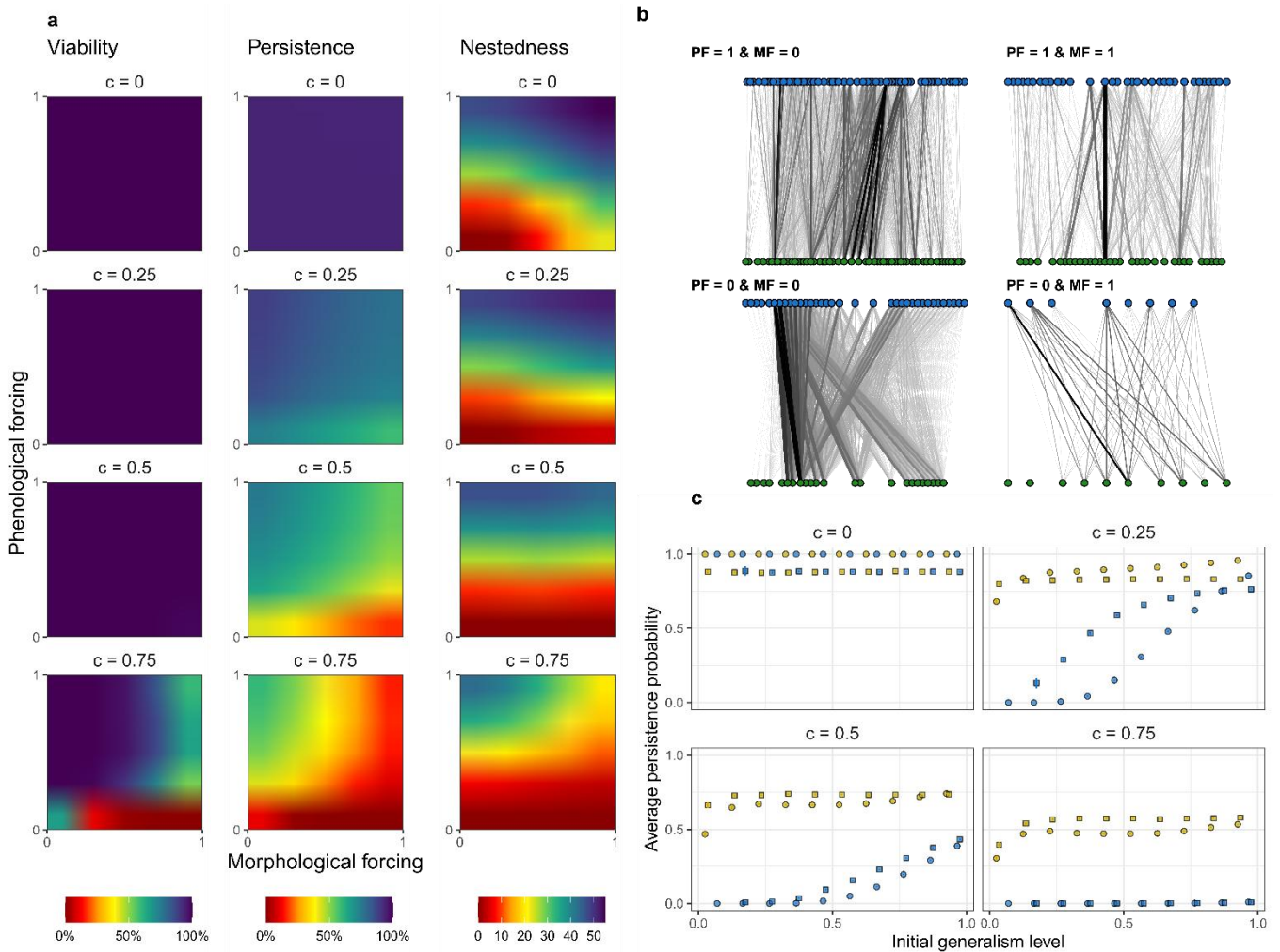
274 *Analysis at the species level*

275 First, we assessed how phenological and morphological traits affect species persistence depending  
276 on their generalism level. Initial and at equilibrium generalism levels were calculated for each species  
277 averaging its interaction strengths in the network, as detailed in supplementary Methods. We grouped  
278 the species by initial generalism level using bins of 0.1 and by the competition coefficient  $c$  of the  
279 simulation. Persistence probability per species group was calculated as the proportion of persisting  
280 species in each group of generalism. Second, we studied the relationships between the persistence  
281 probability and the initial generalism level, and between the species effects generated within-guilds  
282 and the generalism level at equilibrium, comparing simulations with phenological forcing only ( $MF =$   
283  $0$  &  $PF > 0$ ) and simulations with morphological forcing only ( $MF > 0$  &  $PF = 0$ ).

## 284 **Results**

285 Our results show that the structuring effects of phenological and morphological traits on network  
286 viability, persistence and nestedness are the same in the absence of intra-guild competition ( $c = 0$ ) but  
287 they strongly differ when there is intra-guild competition ( $c > 0$ , Fig. 3a). In absence of intra-guild  
288 competition, both phenological and morphological forcings strongly increase network nestedness  
289 while they slightly decrease network persistence and do not affect viability. Such decrease in  
290 persistence is explained by the extinction of species with marginal trait values, which have not enough  
291 mutualistic interactions to persist. When intra-guild competition is present, stronger phenological  
292 forcing (high  $PF$  values) leads to higher network viability, persistence and nestedness (Fig. 3a,b),  
293 while stronger morphological forcing ( $MF$ ) decreases network viability and persistence, and fails to  
294 promote nestedness (Fig. 3a,b). Differences in nestedness between the cases with and without intra-  
295 guild competition are due to species extinctions as nestedness is measured directly on the matrix of  
296 interaction strengths  $I$ , without accounting for species abundances. As expected, higher intra-guild  
297 competition decreases network viability and persistence but our results reveal that such effects are  
298 dampened when the structuring effect of phenology is strong (Fig. 3a).

