

LETTER

Phenological traits foster persistence of mutualistic networks by promoting facilitation

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Abstract

Morphological and phenological traits are key determinants of the structure of mutualistic networks. Both traits 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 favour 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 beneficiate to specialists, the most vulnerable species otherwise, which propagate the most positive effects within guilds and 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.

KEYWORDS

competition, dynamic model, ecological network, indirect interaction, morphology, phenology, plant–pollinator, seasonal structure

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 (Gause, 1934; Volterra, 1928). 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 (Bastolla et al., 2009; Montoya et al., 2006; Neutel et al., 2002, 2007; Okuyama & Holland, 2008; Otto et al., 2007; 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, pollination webs, flower shape and the length of the feeding apparatus of pollinators (Junker et al., 2013; Stang et al., 2006), flowering and flying phenology (Gonzalez & Loiselle, 2016; Junker et al., 2013), floral height (Junker

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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 (Encinas-Viso et al., 2012; Junker et al., 2013; Santamaría & Rodríguez-Gironés, 2007), 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 do 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 minimising 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 (Figure 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 (Figure 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 hypothesise 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 pollinators.

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

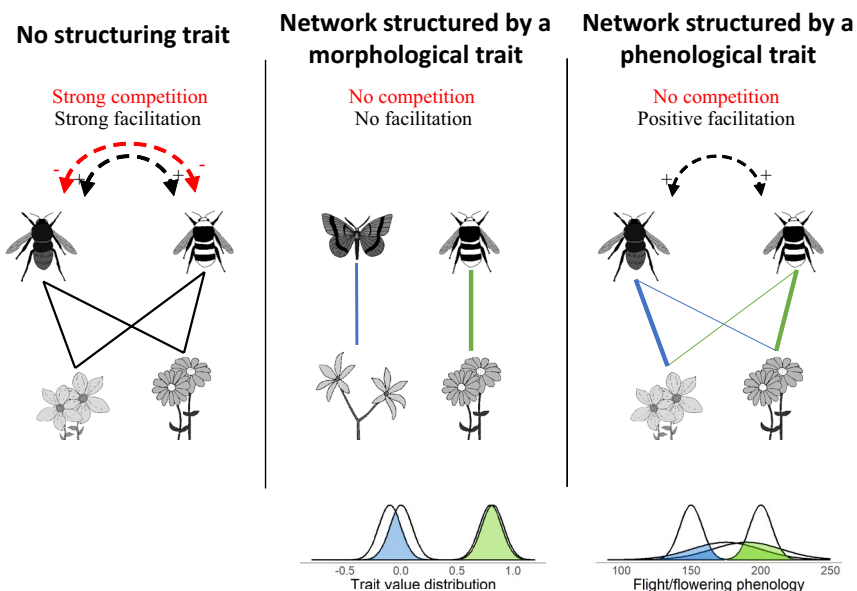


FIGURE 1 Schematic pollination networks with no structuring trait (left), structured by a morphological trait (center) or by a phenological trait (right). Links between pollinators and plants represent mutualistic interactions (+/+) whereas indirect effects within the pollinator guild are represented 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

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.

MATERIALS AND 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; Pascual-García & Bastolla, 2017; Rohr et al., 2014) by modelling competition as a function of plant–pollinator interactions, that is in the functional response of mutualistic interactions, which is a 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 characterised by a phenological and a morphological distribution, both modelled by Gaussian curves. A Gaussian allows to represent a bell shape that often fits well the phenologies of flowering and pollinator activities (Malo, 2002; Rabinowitz et al., 1981; Stewart et al., 2020) or morphological trait distributions (Sletvold et al., 2016). Gaussian parameters have direct biological meaning that 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, that is 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 the species morphologies. These matches are measured as the overlapping area of the Gaussians, modelling 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 force 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 following two matrices:

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

where I_{ij} represents the interaction strength between plant i and 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):

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

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

where 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

TABLE 1 Parameter values of the dynamic model

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

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 1000 initial networks in order to explore a wide set of possible pollination networks.

