Coevolution of phenological traits shapes plant-pollinator coexistence

Keywords: feasibility | emergent properties | morphology | structure | competition | plant | pollinator

Data availability statement:

Codes to perform simulation, to do figures and to analyse empirical networks are available here: https://github.com/f-duchenne/Evolution_pheno_vs_morpho

Empirical plant-pollinator interaction data are available here: https://doi.org/10.5281/zenodo.13270452

Competing Interest Statement:

The authors declare no competing interests.

Author contributions:

FD designed the study and performed all analyses with inputs from VDG and IB. FPM collected the data, with punctual help from IB, and identified plant and insect species. FD wrote the first draft and all authors participated to editing and writing the final version.

Abstract

Previous research has revealed how species traits determine species interactions, and how species interactions influence species coexistence. However, this hierarchical view ignores the coevolutionary feedback from species interactions to species traits and its consequences for species coexistence. Here, we developed a theoretical model to explore how the coevolution of morphological and phenological traits shape the structure and stability of mutualistic interaction networks. We found that, in comparison to morphological traits, phenological traits led to distinctive coevolutionary opportunities for species, which led to different emergent properties at community level. This is because phenological traits promoted facilitation over competition. While morphological coevolution led to modular and specialized interaction networks with a negative diversity-stability trade-off, phenological coevolution was required to achieve nested interaction networks with a positive relationship between diversity and structural stability. Our theoretical results were consistent with empirical observations: across 17 empirical pollination networks we found a high proportion of phenological motifs promoting facilitation over competition, suggesting an important role of phenological coevolution in community assembly. These empirical seasonal structures strongly enhanced the community stability and dampened the diversity-stability trade-off observed when neglecting them. Our results highlight the importance of phenological coevolution in the emergence of diverse and stable communities.

Introduction

Over the last decades, the study of mutualistic communities has developed a deep understanding of the ecological determinants of their stability, leading to key advancements on the fundamental question of how diverse community can be stable (1–8). In mutualistic systems, the balance between negative competitive effects and the positive facilitative effects that each species receives is key for their persistence and is strongly affected by the way the species interactions are distributed in the community (1, 2, 4). For example, a high level of nestedness, a structural pattern which occurs when specialist species interact with generalist ones, has been shown to increase community stability by minimizing within guild competition over facilitation (1, 4, 9). More recently, several studies have suggested that in addition to static structural patterns, the temporal distribution of the interactions is also key to understand the competition-facilitation balance and the stability of mutualistic communities (5, 10, 11).

The increasing availability of mutualistic interactions networks with temporal resolution have highlighted important seasonal dynamics, with high species and interaction turnover within a year (12–14). These temporal dynamics are partially determined by species phenologies (*e.g.* flowering period, activity period) which creates an important species turnover along the season (12, 14–16). This species turnover is expected to have strong consequences for community stability because it can decouple interactions between different partners in time, and thus, decouple competition and facilitation (5, 10, 11). For example, in a plant-pollinator community, two pollinators can interact with the same plant population but at different periods of the season: an early pollinator may do so in spring and a later one in midsummer. This leads to facilitation between the two pollinators on the long term, because they maintain the same plant population, without promoting direct competition between them. Thus, phenology is one of the species traits that can remove competition but maintain facilitation between species. However, to have a positive effect on the balance between facilitation and competition, phenologies need to be organized in such a way that mutualistic partners overlap in time, but competitors do not (Fig. 1). Thus, one of the main questions is how easily can these patterns emerge from coevolutionary dynamics in species-rich communities?

Since natural selection is driven by differences in population fitness and not by community properties, it is not clear if evolutionary dynamics would lead to structure promoting community stability. First, our knowledge on how coevolutionary dynamics affect the stability of mutualistic communities remains fragmented, because the few studies that have explored this used diverse modelling frameworks: modelling trait evolution with quantitative genetics (17) or with adaptive dynamics (18, 19), or directly optimizing species interactions through adaptive foraging (20–22). These studies have also used different metrics of stability, using either the proportion of species persisting (21–23), the resilience (18–20) or the robustness (17) to a perturbation, which complicates the synthesis. In fact, even the studies focusing on the same stability metric, for example the proportion of species persisting, have found either a positive (22, 23) or negative (21) effect of coevolution, highlighting the heterogeneity in potential effects of coevolution on community stability. Second, while some studies have shown that nestedness can emerge from coevolutionary dynamics (20, 24–27), but we know virtually nothing about how mutualistic coevolution can drive the emergence of seasonal structures in interactions, which have been proposed as a key determinant for community stability (5, 11, 28, 29). To fully understand how coevolution affects community stability we need to understand

how coevolution shapes static and temporal structures in the interaction networks, which requires modelling morphological and phenological coevolution simultaneously.