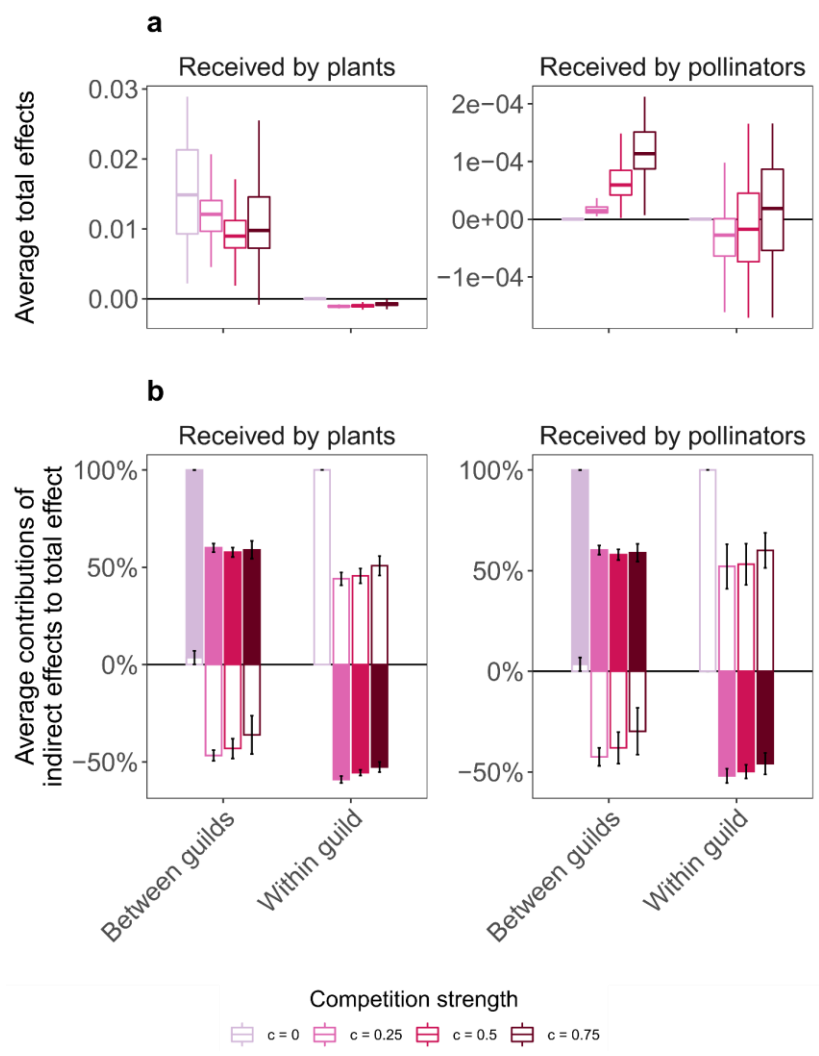
299



300 **Figure 3: Network properties at the ecological equilibrium and species persistence.** (a) Equilibrium  
 301 network properties as a function of the competition strength  $c$ , and phenological and morphological  
 302 forcing parameters. Viability is the percentage of networks with at least one plant and one pollinator  
 303 at equilibrium, persistence is the average percentage of surviving species at equilibrium, and  
 304 nestedness is the weighted NODF of the interaction matrix  $I$  at equilibrium. (b) Example of networks  
 305 at equilibrium for extreme values of phenological forcing (PF) and morphological forcing (MF) and  
 306 for  $c=0.5$ , showing how network persistence and interaction distribution change depending on the  
 307 type of traits structuring networks. Networks were constructed by multiplying the values of interaction  
 308 strengths by the geometric mean of associated species abundances and then by removing links with a  
 309 weight lower than one. Blue points represent pollinators while green points represent plants. (c)  
 310 Pollinator (squares) and plant (circles) persistence probability as a function of the initial generalism  
 311 level and the competition coefficient. Blue points correspond to simulations with a morphological  
 312 forcing only (PF=0 & MF>0) and yellow points correspond to simulations with a phenological  
 313 forcing only (PF>0 & MF=0). Points were staggered to ease readability.

314

315 Differences in network persistence and nestedness between the two types of forcing can be  
 316 understood further by considering species persistence as a function of species initial generalism level  
 317 in the networks. When there is intra-guild competition, specialist species, species with short flight  
 318 period and/or a narrow morphological trait niche, have a lower persistence probability than generalist  
 319 species (Fig. 3c & S1). The lower persistence of specialist species compared to generalists is  
 320 attenuated when networks are structured by a phenological trait compared to when they are structured  
 321 by a morphological trait (Fig. 3c). By maintaining specialist species at equilibrium, the phenological  
 322 forcing thus maintains the heterogeneity in the distribution of generalism levels as required to get a  
 323 nested network. Indeed, nestedness is positively correlated to the variability of generalism levels of  
 324 persistent species (Fig. S2). This explains why networks structured by phenology retain higher



325 nestedness than networks structured by morphology.

326 **Figure 4:** Within and between guilds effects partitioning at equilibrium and their relative  
 327 contributions to total effects. (a) Within and between guilds strength of total effects received by  
 328 species averaged at the guild level for plants and pollinators, per level of competition strength  
 329 represented by different colors. (b) Within and between guilds contributions in percentages of direct  
 330 (filled bars) and indirect (open bars) effects to total effects, averaged at the guild level, per level of  
 331 competition strength represented by different colors. Values represented are the mean of the

332 *distribution over simulations, while error bars represent standard deviation of the mean. In (a)*  
333 *outliers are not represented to preserve readability.*

