

Phenological traits foster persistence of mutualistic networks by promoting facilitation

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All scripts are available here: <https://github.com/f-duchenne/Phenology-favors-persistence-of-mutualistic-communities>. There is no data in this study.

Abstract

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

Introduction

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

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

Contrasting effects of morphological and phenological traits might be especially important in pollination networks because the coexistence of mutualistic networks is expected to strongly depend on the relative importance of indirect competition and indirect facilitation within guilds, either plant or pollinator. Indeed Bastolla *et al.* (2009) showed that the nestedness of mutualistic networks increases

network persistence by minimizing competition while preserving facilitation. In the case of interactions structured by morphological traits, the absence of competition between two pollinators, or plants, is expected to be coupled with the absence of indirect facilitation between these pollinators, or plants, because the species involved do not share mutualistic partners (Fig. 1). In contrast, when interactions are structured by phenological traits, they can be decoupled in time thus removing competition but maintaining facilitation between the two pollinators, as they can still share the same mutualistic partners (Fig. 1). From the schematic example presented in Figure 1, we expect that a network mainly structured by phenological traits buffers competition but maintains facilitation within plant and pollinator guilds, contrary to a network structured by morphological traits. We thus hypothesize that in plant-pollinator networks, differences in phenological traits among species might promote greater coexistence than species differences in morphological traits because phenology differences might increase the relative importance of facilitation over competition among plants and among pollinators.

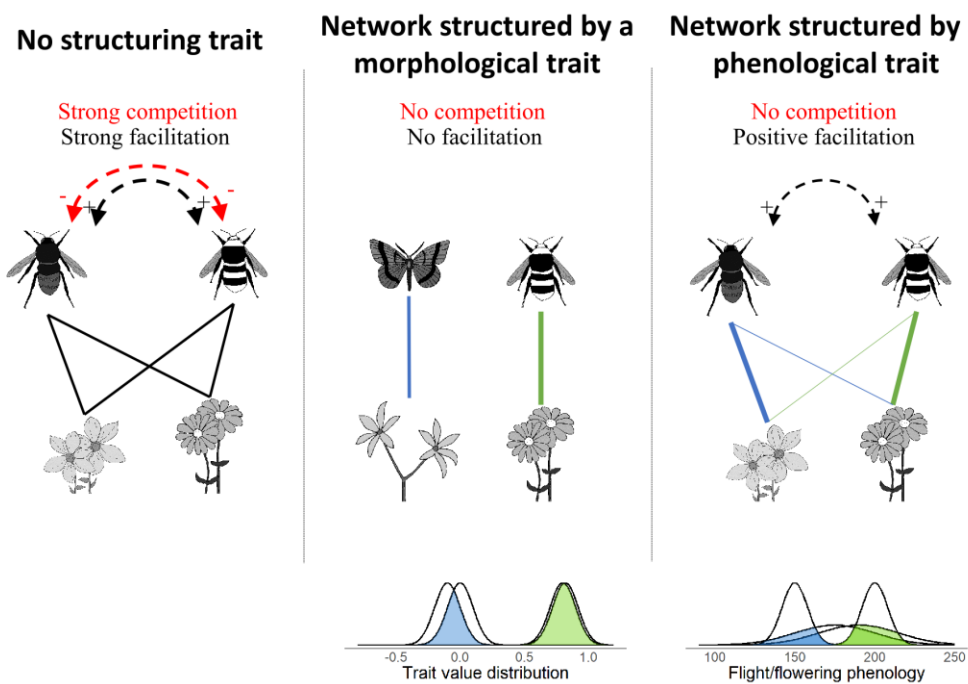


Fig. 1: Schematic pollination networks with no structuring trait (left), structured by a morphological trait (center) or by a phenological trait (right). Links between pollinators and plants represent mutualistic interactions (+/+) whereas indirect effects within the pollinator guild are represented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

Here we test this hypothesis and quantify how phenological and morphological traits affect the relative strength of competition and facilitation and the persistence of plant-pollinator networks. To do so we develop a dynamic model of pollination networks including intra-guild competition for access to mutualistic partners and measure direct and indirect effects among species over all possible paths in the

networks. Our results reveal that niche partitioning due to the phenological and morphological traits, henceforth phenological and morphological forcing respectively, strongly differ in their consequences on pollination network structure and persistence when there is intra-guild competition.

Methods

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

Phenological and morphological traits structure the networks

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

The network interactions between plants and pollinators were defined as a function of the matches among the species phenologies and among the species morphologies. These matches are measured as the overlapping area of the Gaussians, modeling either the phenological or the morphological trait values of plants and pollinators, which is the area under the curve determined by the minimum density of both

Gaussians at each point. These matches were stored in two matrices of dimension $n_f \times n_p$, the number of plant and pollinator species respectively, one containing phenological matches (Phe) and one containing the morphological matches (M). To modulate the structuring effects of phenological and morphological traits, we elevated the terms of the matrices to a power ranging from 0 to 1, with PF (phenological forcing parameter) and MF (morphological forcing parameter) the exponents for phenologies and morphologies respectively. A higher exponent corresponds to a higher forcing (*i.e.* structuring effect of the given trait), 0 meaning that the corresponding trait does not constrain species interactions (*i.e.* no forcing, or structuring effect). Finally, the interaction matrix, called I and of dimension $n_f \times n_p$, was built by doing the Hadamard product (term to term) between the two matrices:

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

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

Dynamic model

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

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

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

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

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

ω is a matrix of dimensions $n_p \times n_p$, containing intra and inter-specific competition terms among pollinators. ω_{kj} depends on D_{kj}^{PF} , which is the intra-guild phenological overlap between the pollinator j and the pollinator k elevated at power PF (phenological forcing), as well as on the strengths of the

interactions between pollinator k and the different plants visited by pollinator j and on the relative dependence of pollinator j on these plants. Competition intensity on pollinator species j thus increases if other pollinators co-occur at the same time (i.e. high phenological overlap) and interact with the plant species on which pollinator j depends. More specifically, competition strength received by pollinator j from pollinator k through plant i is proportional to abundance of pollinator k (P_k) and to the amount of interactions that represents plant i ($I_{ij} \times F_i$) relatively to all interactions maintained by pollinator j ($\sum_{i=1}^{n_j} I_{ij} \times F_i$). So, if a plant becomes extinct it does not promote competition among pollinators anymore, and reciprocally. Note that in our model no phenological overlap ($D_{kj}^{PF} = 0$) means no competition, assuming that there is no resource depletion by earlier species that affects later ones (see Supplementary Methods). An analog matrix called θ is built for plants, meaning that plants also compete for pollinators in the same way.

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

Simulations

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

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

Network indices

We quantified two indices at the network level: the network persistence, which is the percentage of species with an abundance $> 10^{-5}$ at equilibrium and the nestedness of the interaction matrix, calculated as the weighted NODF (Galeano *et al.* 2009) of the interaction matrix I at equilibrium, after we removed extinct species and rounded the interaction strengths I_{ij} to the 5th digit to avoid numerical issues. We also

calculated the network viability over the 1000 networks of each parameter combination, which is the proportion of simulated networks containing at least one plant and one pollinator at equilibrium.

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

Parameter abbreviation	Meaning	Value	Variation among		
			species	1000 initial networks	Parameter combinations
n_f	Initial number of plant species	75	-	No	No
n_p	Initial number of pollinator species	75	-	No	No
K	Plant (K_i) or pollinator (K_j) carrying capacity	$K_i \sim U(10,600)$ $K_j \sim U(1,60)$	Yes	Yes	No
m	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
α	Plant (α_i) or pollinator (α_j) attractiveness rate	$\sim U(0.8,1)$	Yes	Yes	No
β	Plant or pollinator saturation term (handling time)	0.9	No	No	No
c	Intra-guild maximum competition strength	0/0.25/0.5/0.75	No	No	Yes
MFD	Mean Flowering (MFD _i) or Flight (MFD _j) date	$\sim N(190,70)$	Yes	Yes	No
SD	Flowering (SD _i) or Flight (SD _j) period duration (standard deviation)	$\sim U(5,40)$	Yes	Yes	No
TM	Plant (TM _i) or pollinator (TM _j) morphological niche center	$\sim U(-1.5,1.5)$	Yes	Yes	No
G	Width of plant (G_i) or pollinator (G_j) morphological niche (standard deviation)	$\sim U(0.1,0.9)$	Yes	Yes	No
MF	Morphological forcing parameter	0/0.25/0.5/0.75 /1	-	No	Yes
PF	Phenological forcing parameter	0/0.25/0.5/0.75 /1	-	No	Yes

Partitioning of direct, indirect and total effects

To study how the phenological and the morphological structures affect the propagations of indirect effects, we calculated the direct effect, the indirect effect and the sum of both, i.e. the total effect, among each species pair (Fig. 2). Since we were not interested in the equilibrium displacement following a perturbation but in estimating the strength of links among species at equilibrium, we used the analytic formulas demonstrated by Nakajima & Higashi (1995), which considers the net effect of a sustained unit increase in species j on species i growth rate (“abundance to inflow” perturbation, Nakajima & Higashi 1995). This method allowed us to estimate how a species was affected by an increase of the abundance of another species at equilibrium. In this case, the jacobian matrix (A), estimated using persistent species only, represented the direct effects among pairs of species (Nakajima & Higashi 1995). As the competition was implemented in a direct way (equations (2) and (3)), it was considered as a direct effect. Total effects were estimated from the sensitivity matrix (S), which was defined by the inverse of the jacobian matrix:

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

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

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

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

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

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

Analysis of the indirect effect contributions

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

Diversity and nestedness have been shown to affect the importance of indirect effects in ecological networks (Bastolla *et al.* 2009; Iles & Novak 2016). As phenological and morphological forcing might affect network diversity and nestedness at equilibrium, we disentangled the effects mediated by diversity and nestedness from the direct effects of phenological and morphological forcing on the relative contribution of indirect effects to total effects among species within guilds ($\overline{IEC_p}$ or $\overline{IEC_f}$), by performing a path-analysis for each guild. To do so, we used Structural Equation Modeling (SEM) following a previous study (Thébault & Fontaine 2010), as detailed in Supplementary Methods.