To investigate the potential emergence of stabilizing structures in mutualistic communities due to the coevolution of phenological and morphological traits, we first developed a theoretical model, to track static and seasonal structures in interactions over the coevolution process. We used that model to compare the structure and stability of networks produced by phenological coevolution with those produced by morphological coevolution and those produced by the simultaneous coevolution of both traits. Then, we analyzed a set of 17 time-structured empirical plant-pollinator networks to test if the signal of phenological coevolution could be detected, before assessing how the seasonal structures of these of natural communities determined their stability. Our results show that stabilizing seasonal structure can emerge from coevolution of phenological traits, suggesting that temporal dynamics in community ecology can help to answer the longstanding question of how diverse natural communities can be stable.

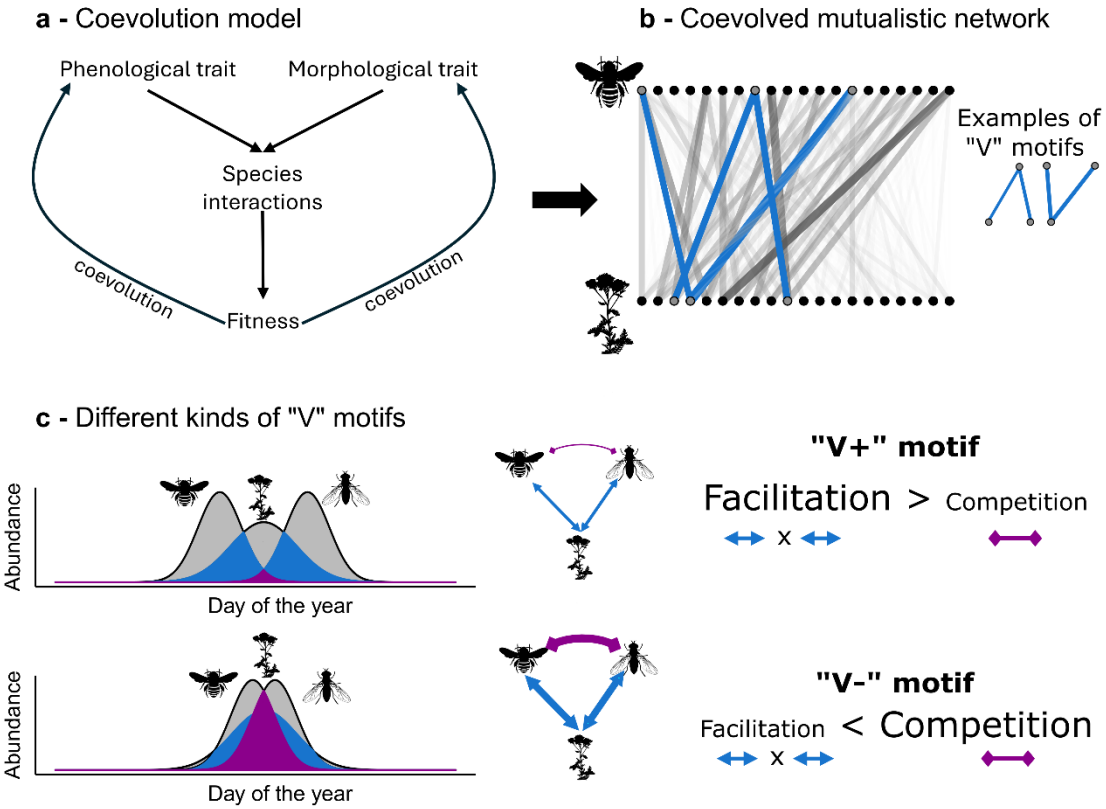

Fig. 1: schematical representation of our coevolution model and the different motifs that can emerge from phenological coevolution. *(a) Schematical representation of our theoretical model and (b) of a coevolved mutualistic interaction network produced by that model. These interaction networks contains hundreds of "V" motifs, which can be classify as "V+" or "V-" motifs depending on whether they promote facilitation over competition or not. (c) On the top a "V" motif promoting facilitation ("V+"), and on the bottom a V motif promoting competition ("V-"). On the top schema, pollinators interact with the same plant but overlap little in time, and hence they almost do not compete with each other to obtain resources but mostly facilitate each other because they maintain the same plant population. The facilitation between pollinators is the positive indirect effect mediated by the plant (the product of the mutualistic interactions). On the bottom schema, pollinators largely overlap in time, a structure which tends to promote competition over facilitation, which can lead to competitive exclusion.*

Methods

We developed a theoretical model to simulate the coevolution of two guilds of species interacting mutualistically among guilds and competing within guilds (Fig. 1), in line with previous models (24, 30, 31). In this model all species were assumed to have similar and constant abundances, while trait values were changing because of natural selection driven by mutualistic and competitive interactions. Our model simulated the reorganization of an interaction network of fixed dimensions (a fixed set of species) due to coevolution. We could then calculate structural properties of that interaction network and the probability for that species assemblage to coexist (*i.e.* its structural stability). For simplicity we took the example of a plant-pollinator community, but the model could apply to any mutualistic community.

Species traits