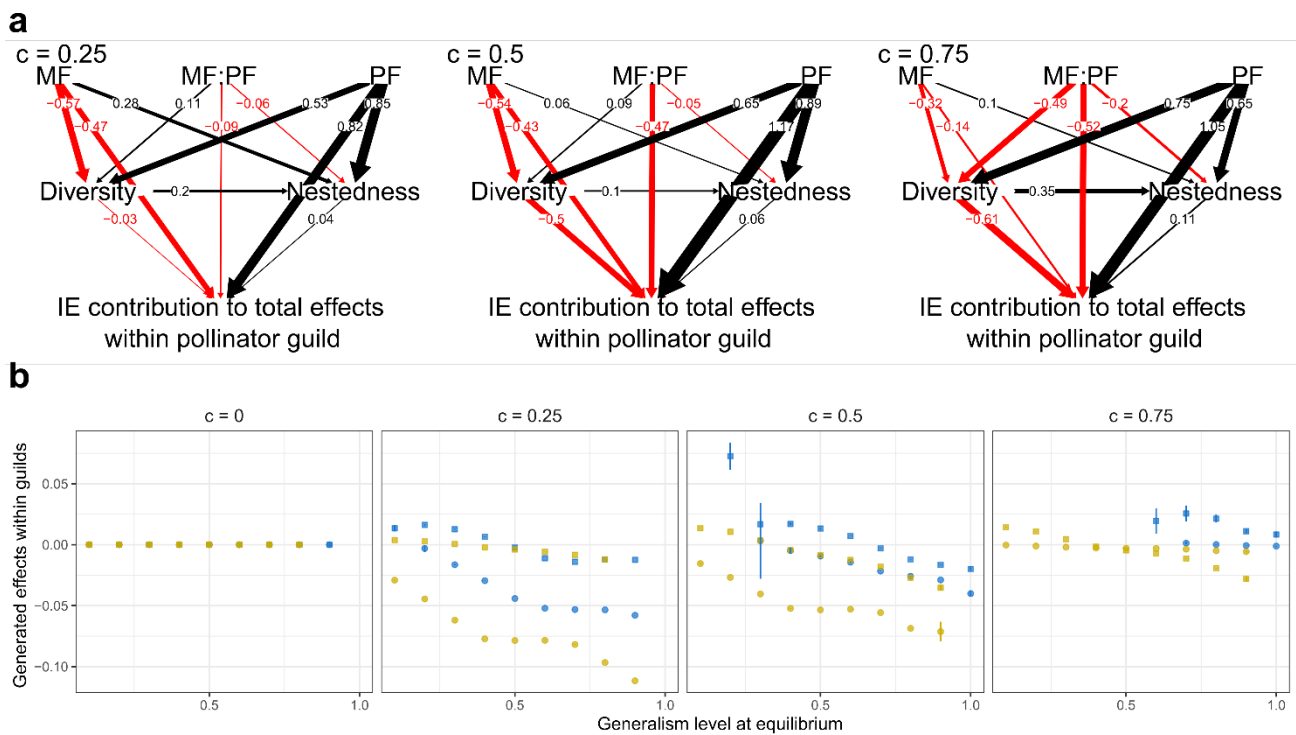
334 As expected, intra-guild competition strongly affects the average strength of direct and indirect  
335 effects among species in the networks at equilibrium, resulting in changes in total effects among  
336 species (Fig. 4a,b). When there is no intra-guild competition, implemented here as a direct effect  
337 within guilds, positive indirect effects are the only contributors to the total effects within guilds, for  
338 both plants and pollinators. In that case, indirect effects between guilds are also positive, but very  
339 weak relatively to direct mutualistic interactions (Fig. 4b). When intra-guild competition is present ( $c$   
340  $> 0$ ), indirect effects are in most cases opposite to direct effects between guilds and within guilds  
341 (Figure 4b, Table S1). Within guilds, indirect effects are positive, opposite to direct competition,  
342 because species from the same guild often maintain common partners thereby benefiting from  
343 facilitation in addition to competing for resources. Further, indirect effects contribute to ~50% of the  
344 total effects within guilds and slightly less between guilds (Fig. 4b). Indirect effects can be strong  
345 enough to balance the competition within guilds and the mutualistic interaction between guilds (Fig. 2,  
346 Fig. 4a, Table S1).