Indirect, direct and total effects at the species level

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

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

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

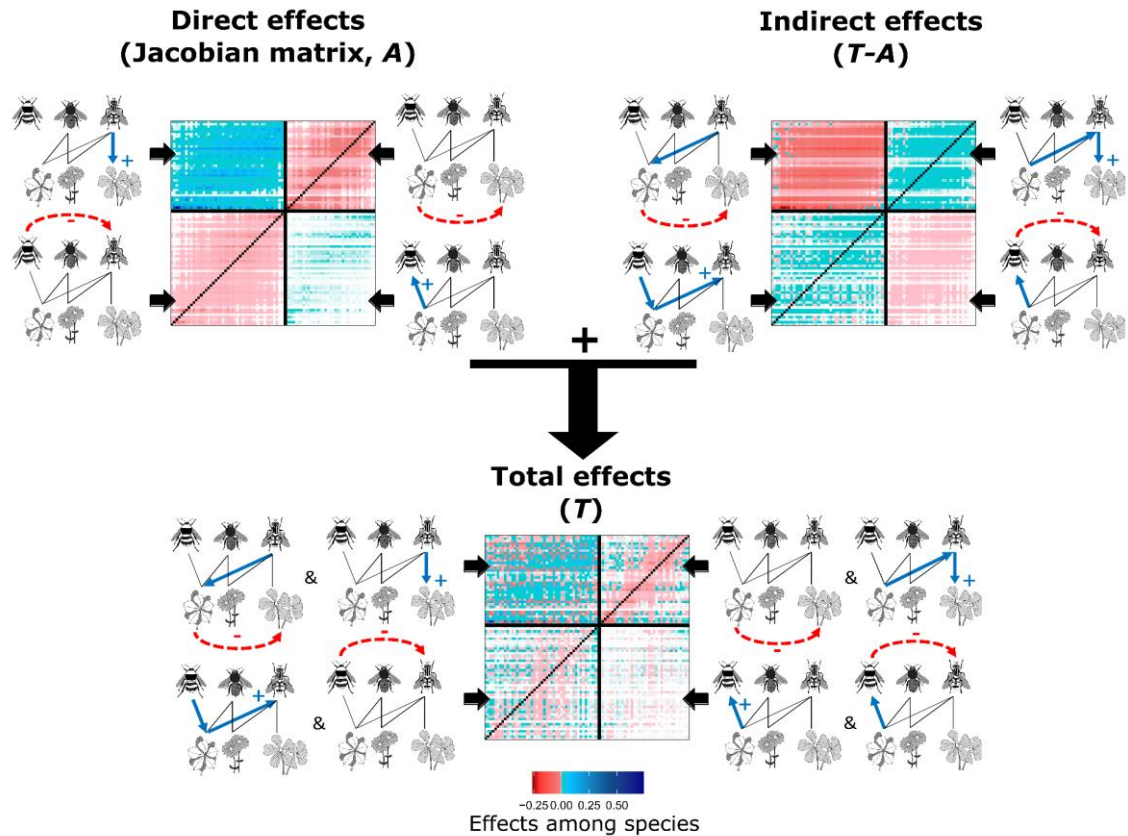


Fig. 2: Example of matrices of direct, indirect and total effects at equilibrium. Jacobian matrix (A, top left), indirect effect matrix (top right, see methods) and total effect matrix (T, bottom) of a network at equilibrium, for MF=0.5, PF=0.5 and $c=0.5$. Blue colors represent positive effects while red colors represent negative effects among species. Matrix diagonals were uncolored to focus on inter-specific relationships (see Methods). In the Jacobian matrix, blocks along the diagonal represent the competition effects within guilds, while off-diagonal blocks represent plant-pollinator direct effects. The total effect matrix (T) represents the sum of the direct and indirect effects among species, so the term to term difference between both matrices ($T - A$) gives the indirect effects only. Schematic networks represent examples of short path indirect effects but in our method we integrated indirect effects over all possible paths.

Analysis at the species level

First, we assessed how phenological and morphological traits affect species persistence depending on their generalism level. Initial and at equilibrium generalism levels were calculated for each species averaging its interaction strengths in the network, as detailed in supplementary Methods. We grouped the species by initial generalism level using bins of 0.1 and by the competition coefficient c of the simulation. Persistence probability per species group was calculated as the proportion of persisting

species in each group of generalism. Second, we studied the relationships between the persistence probability and the initial generalism level, and between the species effects generated within-guilds and the generalism level at equilibrium, comparing simulations with phenological forcing only ($MF = 0$ & $PF > 0$) and simulations with morphological forcing only ($MF > 0$ & $PF = 0$).

Results

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

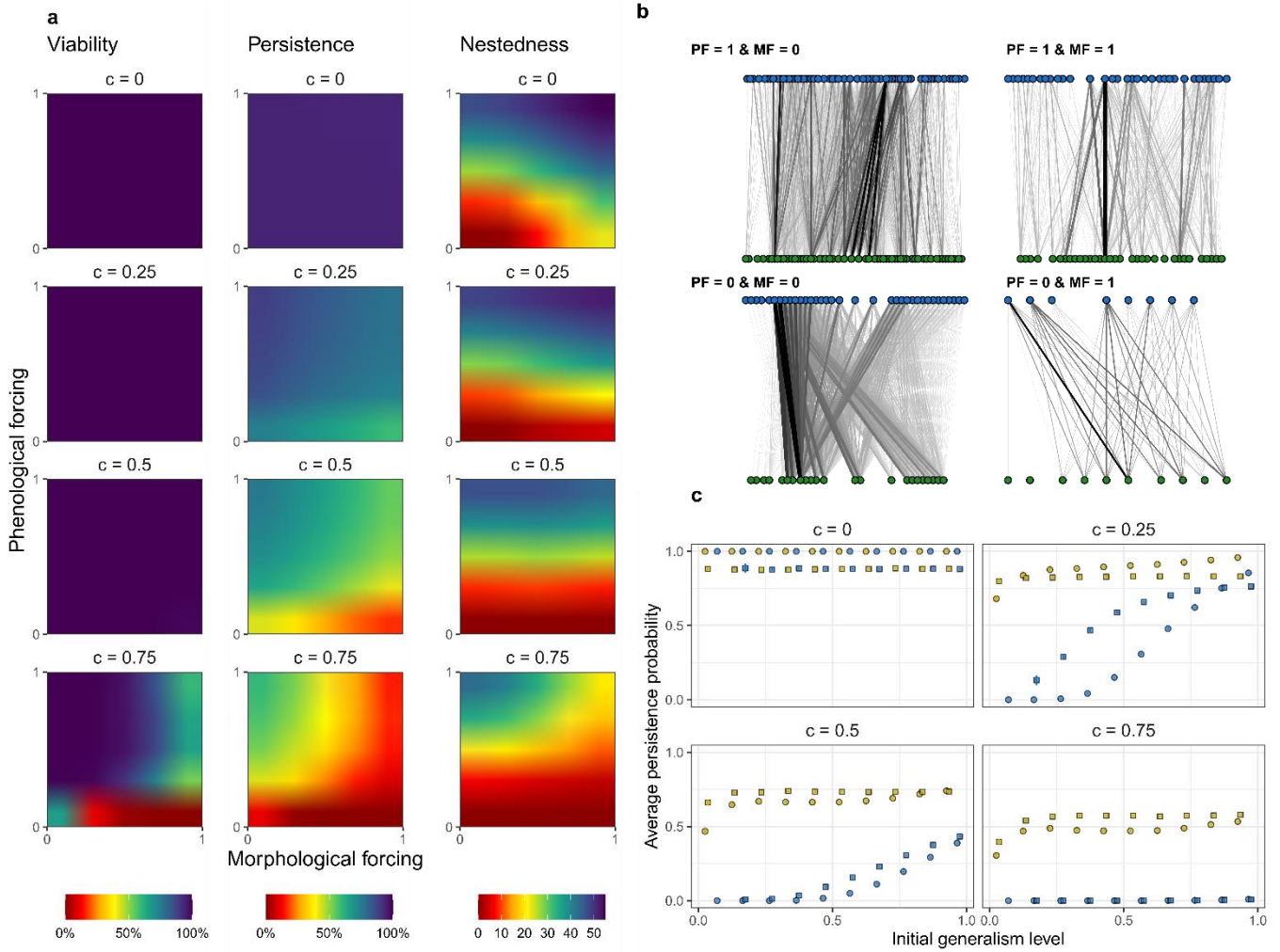


Figure 3: Network properties at the ecological equilibrium and species persistence. (a) Equilibrium network properties as a function of the competition strength c , and phenological and morphological forcing parameters. Viability is the percentage of networks with at least one plant and one pollinator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