Each species was characterized by two gaussian traits: a morphological trait and a phenological trait, with a mean μ_M and μ_P and a standard deviation σ_M and σ_P, respectively. Both traits evolved independently, *i.e.* we assumed no genetic covariance among them. To make comparisons possible between traits, both were treated exactly in the same way, on a scale that goes from 0 to 365. For phenology it obviously recalls the day of the years, while for morphology it can be any abstract scale.

To maintain gaussian distributions within the interval [0,365], we bounded the mean trait value and standard deviation between 80 and 285 and between 1 and 50, respectively. These constraints on trait values had the technical advantage to avoid infinite evolution but also mimicked physiological limits. For example, for phenology, these limits constrained pollinators to be active mostly between days of the year 80 and 285 (*i.e.* spring and summer) simulating empirical pollination seasons that we can observe in temperate areas. For morphology, it would correspond for example to a limit in the length of the corolla or feeding appendices, that cannot be too short neither too long because of physiological constraints. To bound trait values without using a sharp truncation that would create weird behaviors at the bounds, we used a process inspired by generalized linear models, in which the trait evolves on an unbounded latent distribution linked to the effective bounded values through a link function (*cf.* Supplementary Methods I). In the following part, μ and σ, denote the values on the bounded scale (real mean and standard deviation), while $\ddot{\mu}$ and $\ddot{\sigma}$ denote the value on the latent unbounded scale. For example, $\ddot{\mu}$ varied from $-\infty$ to $+\infty$, but μ was bounded between 80 and 285.

Species interactions

The overlap between their morphological (φ_{ij}) and phenological traits (τ_{ij}) determined the interaction strength (γ_{ij}) between a pollinator *j* and a plant *i*:

$$\gamma_{ij} = \varphi_{ij}\tau_{ij} \tag{1}$$

To calculate the overlap between traits, we used the area below the minimum of the two gaussian traits involved (Fig. 1c):

$$\tau_{ij} = \int_0^{365} min\left(\frac{1}{\sigma_{P_i}\sqrt{2\pi}} e^{\frac{-1}{2}\left(\frac{x-\mu_{P_i}}{\sigma_{P_i}}\right)}, \frac{1}{\sigma_{P_j}\sqrt{2\pi}} e^{\frac{-1}{2}\left(\frac{x-\mu_{P_j}}{\sigma_{P_j}}\right)}\right) dx \tag{2}$$

φ_{ij} was calculated according to an equation similar to equation (2). Equation (1) and (2) means that the mutualistic interaction strengths are bounded between zero and one ($0 \leq \gamma_{ij} \leq 1$), because φ_{ij} and τ_{ij} are bounded between zero and one. To neglect phenology in simulation with only a morphological trait, we set $\tau = 1$ for all pairs of species, meaning that all interactions occur simultaneously. In contrast, to ignore morphology when simulating with a phenological trait only, we set $\varphi = 1$, meaning that all species have a perfect morphological match.