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 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_{kj} for plants. ω_{kj} is defined as follows:

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

where 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 the abundance of pollinator k (P_k) and to the amount of interactions that represent plant i ($I_{ij} \times F_i$) relatively to all interactions maintained by pollinator j ($\sum_{i=1}^{n_f} I_{ij} \times F_i$). 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 fifth 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.

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, that is the total effect, among each species pair (Figure 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 formulae demonstrated by Nakajima and 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 in 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 inter-specific relationships. Then, the effect of the species j on the species i through indirect effects (IE_{ij}), was calculated as follows:

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

We further categorised 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 corresponds to their importance relative 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 modelling (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

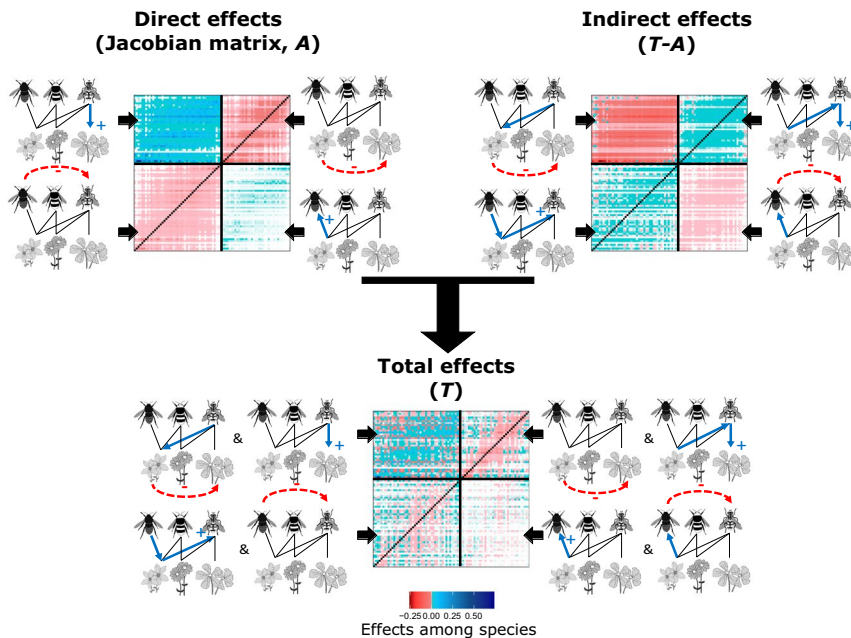


FIGURE 2 Example of matrices of direct, indirect and total effects at equilibrium. Jacobian matrix (A , top left), indirect effect matrix (top right, see methods) and total effect matrix (T , bottom) of a network at equilibrium, for $MF = 0.5$, $PF = 0.5$ and $c = 0.5$. Blue colors represent positive 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

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

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

where n_{peq} is the number of pollinator species persisting at equilibrium. We did the same for plants and indirect and total effects, using E_{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.

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 ($MF = 0$ and $PF > 0$) and simulations with morphological forcing only ($MF > 0$ and $PF = 0$).

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 ($c > 0$, Figure 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 (Figure 3a,b), while stronger morphological forcing (MF) decreases network viability and persistence and