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

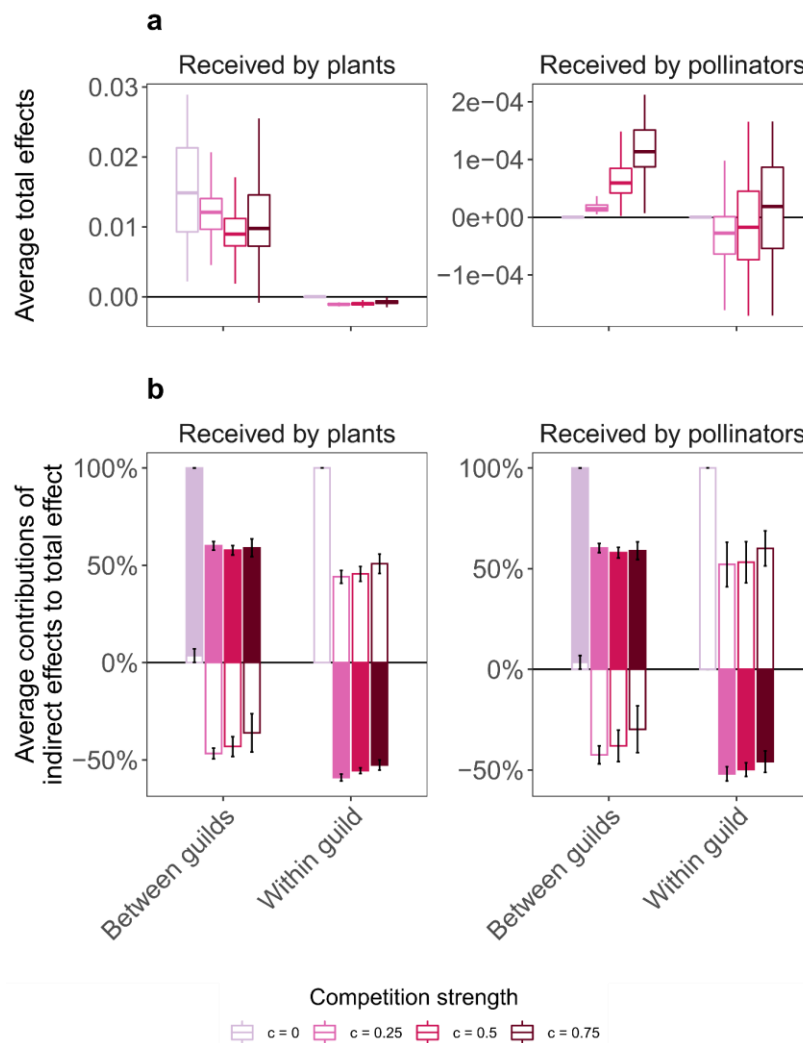


Figure 4: Within and between guilds effects partitioning at equilibrium and their relative contributions to total effects. (a) Within and between guilds strength of total effects received by species averaged at the guild level for plants and pollinators, per level of competition strength represented by different colors. (b) Within and between guilds contributions in percentages of direct (filled bars) and indirect (open bars) effects to total effects, averaged at the guild level, per level of competition strength represented by different colors. Values represented are the mean of the distribution over simulations, while error bars represent standard deviation of the mean. In (a) outliers are not represented to preserve readability.

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

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

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

Importantly, phenological and morphological forcing affect the balance between competition and positive indirect effects within pollinator guild in two different ways: while phenological forcing increases positive indirect effects within the pollinator guild but also competition, morphological forcing does the opposite, decreasing competition but also positive indirect effects (Fig. S4). Thus, the positive

effect of phenological forcing on the contribution of indirect effects to total effects is due to the fact that it increases positive indirect effects more than it increases competition, while morphological forcing does not decrease competition more than it decreases positive indirect effects within pollinator guild. The larger contribution of positive indirect effects to total effects within the pollinator guild when networks are structured by phenological traits might also be linked to the greater persistence of specialists in such networks (Fig. 3c). Indeed, quantifying the effects generated per species, i.e. the effect a species has on the summed growth rates of all other species from the same guild, we show that specialist species tend to generate less negative total effects within guilds than generalists (Fig. 5b). Generalist species generate stronger direct and indirect effects than specialists (Fig. S6) as they have many mutualistic partners and thus many competitors and facilitators. However, specialists tend to generate more positive indirect effects than direct competitive effects (Fig. S6). We detect the same patterns as in Fig. 5a for the contribution of positive indirect effects to total effects within the plant guild, but only for strong intra-guild competition strength (Fig. S5), likely due to the weaker importance of within-guild effects for plants than for pollinators (Fig. 4a).

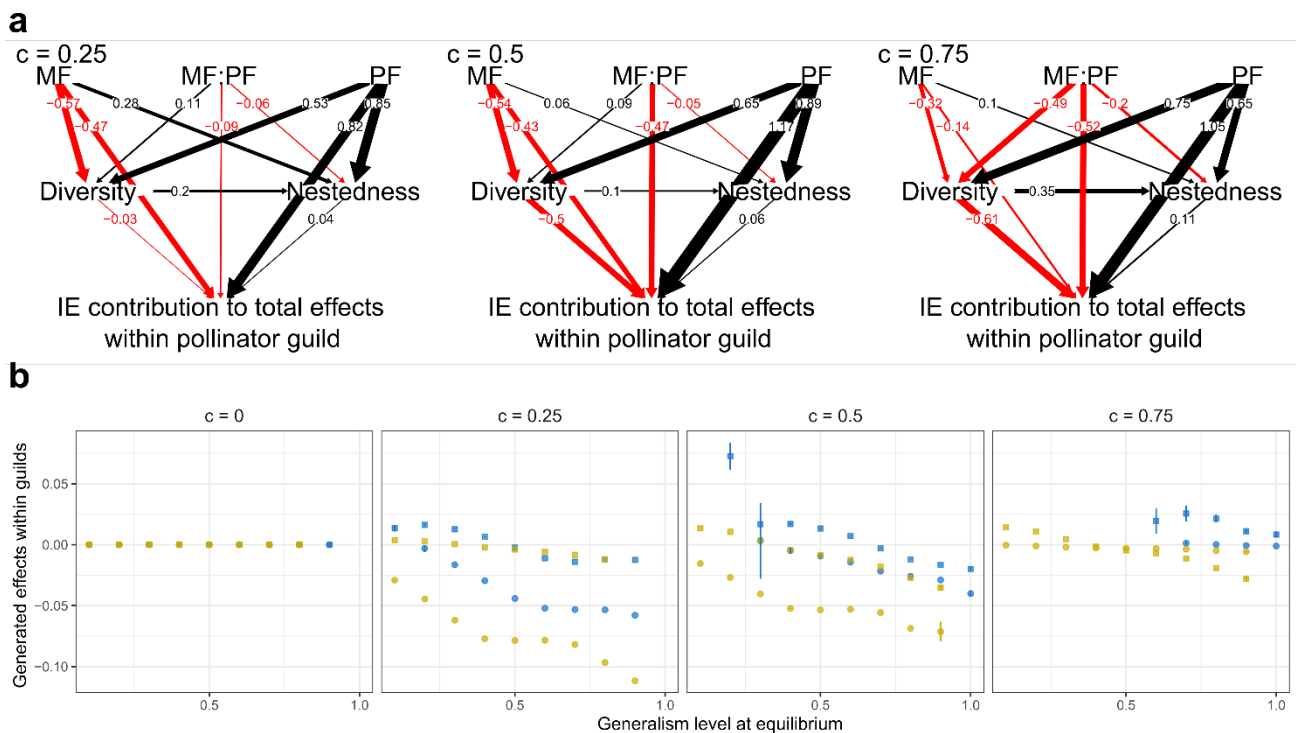


Figure 5: Effects of morphological and phenological forcing parameters on the contribution of indirect effects (IE) within the pollinator guild. (a) Determinants of the contribution of indirect effects (IE) to total effects within the pollinator guild. Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for different values of intra-guild competition strengths c . This model includes an interaction (MF:PF) between the phenological (PF) and morphological (MF) forcing. Diversity is the number of persistent species at equilibrium. (b) Total effects generated within guilds by pollinators (squares) and by plants (circles) as a function of species generalism at equilibrium. Blue points correspond to simulations with a morphological forcing only (PF=0 & MF>0) and yellow points correspond to simulations with a phenological forcing only (PF>0 & MF=0). Error bars are 95% confidence intervals. Values are averaged by tenths of species generalism and points are slightly staggered for readability.

Discussion

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

The benefits of phenological traits mainly occur because they decouple interactions in time, making the balance between facilitation and competition less negative than morphological traits. Our results provide a mechanism that might explain the importance of phenological traits relatively to morphological traits in seasonal pollination networks (Gonzalez & Loiselle 2016; CaraDonna *et al.* 2017; Manincor *et al.* 2020; Sonne *et al.* 2020), and suggest that the seasonal structure is key to the maintenance of diversity in mutualistic communities. These findings can be generalized to other traits than phenology, while they allow to decouple interactions in time or space without leading to resource depletion. Indeed, any trait following this assumption and decoupling interactions in time or space, as for example traits associated with daytime activity and flower opening (e.g. diurnal *vs* night) or with flight and flower heights, should similarly maintain indirect facilitation within guilds and promote species coexistence. For instance, differences in flight and flower heights could allow two pollinator species that fly at different height to avoid competition whilst still interacting with the same plant population, or even with the same individual plant if an individual plant has flowers at different heights. As plant-pollinator interactions have been shown to differ at small spatial and temporal scales (Albrecht *et al.* 2012; Knop *et al.* 2017; Cusser *et al.* 2021), we expect that the mechanisms highlighted in this study are widespread in pollination networks.

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

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

Recent studies showed that climate warming is shifting pollinator flight periods and flowering periods, leading to changes in the seasonal structure of pollinator and plant assemblages, which either increase or decrease phenological overlaps among species depending on the location (Diez *et al.* 2012; Theobald *et al.* 2017; Duchenne *et al.* 2020). Such changes are likely to cause mismatches among interacting species (Memmott *et al.* 2007; Revilla *et al.* 2015) and to decrease the robustness of the network to any other perturbation, thus leading to synergistic effects among perturbations (Revilla *et al.*

2015). Beyond and more insidiously than trophic mismatch, our results highlight that phenological shifts are likely to affect indirect effects such as competition pressures (Rudolf 2019) and facilitation in mutualistic assemblages, with currently unknown consequences for biodiversity. Further, since specialist species are often presented as generally more sensitive to perturbation (Clavel *et al.* 2011) and we showed that they tend to propagate more positive indirect effects than other species, our results suggest that perturbations targeting specialists are likely to increase propagation of negative indirect effects. However, network reorganization following perturbations can also happen (Burkle *et al.* 2013) and might buffer effects of specialist extinctions.

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

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Competing interests

The authors declare no competing interests.

References

- Albrecht, M., Schmid, B., Hautier, Y. & Müller, C.B. (2012). Diverse pollinator communities enhance plant reproductive success. *Proc. R. Soc. B Biol. Sci.*, 279, 4845–4852.
- Bartomeus, I., Saavedra, S., Rohr, R.P. & Godoy, O. (2021). Experimental evidence of the importance of multitrophic structure for species persistence. *Proc. Natl. Acad. Sci.*, 118.
- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci.*, 100, 9383–9387.