347 Consistently with our expectations, when there is intra-guild competition, total effects within guilds  
348 are less negative when there is phenological forcing than when morphological forcing is present (Fig.  
349 S3). However, since networks at equilibrium differ in diversity and nestedness between the two types  
350 of forcing (Fig. 3), we used a path-analysis to disentangle the effects mediated by diversity and  
351 nestedness from those directly due to the phenological and morphological forcings. We focused on the  
352 contribution of indirect effects to total effect within the pollinator guild because pollinator growth  
353 rates strongly depend on within guild total effects while plant growth rates mainly depend on plant-  
354 pollinator interactions (Figure 4a), this because of parametrization choices.

355 The path analysis first reveals that diversity at equilibrium strongly decreases the contribution of  
356 positive indirect effects to total effects within the pollinator guild, while this contribution is slightly  
357 increased by nestedness (Fig. 5a). Second, independently from the effects mediated by diversity and  
358 nestedness, phenological forcing increases the contribution of positive indirect effects to the total  
359 effects within pollinator guild (Fig. 5a). In contrast, morphological forcing strongly decreases the  
360 contribution of positive indirect effects within pollinator guild (Fig. 5a). Further, the interaction  
361 between the phenological and the morphological structuring effects, implemented by forcing  
362 parameters  $PF$  and  $MF$  respectively, has a strong negative effect on the contribution of positive  
363 indirect effects to total effect within pollinator guild, suggesting that combining the two forcings  
364 decreases the contribution of positive indirect effects within pollinator guild (Fig. 5a). Those results  
365 mean that, in contrast to morphological traits, phenological traits, which decouples interaction in time,  
366 favor facilitation over competition within pollinator guild.



367 Importantly, phenological and morphological forcing affect the balance between competition and  
 368 positive indirect effects within pollinator guild in two different ways: while phenological forcing  
 369 increases positive indirect effects within the pollinator guild but also competition, morphological  
 370 forcing does the opposite, decreasing competition but also positive indirect effects (Fig. S4). Thus, the  
 371 positive effect of phenological forcing on the contribution of indirect effects to total effects is due to  
 372 the fact that it increases positive indirect effects more than it increases competition, while  
 373 morphological forcing does not decrease competition more than it decreases positive indirect effects  
 374 within pollinator guild. The larger contribution of positive indirect effects to total effects within the  
 375 pollinator guild when networks are structured by phenological traits might also be linked to the greater  
 376 persistence of specialists in such networks (Fig. 3c). Indeed, quantifying the effects generated per  
 377 species, i.e. the effect a species has on the summed growth rates of all other species from the same  
 378 guild, we show that specialist species tend to generate less negative total effects within guilds than  
 379 generalists (Fig. 5b). Generalist species generate stronger direct and indirect effects than specialists  
 380 (Fig. S6) as they have many mutualistic partners and thus many competitors and facilitators. However,



381 specialists tend to generate more positive indirect effects than direct competitive effects (Fig. S6). We  
 382 detect the same patterns as in Fig. 5a for the contribution of positive indirect effects to total effects  
 383 within the plant guild, but only for strong intra-guild competition strength (Fig. S5), likely due to the  
 384 weaker importance of within-guild effects for plants than for pollinators (Fig. 4a).

385 **Figure 5: Effects of morphological and phenological forcing parameters on the contribution of**  
 386 **indirect effects (IE) within the pollinator guild.** (a) Determinants of the contribution of indirect  
 387 effects (IE) to total effects within the pollinator guild. Values on arrows are standardized coefficients  
 388 of the multi-group path-analysis performed on data for different values of intra-guild competition  
 389 strengths  $c$ . This model includes an interaction (MF:PF) between the phenological (PF) and  
 390 morphological (MF) forcing. Diversity is the number of persistent species at equilibrium. (b) Total



391 effects generated within guilds by pollinators (squares) and by plants (circles) as a function of species  
392 generalism at equilibrium. Blue points correspond to simulations with a morphological forcing only  
393 ( $PF=0$  &  $MF>0$ ) and yellow points correspond to simulations with a phenological forcing only  
394 ( $PF>0$  &  $MF=0$ ). Error bars are 95% confidence intervals. Values are averaged by tenths of species  
395 generalism and points are slightly staggered for readability.