The competition between plant *i* and *k* was defined as the intersection of their mutualistic interactions divided by the union of their niche, multiplied by the temporal co-occurrence between plant *i* and *k* (τ_{ik}):

$$\alpha_{ik} = \tau_{ik} \frac{\sum_{j=1}^{n_A} \gamma_{ij}\gamma_{kj}}{\frac{1}{2}\sum_{j=1}^{n_A} \gamma_{ij} + \gamma_{kj}} \tag{3}$$

where n_A was the number of pollinator species. We set the intraspecific competition to one, $\alpha_{i,k=i} = 1$, to ensure diagonal dominance of our system. The competition coefficient among pollinator species was calculated with an equation similar to equation (2). These competition coefficients represent only the competition for mutualistic partners among species from the same guild, as here we ignored competition for abiotic resources or space, because we wanted to focus on the role of mutualistic interactions in driving coevolution.

Species fitness and trait evolution

The plant-pollinator population dynamics can be described by a generalized Lotka-Volterra model, as often done (1, 2). In this model, the variation in the population size of plant *i* was:

$$\frac{dN_i}{dt} = N_i \left(r_i - c \sum_{k=1}^{n_P} \alpha_{ik} N_k + \sum_{j=1}^{n_A} \gamma_{ij} N_j \right) \tag{4}$$

where r_i was the basal per-capita growth rate of species *i*, and c was the overall importance of competition, relative to mutualism. The variation in population size of pollinators was described by a similar equation.

We used the Lotka-Volterra model to define the fitness of species *i* (W_i), which was the total population growth rate. Since we were interested in the fitness components that depended on trait values only, this total growth rate could be summarized as the balance between competition and mutualism. In addition, since we used equal and constant population sizes ($N_i = N, \forall i$), species abundances could be dropped, leading to the following fitness function:

$$W_i = -c \sum_{k=1}^{n_P} \alpha_{ik} + \sum_{j=1}^{n_A} \gamma_{ij} \tag{5}$$

At each time step we introduced independent mutations on trait parameters (μ_M, μ_P, σ_M and σ_P). For each parameter we introduced deterministic positive (e.g. $\ddot{\mu}_M + \varepsilon$) and negative mutations (e.g. $\ddot{\mu}_M - \varepsilon$), with a mutation size ε. We calculated the fitness associated with the three trait values, unmuted (resident), positive and negative mutation. Among these three

values, we kept the trait parameter value associated with the highest fitness for the next time step.

Simulations and parametrization

Our simulations required very few parameterizations, because most of the coefficients were determined by the evolving trait values, but we needed to draw initial values for traits and to fix a value for the competition importance (c) and for the mutation size (ε).

For the traits, we drew initial values on the modified logit scale (*cf.* Supplementary Methods I) from a uniform distribution for the mean and the standard deviation: $\ddot{\mu}_{i,t=0} \sim U(-2.5,2.5)$ and $\ddot{\sigma}_{i,t=0} \sim U(-2.5,2.5)$. We generated 100 initial conditions for 3 different values of initial diversity: 10, 20 and 30 species per guild.

Since our competition coefficients were always smaller than the mutualistic interaction strength (*cf.* equation (2)), we needed c>1 to avoid mutualistic orgies, a common behavior in linear models of mutualistic communities (32). A mutualistic orgy would lead to all species quickly converging to the same trait value, and would thus not be realistic. We performed simulations with three values of competition to simulate 3 cases: low importance of competition ($c = 2$), a moderate importance ($c = 4$) and a high importance ($c = 6$). These three values were chosen to have an average ratio of mutualism/competition across the 100 initial conditions (when considering a phenological trait) that was >1 (mutualism stronger than competition), 0.5<x<1 (competition slightly stronger than mutualism) and <0.5 (competition stronger than mutualism, Fig. S1).

The mutation size ε was fixed to 0.01, which allows a smooth evolution (without big jumps due to a high mutation size) but fast enough to allow simulation to reach a stationary state (Fig. S2).

We performed simulations over 2000 time steps. In our time-discrete model, trait values never reach an equilibrium because all species traits change simultaneously, but trait evolution was fast in the first 200 steps, before slowing down and reaching stationary states asymptotically (Fig. S2). For each initial condition, the simulation was run three times, considering a morphological trait or a phenological trait only, and considering both traits together. This allowed us comparing trait coevolutionary dynamics in isolation and when they were mixed.