498 Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B. & Bascompte, J. (2009). The
499 architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*,
500 458, 1018–1020.

501 Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013). Plant-Pollinator Interactions over 120 Years: Loss of
502 Species, Co-Occurrence, and Function. *Science*, 339, 1611–1615.

503 Campbell, D.R. (1985). Pollinator Sharing and Seed Set of *Stellaria pubera*: Competition for Pollination.
504 *Ecology*, 66, 544–553.

505 CaraDonna, P.J., Burkle, L.A., Schwarz, B., Resasco, J., Knight, T.M., Benadi, G., *et al.* (2021). Seeing
506 through the static: the temporal dimension of plant–animal mutualistic interactions. *Ecol. Lett.*,
507 24, 149–161.

508 CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., *et al.*
509 (2017). Interaction rewiring and the rapid turnover of plant–pollinator networks. *Ecol. Lett.*, 20,
510 385–394.

511 Clavel, J., Julliard, R. & Devictor, V. (2011). Worldwide decline of specialist species: toward a global
512 functional homogenization? *Front. Ecol. Environ.*, 9, 222–228.

513 Cusser, S., Haddad, N.M. & Jha, S. (2021). Unexpected functional complementarity from non-bee
514 pollinators enhances cotton yield. *Agric. Ecosyst. Environ.*, 314, 107415.

515 Diez, J.M., Ibáñez, I., Miller-Rushing, A.J., Mazer, S.J., Crimmins, T.M., Crimmins, M.A., *et al.* (2012).
516 Forecasting phenology: from species variability to community patterns. *Ecol. Lett.*, 15, 545–
517 553.

518 Duchenne, F., Thébault, E., Michez, D., Elias, M., Drake, M., Persson, M., *et al.* (2020). Phenological
519 shifts alter the seasonal structure of pollinator assemblages in Europe. *Nat. Ecol. Evol.*, 4, 115–
520 121.

521 Encinas-Viso, F., Revilla, T.A. & Etienne, R.S. (2012). Phenology drives mutualistic network structure
522 and diversity: Effects on the dynamics of mutualistic networks. *Ecol. Lett.*, 15, 198–208.

523 Galeano, J., Pastor, J.M. & Iriondo, J.M. (2009). Weighted-Interaction Nestedness Estimator (WINE):
524 A new estimator to calculate over frequency matrices. *Environ. Model. Softw.*, 24, 1342–1346.

525 Gardner, M.R. & Ashby, W.R. (1970). Connectance of Large Dynamic (Cybernetic) Systems: Critical
526 Values for Stability. *Nature*, 228, 784–784.

527 Gause, G.F. (1934). Experimental Analysis of Vito Volterra’s Mathematical Theory of the Struggle for
528 Existence. *Science*, 79, 16–17.

529 Gonzalez, O. & Loiselle, B.A. (2016). Species interactions in an Andean bird–flowering plant network:
530 phenology is more important than abundance or morphology. *PeerJ*, 4, e2789.

531 Guimarães, P.R., Pires, M.M., Jordano, P., Bascompte, J. & Thompson, J.N. (2017). Indirect effects
532 drive coevolution in mutualistic networks. *Nature*, 550, 511–514.

533 Henry, M. & Rodet, G. (2018). Controlling the impact of the managed honeybee on wild bees in
534 protected areas. *Sci. Rep.*, 8, 9308.

535 Iles, A.C. & Novak, M. (2016). Complexity Increases Predictability in Allometrically Constrained Food
536 Webs. *Am. Nat.*, 188, 87–98.

537 Jones, E.I., Bronstein, J.L. & Ferrière, R. (2012). The fundamental role of competition in the ecology
538 and evolution of mutualisms. *Ann. N. Y. Acad. Sci.*, 1256, 66–88.

539 Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, H.M., *et al.* (2013).
540 Specialization on traits as basis for the niche-breadth of flower visitors and as structuring
541 mechanism of ecological networks. *Funct. Ecol.*, 27, 329–341.

542 Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M. & Fontaine, C. (2017). Artificial light at night as
543 a new threat to pollination. *Nature*, 548, 206–209.

544 Levin, D.A. & Anderson, W.W. (1970). Competition for Pollinators between Simultaneously Flowering
545 Species. *Am. Nat.*, 104, 455–467.

546 Malo, J.E. (2002). Modelling unimodal flowering phenology with exponential sine equations. *Funct.*
547 *Ecol.*, 16, 413–418.

548 Manincor, N. de, Hautekeete, N., Piquot, Y., Schatz, B., Vanappelghem, C. & Massol, F. (2020). Does
549 phenology explain plant–pollinator interactions at different latitudes? An assessment of its
550 explanatory power in plant–hoverfly networks in French calcareous grasslands. *Oikos*, 129,
551 753–765.

552 May, R.M. (1972). Will a Large Complex System be Stable? *Nature*, 238, 413–414.

553 Mazancourt, C.D., Johnson, E. & Barraclough, T.G. (2008). Biodiversity inhibits species' evolutionary
554 responses to changing environments. *Ecol. Lett.*, 11, 380–388.

555 Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007). Global warming and the disruption of
556 plant–pollinator interactions. *Ecol. Lett.*, 10, 710–717.

557 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and indirect
558 effects in real food webs. *Ecology*, 90, 2426–2433.

559 Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006). Ecological networks and their fragility. *Nature*, 442,
560 259–264.

561 Nakajima, H. & Higgashi, M. (1995). Indirect effects in ecological interaction networks II. The conjugate
562 variable approach. *Math. Biosci.*, 130, 129–150.

563 Neutel, A.-M., Heesterbeek, J.A.P., Koppel, J. van de, Hoenderboom, G., Vos, A., Kaldewey, C., *et al.*
564 (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449,
565 599–602.

566 Neutel, A.-M., Heesterbeek, J.A.P. & Ruiter, P.C. de. (2002). Stability in Real Food Webs: Weak Links
567 in Long Loops. *Science*, 296, 1120–1123.

568 Okuyama, T. & Holland, J.N. (2008). Network structural properties mediate the stability of mutualistic
569 communities. *Ecol. Lett.*, 11, 208–216.

570 Otto, S.B., Rall, B.C. & Brose, U. (2007). Allometric degree distributions facilitate food-web stability.
571 *Nature*, 450, 1226–U7.

572 Pascual-García, A. & Bastolla, U. (2017). Mutualism supports biodiversity when the direct competition
573 is weak. *Nat. Commun.*, 8, 1–13.

574 Pires, M.M., O'Donnell, J.L., Burkle, L.A., Díaz-Castelazo, C., Hembry, D.H., Yeakel, J.D., *et al.*
575 (2020). The indirect paths to cascading effects of extinctions in mutualistic networks. *Ecology*,
576 101, e03080.

577 Pleasants, J.M. (1980). Competition for Bumblebee Pollinators in Rocky Mountain Plant Communities.
578 *Ecology*, 61, 1446–1459.

579 Rabinowitz, D., Rapp, J.K., Sork, V.L., Rathcke, B.J., Reese, G.A. & Weaver, J.C. (1981). Phenological
580 Properties of Wind- and Insect-Pollinated Prairie Plants. *Ecology*, 62, 49–56.

581 Revilla, T.A., Encinas-Viso, F. & Loreau, M. (2015). Robustness of mutualistic networks under
582 phenological change and habitat destruction. *Oikos*, 124, 22–32.

583 Rohr, R.P., Saavedra, S. & Bascompte, J. (2014). On the structural stability of mutualistic systems.
584 *Science*, 345.

585 Rudolf, V.H.W. (2019). The role of seasonal timing and phenological shifts for species coexistence.
586 *Ecol. Lett.*, 22, 1324–1338.

587 Saavedra, S., Stouffer, D.B., Uzzi, B. & Bascompte, J. (2011). Strong contributors to network
588 persistence are the most vulnerable to extinction. *Nature*, 478, 233–235.

589 Salas, A.K. & Borrett, S.R. (2011). Evidence for the dominance of indirect effects in 50 trophic
590 ecosystem networks. *Ecol. Model.*, 222, 1192–1204.

591 Santamaría, L. & Rodríguez-Gironés, M.A. (2007). Linkage Rules for Plant–Pollinator Networks: Trait
592 Complementarity or Exploitation Barriers? *PLOS Biol.*, 5, e31.

593 Schiestl, F.P. (2010). The evolution of floral scent and insect chemical communication. *Ecol. Lett.*, 13,
594 643–656.

595 Sletvold, N., Trunschke, J., Smit, M., Verbeek, J. & Ågren, J. (2016). Strong pollinator-mediated
596 selection for increased flower brightness and contrast in a deceptive orchid. *Evolution*, 70, 716–
597 724.

598 Soetaert, K., Petzoldt, T. & Setzer, R.W. (2010). Solving Differential Equations in R: Package deSolve.
599 *J. Stat. Softw.*, 33, 1–25.

600 Sonne, J., Vizenin-Bugoni, J., Maruyama, P.K., Araujo, A.C., Chávez-González, E., Coelho, A.G., *et al.*
601 (2020). Ecological mechanisms explaining interactions within plant–hummingbird
602 networks: morphological matching increases towards lower latitudes. *Proc. R. Soc. B Biol. Sci.*,
603 287, 20192873.

604 Stang, M., Klinkhamer, P.G.L. & Meijden, E.V.D. (2006). Size constraints and flower abundance
605 determine the number of interactions in a plant–flower visitor web. *Oikos*, 112, 111–121.

- Stewart, J.E., Illán, J.G., Richards, S.A., Gutiérrez, D. & Wilson, R.J. (2020). Linking inter-annual variation in environment, phenology, and abundance for a montane butterfly community. *Ecology*, 101, e02906.
- Tarantola, A. (2005). *Inverse problem theory and methods for model parameter estimation*. SIAM.
- Thébaud, E. & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*, 329, 853–856.
- Theobald, E.J., Breckheimer, I. & HilleRisLambers, J. (2017). Climate drives phenological reassembly of a mountain wildflower meadow community. *Ecology*, 98, 2799–2812.
- Valdovinos, F.S. (2019). Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.*, 22, 1517–1534.
- Volterra, V. (1928). Variations and Fluctuations of the Number of Individuals in Animal Species living together. *ICES J. Mar. Sci.*, 3, 3–51.