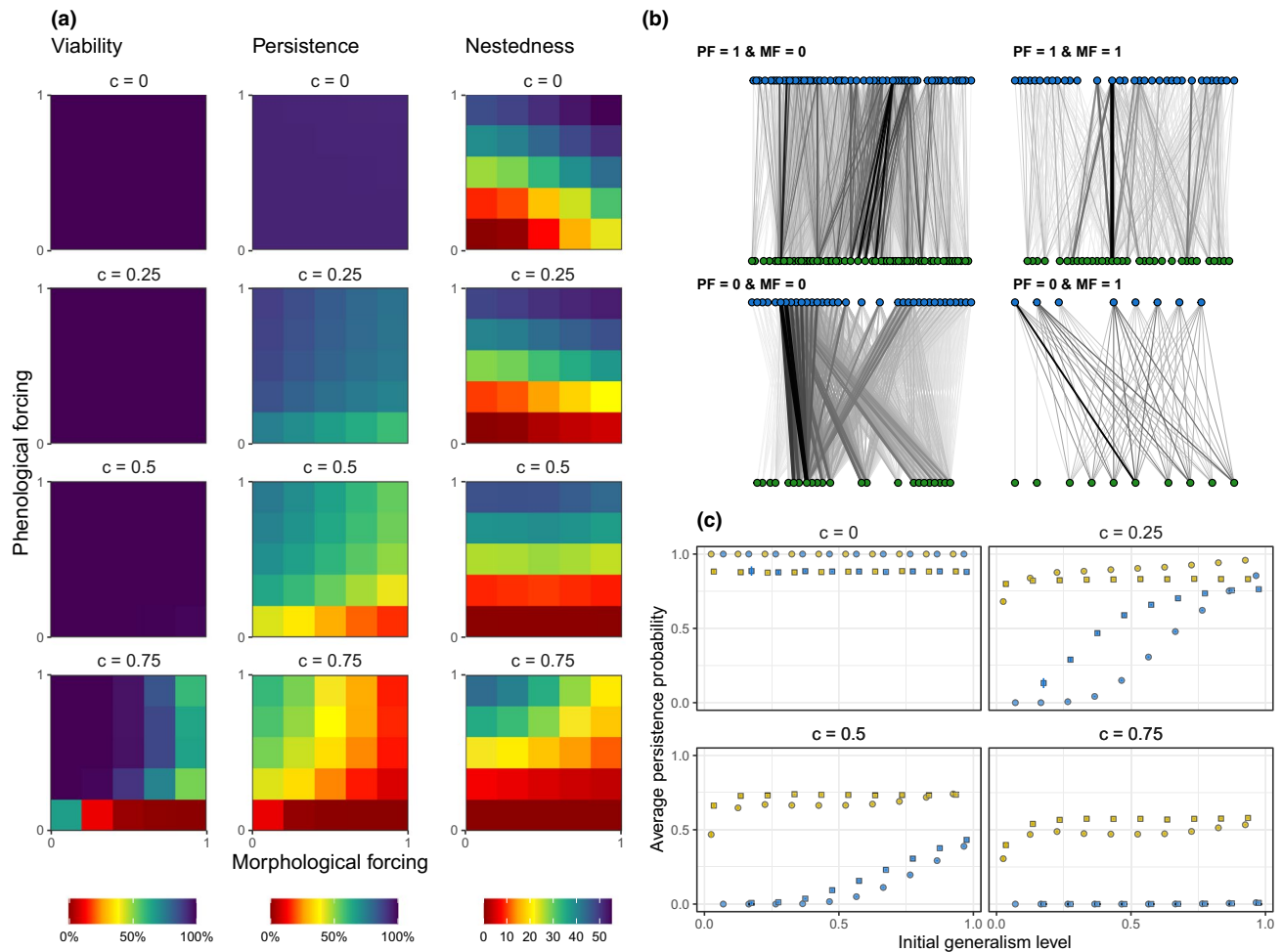


FIGURE 3 Network properties at the ecological equilibrium and species persistence. (a) Equilibrium network properties as a function of the competition strength c , and phenological and morphological forcing parameters. Viability is the percentage of networks with at least one plant and one pollinator 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

fails to promote nestedness (Figure 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 (Figure 3a).

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 (Figure 3c and Figure S1). The lower persistence of specialist species compared with generalists is attenuated when networks are structured by a phenological trait compared with when they are structured by a morphological trait (Figure 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 (Figure S2). This explains why networks structured by phenology retain higher nestedness than networks structured by morphology.