Network structure, motifs and stability

To assess how coevolutionary dynamics affect the structure and the stability of the evolving interaction networks, we measured indices describing the mutualistic interaction network. Since evolution slowed down with time (Fig. S2), we measured these metrics at 10 time steps, that were evenly distributed on a square-rooted time scale (t = 0, 20, 100, 220, 400, 620, 890, 1210, 1580, 2000).

To measure how evolution affected the balance between mutualism and competition we computed the average competition strength, which is the average of all α_{ij}, and the balance between mutualism and competition as $\frac{\bar{\gamma}}{c\bar{\alpha}}$, where $\bar{\gamma}$ and $\bar{\alpha}$ are the average of all pairwise terms of mutualistic interaction and competition (across both guilds), respectively. To test if co-evolutionary dynamics can lead to phenological motifs that promote facilitation over competition, among the hundreds or thousands of "V" motifs we calculate the proportion of

them promoting facilitation, *i.e.* "V+" motifs (Fig. 1c). This kind of motifs can be present only in the phenological scenario because they require that two mutualistic partners of a given species are decoupled in time. In contrast, when considering morphological traits, all interactions happen simultaneously ($\tau = 1$) thus "V+" motifs are impossible. Details of the calculation are provided in Supplementary Methods II.

To measure structural properties we measured the connectance, nestedness, modularity, specialization and interaction evenness with different indices implemented in the *bipartite* R package (33). Details of the calculations are also provided in Supplementary Methods II. To track network structure over time, we performed a Principal Component Analysis (PCA) with the structural metrics, across all simulations and time steps. We used the two first dimensions of this PCA which explained 93% of the total variance, to characterize the evolutionary trajectories of the simulated communities.

Finally, to understand how evolutionary dynamics affected the ecological stability of our system, we measured the community structural stability. Structural stability is a measure of ecological stability that aims to quantify the range of environmental conditions, modelled through the per capita basal growth rates (r), in which all species can coexist indefinitely (2, 3, 34). The range of environmental conditions, or growth rates, in which all species can coexist is called the feasibility domain, and the structural stability is quantified as the size of the feasibility domain scaled by the number of species in the community, which gives an average measure of species persistence (ω). To calculate the structural stability of our communities, we used the generalized Lotka-Volterra model presented in equation (4), using the *Omega* R function provided by Song *et al.* (34). Details of the calculation are also provided in Supplementary Methods II.

Diversity-Stability trade off

To study how coevolution affected the relationships between the structural stability and the diversity, we modelled structural stability as a function of diversity using a Generalized Linear Model (GLM) with a quasibinomial error structure and a logit link function. To model one diversity-stability trade off per coevolution scenario, for initial and coevolved networks, we included a quadruple interaction between the diversity (number of species per guild), the kind of coevolution scenario, the kind of network (initial *versus* coevolved) and the importance of competition in the model. The GLM was described by the following equation:

$$logit(\omega(A)_{ticn}) = \beta_{0_{tic}} + \beta_{1_{tic}} \times diversity_n \quad (6)$$

where $\omega(A)_{ticj}$ was the structural stability at time t, of the initial ($t = 0$) or coevolved networks ($t = 2000$), for coevolution scenario i (phenological, morphological or mixed coevolution), competition importance c, and for a simulated diversity n (number of species per guild). $\beta_{0_{tic}}$ and $\beta_{1_{tic}}$ were the intercept and the slope of the diversity-stability relationships, respectively.

Analyses of empirical plant-pollinator interaction networks

We used a set of 17 time-structured plant-pollinator interaction networks, sampled in the area of the Doñana National park, near Sevilla, in Spain, with the protocol described in *ref.* (35). These networks have been sampled at bi-weekly intervals during the peak season (February to May), for one to 8 years (Table S1). Interactions have been recorded at each

sampling occasion along a 100m transect during 30 effective minutes, and flower abundances per species have also been recorded along that transect in a standardized way (35).