Supplementary Materials for
Phenological traits foster persistence of mutualistic networks by
promoting facilitation

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Supplementary Methods.....	2
Details on some assumptions of the model	2
Contribution of the indirect effects to the total effects among species.....	4
Path analysis.....	4
Species generalism level	5
Supplementary Figures.....	6
Supplementary Table.....	14

Supplementary Methods

Details on some assumptions of the model

Obligate mutualism. This is a common assumption of mutualistic networks (Thébault & Fontaine 2010; Valdovinos *et al.* 2013; Valdovinos 2019): pollinators need to feed on plants to reproduce and plants need to be pollinated by pollinators to reproduce. This assumption allows to focus on the effect of mutualistic interactions and competition for mutualistic partners on persistence, without any additional effects of baseline growth rates. In nature, some pollinators can find some alternative resources to feed and some plants can be pollinated in another way, but here we focus on guilds that depend on each other.

Trait distributions. We use theoretical trait distributions for morphology and phenology, in order to calculate the overlaps that determine the interaction strengths between plants and pollinators and competition intensity among species within guilds. We drew phenological traits from a gaussian distribution centered on summer, as observed in pollination systems in temperate areas (CaraDonna *et al.* 2014, 2017; Duchenne *et al.* 2020). For morphological traits, since morphology is represented by an abstract unidimensional niche, we used an arbitrary scale centered on 0. In addition to their biological meaning (see Methods part of the main text), Gaussian distributions are very convenient to define overlaps that are bounded between 0 and 1. Since the equations of our model only depend on overlap values among trait distributions, any other kind of trait distributions would affect our results only by changing overlap values. To assess the impact of the differences in trait distributions for morphology and phenology in our model, we also performed model simulations as explained in the main text but this time drawing morphological trait values in the same distribution than phenological trait values, thus using a circular wrapped Gaussian distribution bounded between 0 and 365 to model morphology. Results presented in Fig. S7 show exactly the same pattern than results shown in Fig. 2a of the paper, highlighting that our findings result from fundamental differences between the two types of traits and not from differences in their modelled distributions.

Overlap calculation. Here we calculated phenological and morphological overlap as the area under the curve which is determined in each point by the minimum density value between the two Gaussians representing traits of the given pair of species. By doing so, we assume that a plant and a pollinator with the same average value of trait would interact in a stronger way if both have narrow or wider niches (phenological or morphological) than if one has a narrow niche and the other one a wide niche (Fig. S8). It is because the trait (morphology or phenology) niche width represents the intraspecific variability of trait values among individuals from the same species and not the generalism of the species itself. For phenological trait it means that phenology duration represents the asynchrony between individuals of the same species rather than life span of the species. For morphology it means that morphological niche width of a species is determined by its morphological variability among individuals. Thus, between a

plant with a narrow morphological niche and a pollinator with a wide morphological niche, as represented in Fig. S8c, a small proportion of individuals have compatible trait values, thus the morphological overlap is low. This explains why we did not implemented a trade-off between the generalism level (correlated with the width of the morphological/phenological niche in our model) and the interaction strengths, like it is sometimes done in mutualistic models (Saavedra *et al.* 2017).

Phenological overlap and competition. Here we assume that no phenological overlap means no competition. For instance, we thus assume that visits by a pollinator earlier in time of a given plant species does not lead to depletion of resources for pollinators visiting the same plant species later. We make this assumption because resource production occurs on a much smaller temporal scale than phenological overlap, the latter representing seasonal overlaps in our model. Indeed, nectar production takes often less than few hours and is often continuous over time (Cavalcante *et al.* 2018), flower nectar being the main resource for pollinators in plant-pollinator networks.

Competition structure and traits. The main difference between morphology and phenology is that, if both structure mutualistic interactions, phenology also directly structures competition for mutualistic partners. Indeed, competition is structured by interactions, thus indirectly by morphology and phenology, but it is re-structured by phenology again (equation (4) of the main text). We did this choice because we consider that to compete species should use the same mutualistic partners, at the same time. This double role of phenology in structuring competition (indirectly through mutualistic interactions, and directly through phenological overlap among species from the same guild) is the main difference with morphology, which structures competition only in an indirect way, through mutualistic interactions.

Intra and inter-specific competition. It is valuable to note that in this model, the competition coefficient for mutualistic partners could be stronger inter-specifically (ω_{kj}) than intra-specifically (ω_{jj}). Indeed, if we focus on the competition received by a pollinator j from another pollinator k , the competition coefficient (neglecting pollinator abundances and the scaling value c) is equal to $\frac{1}{\sum_{i=1}^{n_f} I_{ij} \times F_i} \times D_{kj}^{PF} \times \sum_{i=1}^{n_f} F_i \times I_{ik} \times I_{ij}$. In this equation, let's neglect all terms that do not depend on k , thus considering $D_{kj}^{PF} \times \sum_{i=1}^{n_f} I_{ik} \times I_{ij}$. The first term is the phenological overlap among pollinators elevated at power PF (D_{kj}^{PF}), and it tends to increase intra-specific competition relatively to inter-specific competition because it is equal to one if $k = j$, and it is below one if $k \neq j$. The second term ($\sum_{i=1}^{n_f} I_{ik} \times I_{ij}$) corresponds to the multiplicative intensity of the interactions of the two pollinators with a same plant, summed over all plants. This term can be higher when $k \neq j$ (inter-specifically) than when $k = j$ (intra-specifically), because I_{ik} can obviously be higher than I_{ij} . Thus, the product of these two terms can be higher when $k \neq j$ than when $k = j$, meaning that competition coefficients for mutualistic partners could be higher inter-specifically than intra-specifically. The same logic applies similarly for plants. This is

not a classical assumption of models, but it follows a biological rationale since there is no reason to think that competition for partners should be higher intra-specifically than inter-specifically.

Contribution of the indirect effects to the total effects among species

We calculated the average contributions of indirect effects to total effects among species (in percentage) by considering four types of total effects: the effects of an increase in pollinator abundance on growth rates of other pollinators (corresponding average contribution: $\overline{IEC_p}$), the effects of an increase in plant abundance on growth rates of other plants (corresponding average contribution: $\overline{IEC_f}$), the effects of an increase in pollinator abundance on growth rates of plants (corresponding average contribution: $\overline{IEC_{pf}}$), and the effects of an increase in plant abundance on growth rates of pollinators (corresponding average contribution: $\overline{IEC_{fp}}$).

The average contribution of indirect effects to total effects among pollinators (in %) was defined as follow:

$$\overline{IEC_p} = \frac{1}{n_{peq}^2 - n_{peq}} \left(\sum_{j=1}^{n_{peq}} \sum_{i=1, i \neq j}^{n_{peq}} \frac{IE_{ji}}{|IE_{ji}| + |A_{ji}|} \right) \times 100 \quad (9)$$

Where IE_{ji} and A_{ji} are the strength of the indirect and direct effects, respectively, of species j on species i (see Methods), and n_{peq} is the number of pollinator species persisting at equilibrium. The calculation of the average contribution of indirect effects to total effects among plants $\overline{IEC_f}$ was done by using a formula equivalent to equation (9).

The contribution of indirect effects to total effects received by plants from pollinators ($\overline{IEC_{pf}}$) was calculated as follow:

$$\overline{IEC_{pf}} = \frac{1}{n_{peq} \times n_{feq}} \left(\sum_{j=1}^{n_{peq}} \sum_{i=n_{peq}+1}^{n_{peq}+n_{feq}} \frac{IE_{ji}}{|IE_{ji}| + |A_{ji}|} \right) \times 100 \quad (10)$$

The calculation of $\overline{IEC_{fp}}$ was done using a formula equivalent to equation (10). n_{feq} is the number of plant species persisting at equilibrium

Path analysis

We tested all linear relationships presented in the Figure 4, using a multigroup approach as implemented in the R package *PiecewiseSEM* (Lefcheck 2016) for each competition coefficient. We excluded simulations with no competition, $c = 0$, as it did not exhibit any variation in intra-guild indirect effect contributions, this because there was no direct link among species from the same guild and thus the indirect effects were equal to the total effects. We used linear mixed-effect models with a random network effect implemented in the R package *nlme* (Pinheiro *et al.* 2020) to account for the fact that the 100 parameter combinations were run on a set of 1000 initial networks. Finally, we showed standardized coefficients for each relationship. We performed this analysis on the average contribution of indirect

effects to total effects among pollinators ($\overline{IEC_p}$) and among plants ($\overline{IEC_f}$), as well as on the average direct and average indirect effects among pollinators.

Species generalism level

To position species on the specialist-generalist gradient, for each species we calculated the average of its interaction strengths in the network, i.e. the average of all values of matrix I belonging to its corresponding column for pollinators, or row for plants. Specialist species have a lower average value of interaction strengths than generalists as they have weak interaction strengths with most species in the network. We did that with the initial interaction matrix I to calculate the initial generalism level, and with the final interaction matrix obtained by removing extinct species from I , to calculate the generalism level at equilibrium.

References:

- Cavalcante, M.C., Galetto, L., Maués, M.M., Pacheco Filho, A.J.S., Bomfim, I.G.A. & Freitas, B.M. (2018). Nectar production dynamics and daily pattern of pollinator visits in Brazil nut (*Bertholletia excelsa* Bonpl.) plantations in Central Amazon: implications for fruit production. *Apidologie*, 49, 505–516.
- Lefcheck, J.S. (2016). piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.*, 7, 573–579.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). *nlme: Linear and Nonlinear Mixed Effects Models*.
- Saavedra, S., Rohr, R.P., Bascompte, J., Godoy, O., Kraft, N.J.B. & Levine, J.M. (2017). A structural approach for understanding multispecies coexistence. *Ecol. Monogr.*, 87, 470–486.
- Thébault, E. & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science*, 329, 853–856.
- Valdovinos, F.S. (2019). Mutualistic networks: moving closer to a predictive theory. *Ecol. Lett.*, 22, 1517–1534.
- Valdovinos, F.S., Espanés, P.M. de, Flores, J.D. & Ramos-Jiliberto, R. (2013). Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, 122, 907–917.