396

## 397 **Discussion**

398 Our results show that the structuring effect of phenological traits on plant-pollinator interactions  
399 dampens the negative effects of competition for mutualistic partners on species persistence, leading to  
400 greater diversity and network nestedness than when interactions are structured by morphological traits.  
401 As hypothesized, we find that these two types of traits affect indirect effects in two very distinct ways:  
402 while the structure imposed by morphological traits decreases both competition and positive indirect  
403 effects among species from the same guild, the structure imposed by phenological traits increases  
404 competition and positive indirect effects among species from the same guild. Most importantly, once  
405 differences in network nestedness and diversity are accounted for, we show that phenological traits  
406 lead to a less negative, or more positive, balance between competition and positive indirect effects  
407 within guilds at equilibrium than morphological traits. Since indirect effect estimation is based on a  
408 linear approximation around the equilibrium state, we cannot estimate indirect effects during the  
409 transient dynamics leading to the equilibrium, which prevents us from properly assessing if they are a  
410 cause or a consequence of network persistence. However, there is no difference in persistence between  
411 networks structured by phenology (*i.e.* with a phenological forcing) and networks structured by  
412 morphology (*i.e.* with a morphological forcing) when intra-guild competition is null. This suggests  
413 that the positive effect of phenological forcing on persistence results from changes in net effects of  
414 competition and facilitation between species from the same guild. Taken together, our results show  
415 that the type of species traits shaping interactions in mutualistic networks affect species coexistence,  
416 by altering the balance between competition and facilitation among species from the same guild.

417 The benefits of phenological traits mainly occur because they decouple interactions in time, making  
418 the balance between facilitation and competition less negative than morphological traits. Our results  
419 provide a mechanism that might explain the importance of phenological traits relatively to  
420 morphological traits in seasonal pollination networks (Gonzalez & Loiselle 2016; CaraDonna *et al.*  
421 2017; Manincor *et al.* 2020; Sonne *et al.* 2020), and suggest that the seasonal structure is key to the  
422 maintenance of diversity in mutualistic communities. These findings can be generalized to other traits  
423 than phenology, while they allow to decouple interactions in time or space without leading to resource  
424 depletion. Indeed, any trait following this assumption and decoupling interactions in time or space, as  
425 for example traits associated with daytime activity and flower opening (e.g. diurnal vs night) or with  
426 flight and flower heights, should similarly maintain indirect facilitation within guilds and promote  
427 species coexistence. For instance, differences in flight and flower heights could allow two pollinator

428 species that fly at different height to avoid competition whilst still interacting with the same plant  
429 population, or even with the same individual plant if an individual plant has flowers at different  
430 heights. As plant-pollinator interactions have been shown to differ at small spatial and temporal scales  
431 (Albrecht *et al.* 2012; Knop *et al.* 2017; Cusser *et al.* 2021), we expect that the mechanisms  
432 highlighted in this study are widespread in pollination networks.

433 Competition is known as an important evolutionary and ecological driver of plant-pollinator  
434 interactions (Levin & Anderson 1970; Jones *et al.* 2012; Bartomeus *et al.* 2021) because plants or  
435 pollinators strongly compete among them to access to their mutualistic partners in pollination  
436 networks (Pleasants 1980; Campbell 1985; Henry & Rodet 2018). However, most of the theoretical  
437 studies tackling this point modeled competition independently from plant-pollinator interactions  
438 (Bastolla *et al.* 2009; Pascual-García & Bastolla 2017), while few other studies suggest that  
439 accounting for the seasonal structure in competition increases network persistence (Encinas-Viso *et al.*  
440 2012; Rudolf 2019). Our modeling approach allows structuring competition depending on the sharing  
441 of mutualistic partners in time. Doing so, we show that competition is a major driver of the persistence  
442 of plant-pollinator networks and that the differential effects of phenological and morphological traits  
443 depend on the presence of competition, our scenario with no competition being a null expectation or a  
444 control. Further, we also show that when competition is present, the structuring effect of phenological  
445 traits favors positive indirect effects within guilds, i.e. facilitation, thereby maintaining diversity. Such  
446 effect not only comes from indirect effects among species sharing mutualistic partners, i.e. paths of  
447 length two, but also from indirect effects among species from the same guild over longer paths as our  
448 calculation includes all possible paths.