From these empirical interaction data and flower counts we could assess the number of "V+" motifs, in which the (geometric) average overlap between mutualistic partners was higher than the overlap between the two competitors. To get a measure comparable with our simulations and among networks, as before, we estimated the proportion of "V+" motifs over the total number of "V" shape motifs (*cf.* Supplementary Methods III). To compare these proportion of "V+" motifs with the proportion we obtained in our theoretical simulations, we performed a new set of simulation using the number of plant and pollinator species of the empirical networks. For each of the 17 empirical networks, we performed these simulations with a mixed coevolution scenario (morphological and phenological coevolution together), for a moderate importance of competition (c = 4) and for a set of 10 different random initial conditions of randomly distributed traits values, using the same uniform distribution as for the theoretical simulations to draw trait values.

Finally, to see how considering the seasonal structure in interactions affected the structural stability of these communities, we estimated the structural stability (ω) with and without considering the seasonal structure in the interactions (*cf.* Supplementary Methods III).

Results

The initial average competition strength differed between initial networks with or without phenology (Fig. 2), because decoupling interactions in time, even randomly, decreases competition strength. Moreover, the scenario combining both phenological and morphological traits exhibited less mutualism strength in average at initial state, because combining two randomly distributed traits provided less opportunity for trait matching than when using only one trait. However, what most interested us was seeing how coevolution shaped the networks, *i.e.* the trajectory over time of the different structural metrics. When coevolutionary dynamics unfolded, trait modifications quickly reorganized species interactions, affecting the overall strength of competitive and mutualistic interactions and their balance, with distinctive trajectories across coevolution scenarios (Fig. 2 & S3).

Regardless the importance of competition (parameter c), morphological coevolution tended to decrease the average amount of mutualistic interactions, and consequently the average amount of competition for partners in the systems, which leads to a slight increase in the mutualism/competition balance (Fig 2a-c). This restructuring of the community can be understood by examining the distribution of species traits: morphological coevolution produced only specialist species, characterized by the small standard deviation of their morphological trait, indicating a very narrow morphological niche (Fig. S4). In contrast, phenological and mixed coevolution tended to produce some generalist species, characterized by long phenology (large standard deviation, Fig. S4), in a proportion that depended on the importance of competition. The lower the competition importance, the more generalist species (Fig. S4), and thus the more mutualism and competition in the community (Fig. 2). When giving low importance to competition (c = 2), phenological and mixed coevolution tended to maximize trait matching across a maximum of species, leading to strong trait convergence, regardless the amount of competition it generated. In contrast, when competition had moderate or high importance (c = 4 or c = 6), phenological and mixed coevolution produced interaction networks

that tended to maximize the mutualism-competition balance (Fig. 2c) and tended to reorganize phenologies in a way that potential competitors did not overlap in time. This reorganization creates "V+" motifs that promote facilitation (Fig. 2d & S3), patterns that cannot be produced by morphological coevolution.