Supplementary Figures

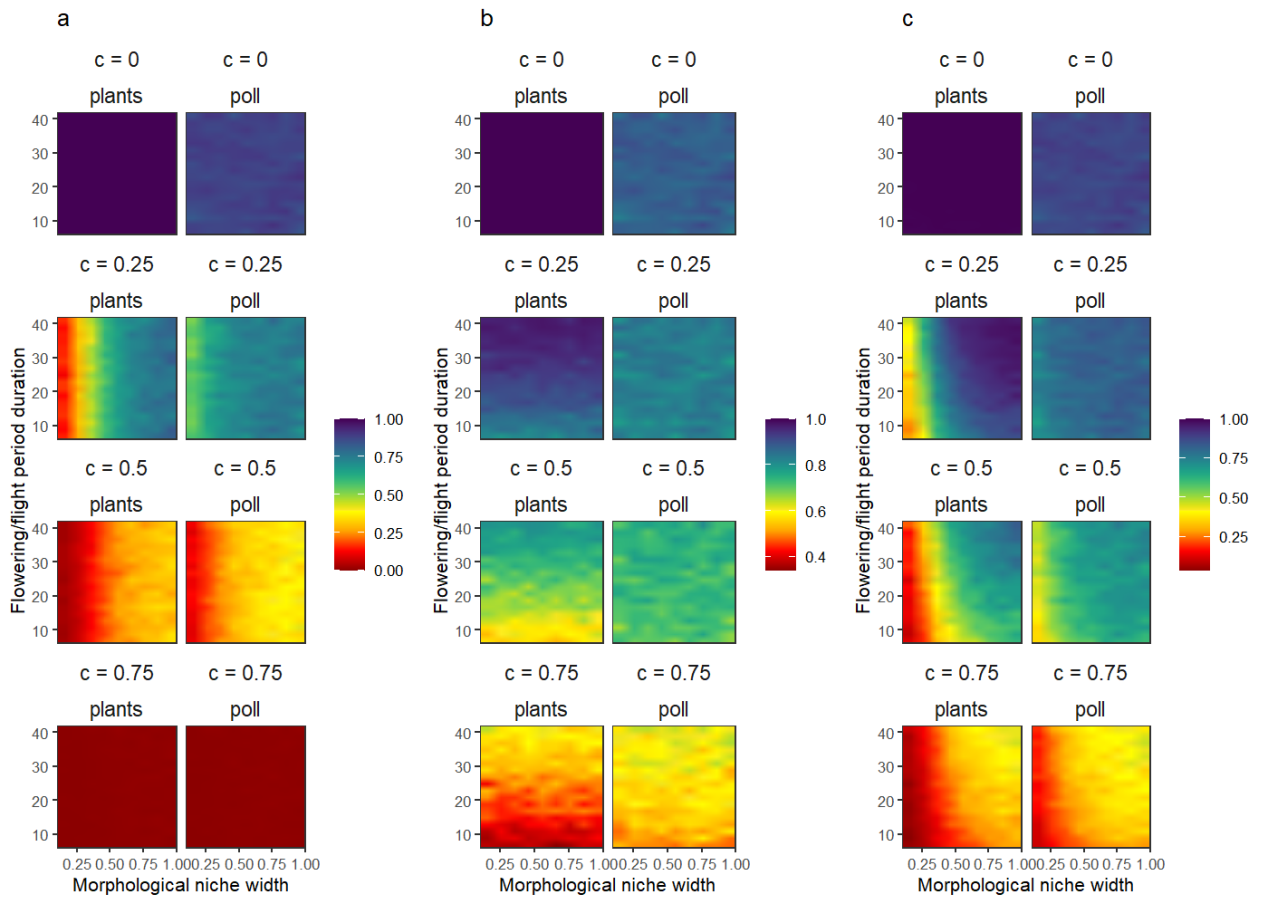


Figure S1: Persistence probability as a function of the species flowering/flight period duration and of the morphological niche width. (a) Case with morphological forcing only ($MF > 0$ & $PF = 0$), (b) case with phenological forcing only ($MF = 0$ & $PF > 0$), (c) case with both phenological and morphological forcing ($MF > 0$ & $PF > 0$). Values are shown for plants and pollinators (poll).

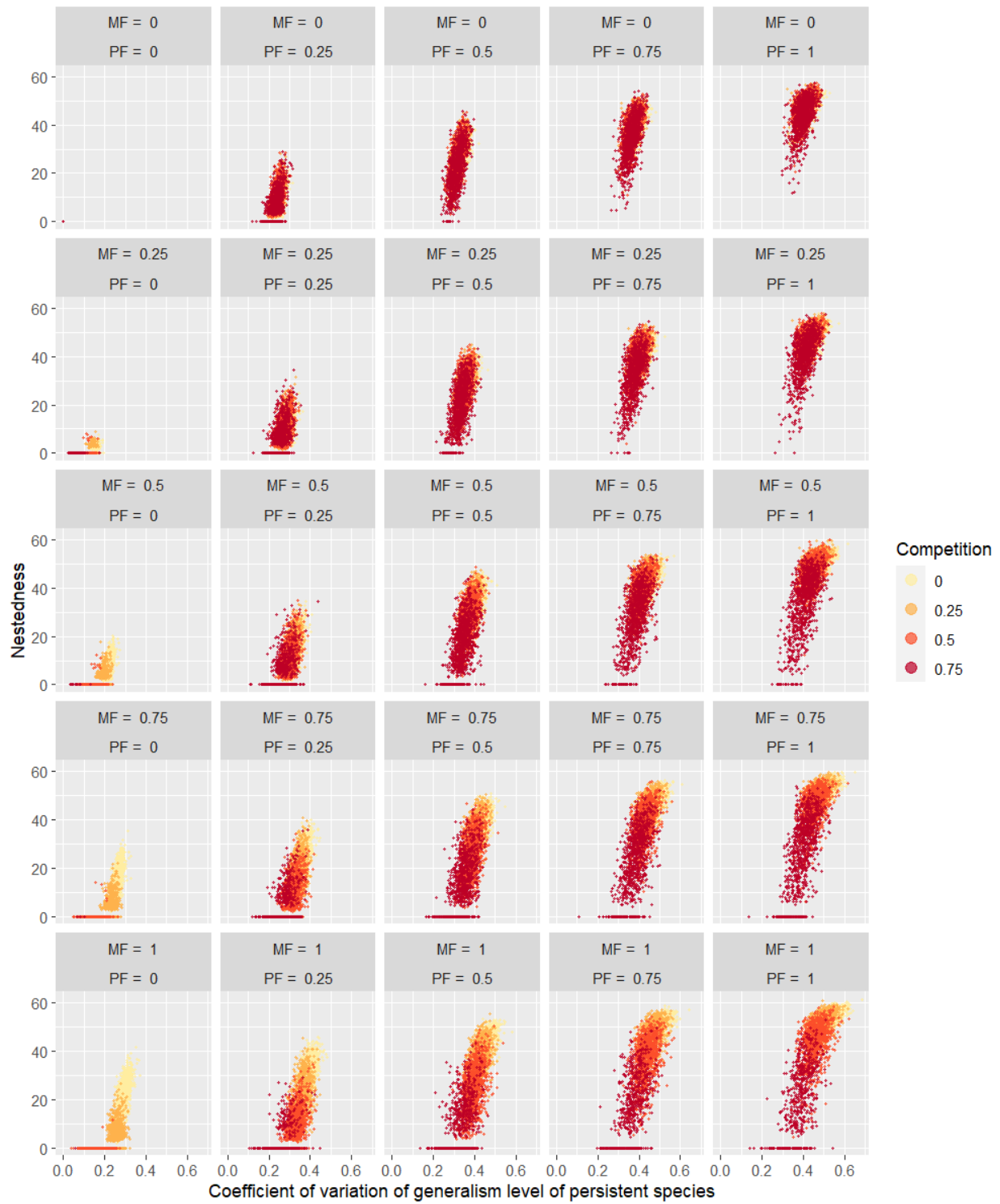


Figure S2: Relationships between nestedness and the coefficient of variation of the generalism level of persistent species at equilibrium for different levels of phenological and morphological forcing. PF and MF are the phenological and morphological forcing, respectively. Colors correspond to the competition strength c .