449 Furthermore, our results highlight that the persistence of specialist species is key to understand the  
450 structuring effects of phenology at equilibrium. As revealed by Saavedra *et al.* (2011), we found that  
451 specialists are the species that promote the most the nestedness of networks at equilibrium, as they  
452 create heterogeneity in degree distribution (Bascompte *et al.* 2003), but they are also the most  
453 vulnerable species. Including a seasonal structure better protects specialist species from extinction,  
454 which provides new insights on mechanisms that could maintain those vulnerable species in networks.  
455 Consequently, we find that phenological forcing increases nestedness much more than morphological  
456 forcing, which is expected to increase the resilience and the robustness of the networks to  
457 perturbations (Memmott *et al.* 2007; Thébault & Fontaine 2010). Moreover, we find that specialist  
458 species propagate more positive indirect effects to other species relatively to their direct competitive  
459 effects than generalists. Thus, in addition to promoting positive indirect effects within guilds by  
460 decoupling interactions in time, the structuring effect of phenology protects species that have a lower  
461 negative balance between positive indirect effects and competitive effects, thereby tilting the balance  
462 even more towards facilitation rather than competition.

463 Recent studies showed that climate warming is shifting pollinator flight periods and flowering  
464 periods, leading to changes in the seasonal structure of pollinator and plant assemblages, which either  
465 increase or decrease phenological overlaps among species depending on the location (Diez *et al.* 2012;  
466 Theobald *et al.* 2017; Duchenne *et al.* 2020). Such changes are likely to cause mismatches among  
467 interacting species (Memmott *et al.* 2007; Revilla *et al.* 2015) and to decrease the robustness of the  
468 network to any other perturbation, thus leading to synergistic effects among perturbations (Revilla *et al.*  
469 *et al.* 2015). Beyond and more insidiously than trophic mismatch, our results highlight that phenological  
470 shifts are likely to affect indirect effects such as competition pressures (Rudolf 2019) and facilitation  
471 in mutualistic assemblages, with currently unknown consequences for biodiversity. Further, since  
472 specialist species are often presented as generally more sensitive to perturbation (Clavel *et al.* 2011)  
473 and we showed that they tend to propagate more positive indirect effects than other species, our results  
474 suggest that perturbations targeting specialists are likely to increase propagation of negative indirect  
475 effects. However, network reorganization following perturbations can also happen (Burkle *et al.* 2013)  
476 and might buffer effects of specialist extinctions.

477 Our results are mostly theoretical and focus on ecological dynamics only. Since in diverse  
478 communities competition can constrain species' evolutionary trajectories (Mazancourt *et al.* 2008), it  
479 is likely that ecological and evolutionary equilibrium differ. An interesting perspective would be to  
480 investigate the consequences of eco-evolutionary dynamics of morphological and phenological traits  
481 on the competition-facilitation balance and related network persistence. In addition, future steps would  
482 be to estimate the real benefits of empirical seasonal structures on coexistence. To do so, the challenge  
483 is not only to assess the relative importance of phenological and morphological overlaps among  
484 species within ecological networks (CaraDonna *et al.* 2017, Sonne *et al.* 2020) but also to solve the  
485 complex "inverse problem" to parametrize models using empirical seasonal and morphological  
486 structures (Tarantola 2005).

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#### 496 **Competing interests**

497 The authors declare no competing interests.

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