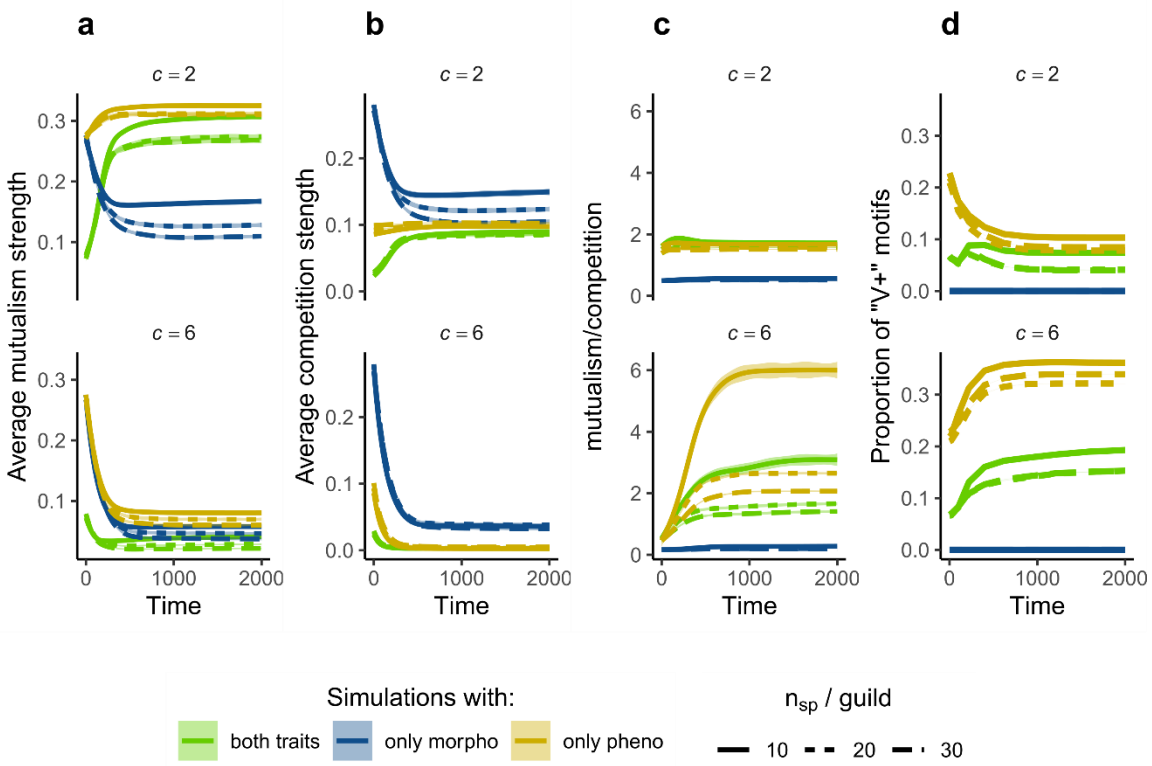

Fig. 2: motifs promoting facilitation can emerge from phenological coevolution. *(a) average mutualistic strength, (b) average competition strength, (c) mutualism/competition balance (cf. methods) and (d) proportion of "V+" motifs (over all "V" motifs), as a function of time, diversity and simulation scenarios for low (c=2) and high (c=6) competition strengths. In (a)-(d) the lines and ribbon show the estimated values and their 95% confidence interval, respectively, obtained by a locally estimated scatterplot smoothing (LOESS) of the values across time. V+ motifs did not exist when performing coevolution with morphological trait only (cf. Methods). See Fig. S3 for simulations with c = 4.*

To understand how coevolution affected network structure and stability, we then focus on simulations in which competition was moderate ($c = 4$) or important ($c = 6$), as it appears to be the case in many mutualistic systems (36–38). In this context, our simulations highlighted significant differences across various aspects of network structure between the coevolution scenarios including phenological traits (mixed or phenological coevolution) and the scenario with morphological traits only (Fig. 3 & S5). Mixed and phenological coevolution tended to produce mutualistic networks with a very similar structure, more nested and less modular than mutualistic networks produced by morphological coevolution. Differences in network structure between coevolution scenarios became apparent mostly when simulating big networks (*i.e.* high diversity of species, Fig. 3d-e), which offers more degree of freedom for the emergence of patterns.

These first results suggest that phenological coevolution is more likely to decrease the competitive exclusion than morphological coevolution, because of a better optimization of the ratio between mutualism and competition (Fig. 2), and because of the emergence of stabilizing structures, such as nestedness (Fig. 3). Importantly, when both traits coevolved, the outputs of the coevolved networks were more similar to the ones obtained by phenological coevolution than to the ones obtained by morphological coevolution, suggesting that coevolution of species phenologies is key in determining emergent properties at community level.