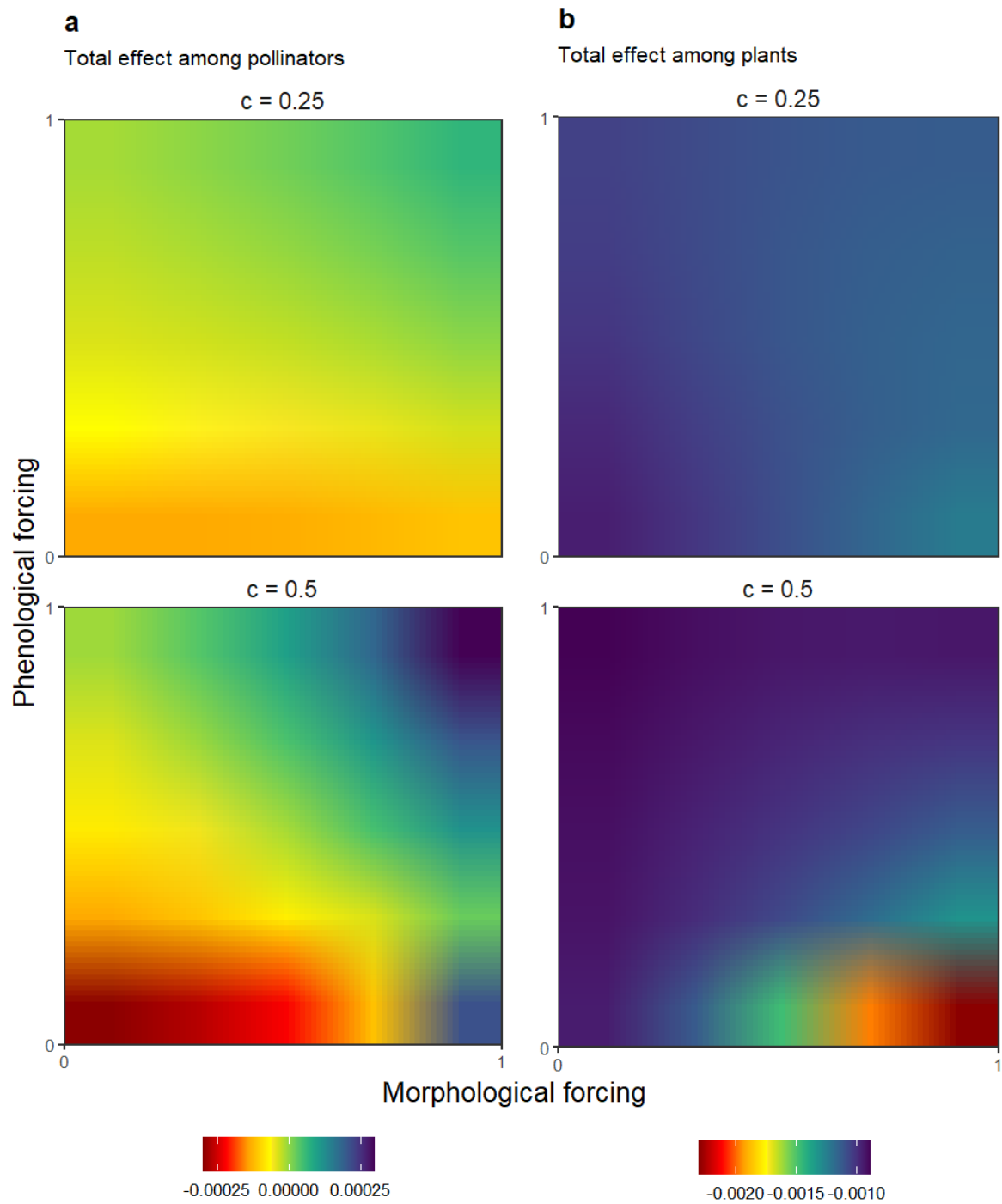


Figure S3: Average total effect among species from the same guild as a function of phenological and morphological forcing. (a) Among pollinators and (b) among plants for the two intermediate levels of intra-guild competition c .

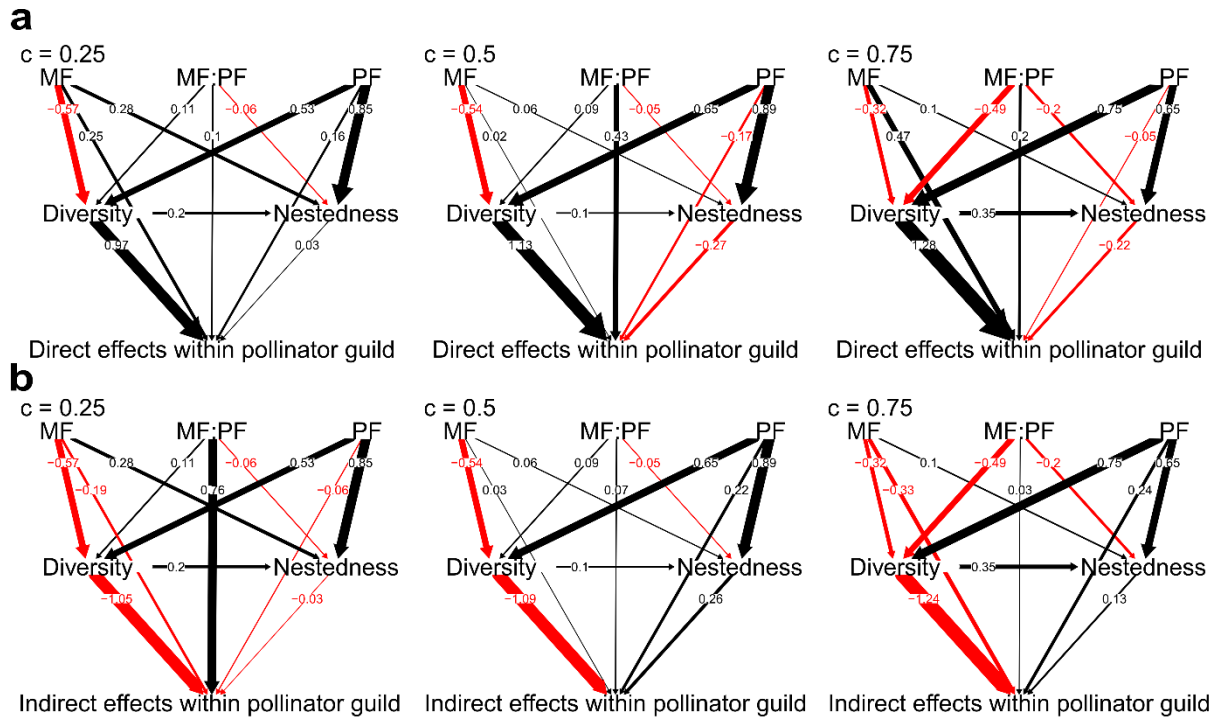


Figure S4: Effects of morphological and phenological forcing on direct and indirect effect strengths among pollinators. Determinant factors of the (a) direct and (b) indirect effect strength among pollinators. Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for different values of intra-guild competition strengths c . This model includes an interaction (MF:PF) between the phenological (PF) and morphological (MF) forcing. Diversity is the number of persistent species at equilibrium.

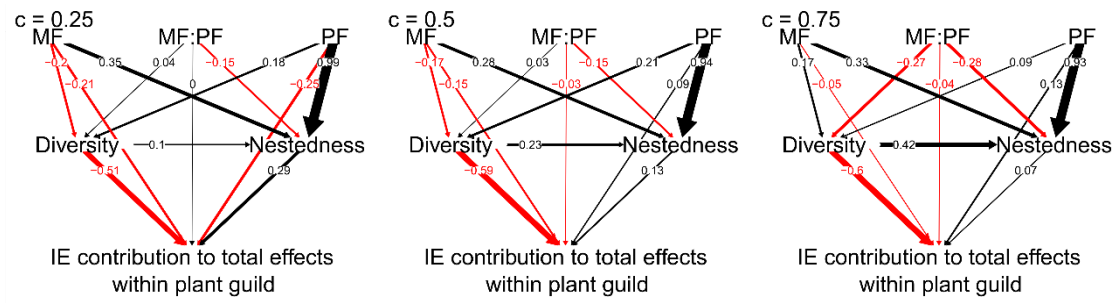


Figure S5: Effects of morphological and phenological forcing on the contribution of indirect effects (IE) among plants. (a) Determinant factors of the indirect effects (IE) contribution to total effects among plants. Values on arrows are standardized coefficients of the multi-group path-analysis performed on data for different values of intra-guild competition strengths c . This model includes an interaction (MF:PF) between the phenological (PF) and morphological (MF) forcing. Diversity is the number of persistent species at equilibrium.

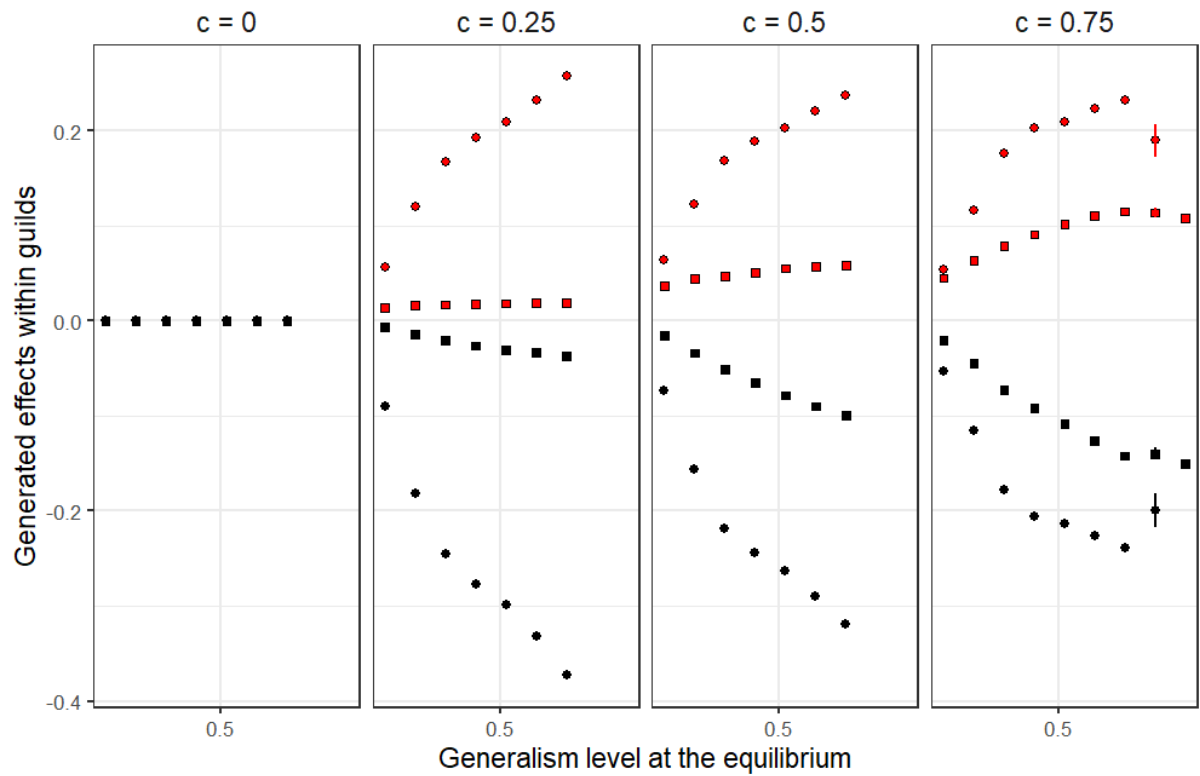


Figure S6: Average direct and indirect effects propagated by species as a function of their generalism level. Propagated effects within guilds by plants (circles) and pollinators (squares), for indirect (red) and direct (black) effects, averaged over all simulations with a phenological forcing and a morphological forcing ($MF > 0$ & $PF > 0$). The generalism level is the amount of interactions (see Methods), the higher it is the more generalist the species is. Error bars are 95% confidence interval.