As expected, intra-guild competition strongly affects the average strength of direct and indirect effects among species in the networks at equilibrium, resulting

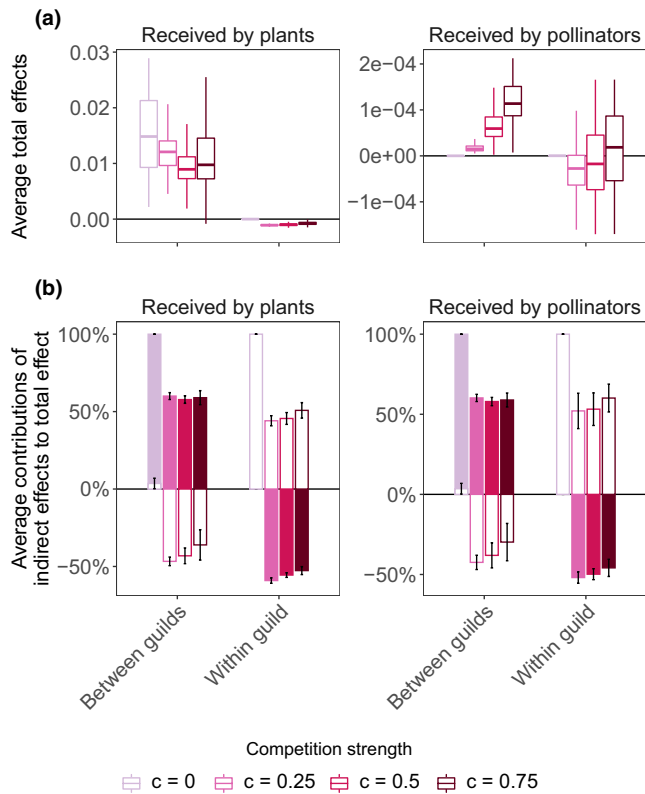


FIGURE 4 Within and between guilds effects partitioning at equilibrium and their relative contributions to total effects. (a) Within and between guilds strength of total effects received by species averaged at the guild level for plants and pollinators, per level of competition strength represented by 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

in changes in total effects among species (Figure 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 (Figure 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 (Figure 4b). Indirect effects can be strong enough to balance the competition within guilds and the mutualistic interaction between guilds (Figure 2, Figure 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 (Figure S3). However, since networks at equilibrium differ in diversity and nestedness between the two types of forcing (Figure 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 parameterisation 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 (Figure 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 (Figure 5a). In contrast, morphological forcing strongly decreases the contribution of positive indirect effects within pollinator guild (Figure 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 (Figure 5a). Those results mean that, in contrast to morphological traits, phenological traits, which decouples interaction in time, favour 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 (Figure 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 (Figure 3c). Indeed, quantifying the effects generated per species, that is 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 (Figure 5b). Generalist species generate stronger direct and indirect effects than specialists (Figure 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 (Figure S6). We detect the same patterns as in Figure 5a for the contribution of positive indirect effects to total effects within the plant guild, but only for strong intra-guild competition strength (Figure S5), likely due to the weaker importance of within-guild effects for plants than for pollinators (Figure 4a).

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 hypothesised, 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 affects 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 (CaraDonna et al., 2017; Gonzalez & Loiselle, 2016; 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 generalised 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 heights to avoid competition while 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; Cusser et al., 2021; Knop et al., 2017), 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 (Bartomeus et al., 2021; Jones et al., 2012; Levin & Anderson, 1970) because plants or pollinators strongly compete among them to access their mutualistic partners in pollination networks (Campbell, 1985; Henry & Rodet, 2018; Pleasants, 1980). However, most of the theoretical studies tackling this point modelled competition independently from plant to 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 modelling 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 favours positive indirect effects within guilds, that is facilitation, thereby maintaining diversity. Such effect not only comes from indirect effects among species sharing mutualistic partners, that is 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

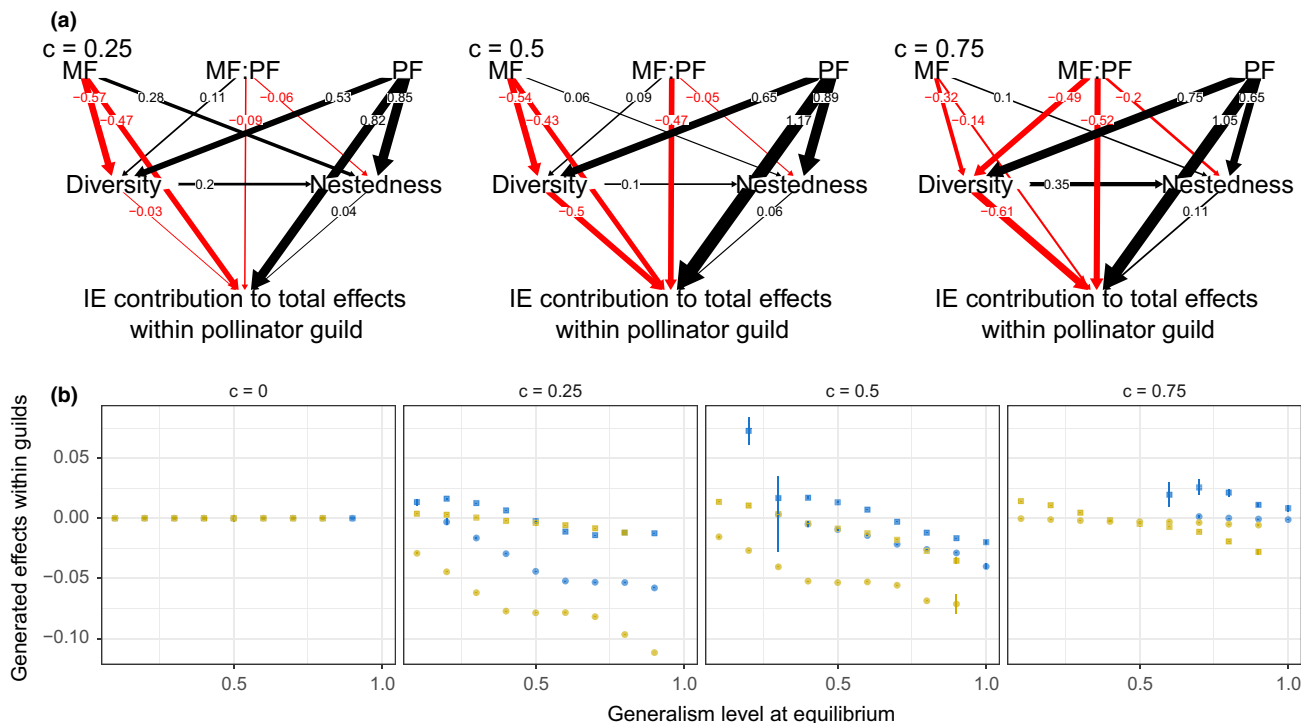


FIGURE 5 Effects of morphological and phenological forcing parameters on the contribution of indirect effects (IE) within the pollinator guild. (a) Determinants of the contribution of IE to total effects within the pollinator guild. Values on arrows are standardized coefficients of the multi-group path-analysis 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

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; Thébaud & Fontaine, 2010). Moreover, we find that specialist species propagate more positive indirect effects to other species relative 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; Duchenne et al., 2020; Theobald

et al., 2017). 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 the propagation of negative indirect effects. However, network reorganisation following perturbations can also happen (Burkle et al., 2013) and might buffer the effects of specialist extinctions.

Our results are 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 parametrise models using empirical seasonal and morphological structures (Tarantola, 2005).

COMPETING INTERESTS

The authors declare no competing interests.

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AUTHOR CONTRIBUTIONS

FD, CF, ETe and ETh designed the study. FD performed all the simulations and statistical analyses and wrote the paper with contributions from all authors.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13836>.

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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