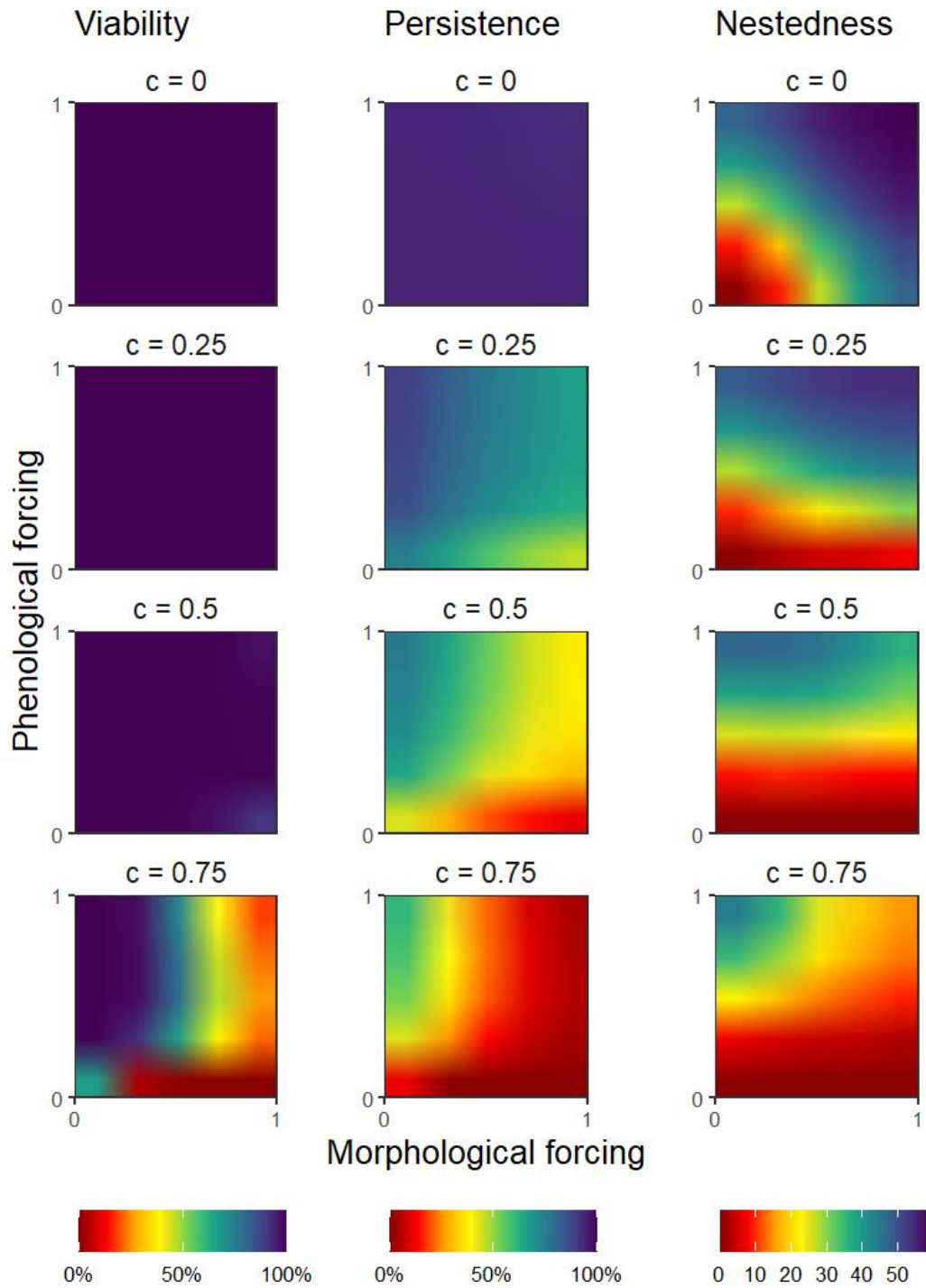


Figure S7: Same Figure than the Figure 2a of the paper, but trait values were sampled in the same distributions for morphology and phenology. Equilibrium network properties as a function of the competition strength c , and phenological and morphological forcings. Viability is the percentage of networks with at least one plant and one pollinator at equilibrium, persistence is the average percentage of surviving species at equilibrium, and nestedness is the weighted NODF of the interaction matrix I at equilibrium.

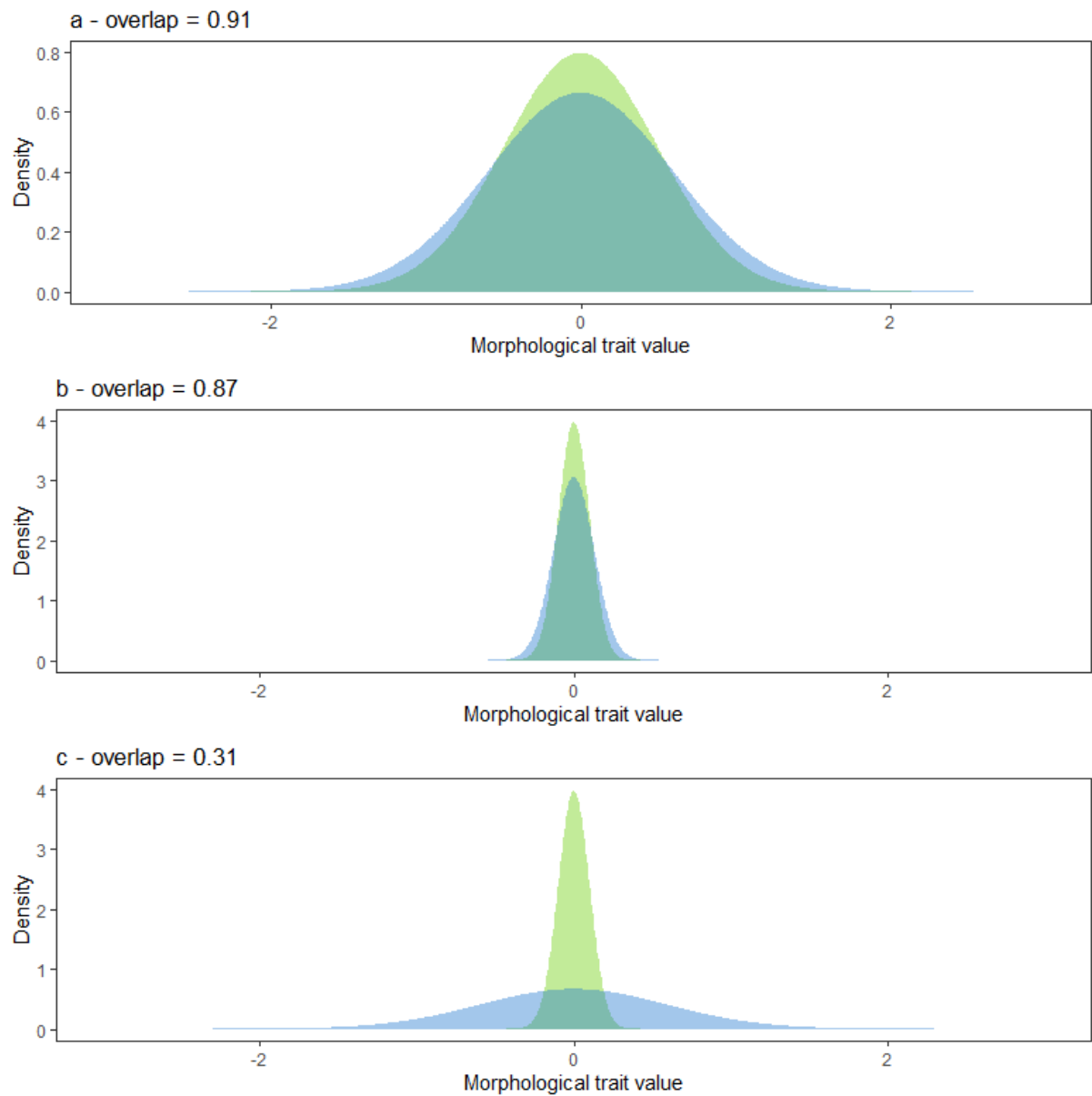


Figure S8: Three examples of morphological overlaps between a plant species (green) and a pollinator (blue). In all panels species have the same morphological niche centroid (0), but different morphological niche width. In (a) both species have a wide morphological niche, in (b) both species have a narrow morphological niche while in (c) the plant has a narrow morphological niche and the pollinator a wide one. The same logic applies for phenological overlaps.

Supplementary Table

Table S1: *Sign of effects within and among guilds.* A sign followed by « (mostly) » indicates that this sign corresponds to a majority of cases but it is not always the case. “c” refers to the maximum competition strength (see Methods).

	plant-pollinator	plant-plant	pollinator-pollinator
Direct effects	+	if $c > 0$: - if $c = 0$: nul	if $c > 0$: - if $c = 0$: nul
Indirect effects	if $c > 0$: - (mostly) if $c = 0$: +	if $c > 0$: + (mostly) if $c = 0$: +	if $c > 0$: + (mostly) if $c = 0$: +
Total effects	if $c > 0$: + or - if $c = 0$: +	if $c > 0$: + or - if $c = 0$: +	if $c > 0$: + or - if $c = 0$: +