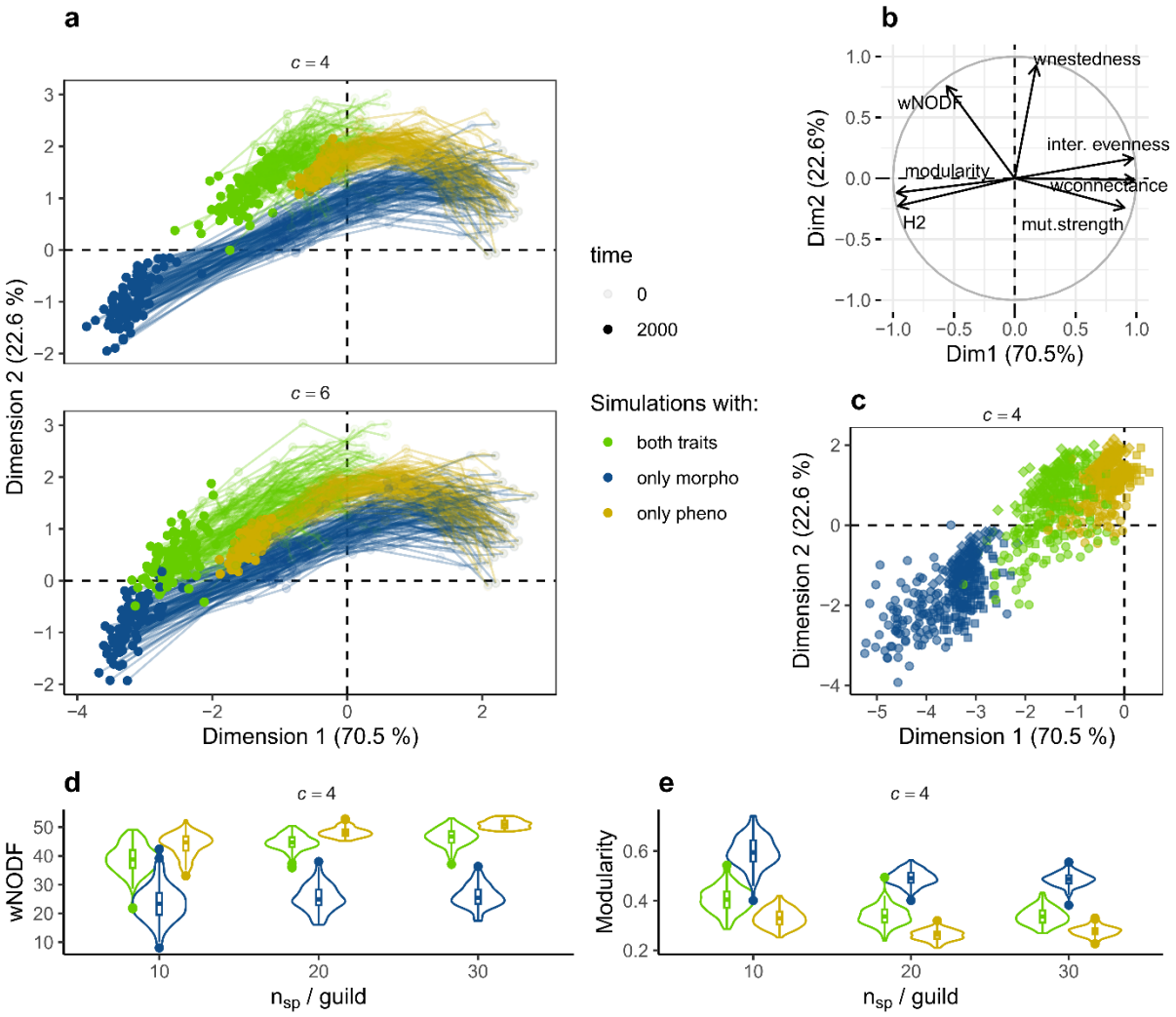

Fig. 3: phenological and morphological coevolution led to divergent evolutionary trajectories of communities. *(a) Location of each network at different time steps, in a multidimensional space of network structure, for different importance of competition (c = 4 & c = 6). The multidimensional space of network structure was created using the Principal Component Analysis (PCA) illustrated in (b). In (a) only the simulations with 30 species per guild are represented for readability. (b) PCA loading plot, where wNODF is a weighted measure of nestedness and H2 a measure of specialisation, and mutualism (mut.) strength a measure of connectance (cf. methods). (c) Final location of each community in the multidimensional space of network structure, when c = 4 (cf. Figure S4 for c = 6). Circles represent simulations with 10 species per guild, squares 20 species per guild and diamonds 30 species per guild. (d) and (e) represent the nestedness (measured as wNODF) and the modularity of the final networks, as a function of the number of species per guild and kind of trait, when c =4.*

In the initial state, communities structured by morphological traits exhibited lower structural stability than those structured by phenological traits or by both traits (Fig. 4a). This is consistent with previous findings (5, 10), and happens because decoupling interactions in time, even randomly, decreases competition strength (Fig. 2b-c). All initial networks showed a negative relationship between diversity and stability: the more diverse, the less stable (Fig. 4b-c). Once the coevolutionary dynamics unfolded, it increased the structural stability and dampened the diversity-stability trade-off in all coevolution scenarios (Fig. 4b-c). However, only the phenological and mixed coevolution reversed the diversity-stability trade-off to a positive relationship (Fig. 4b-c). This suggests that the seasonal structure in interactions is key to create diverse and stable communities.

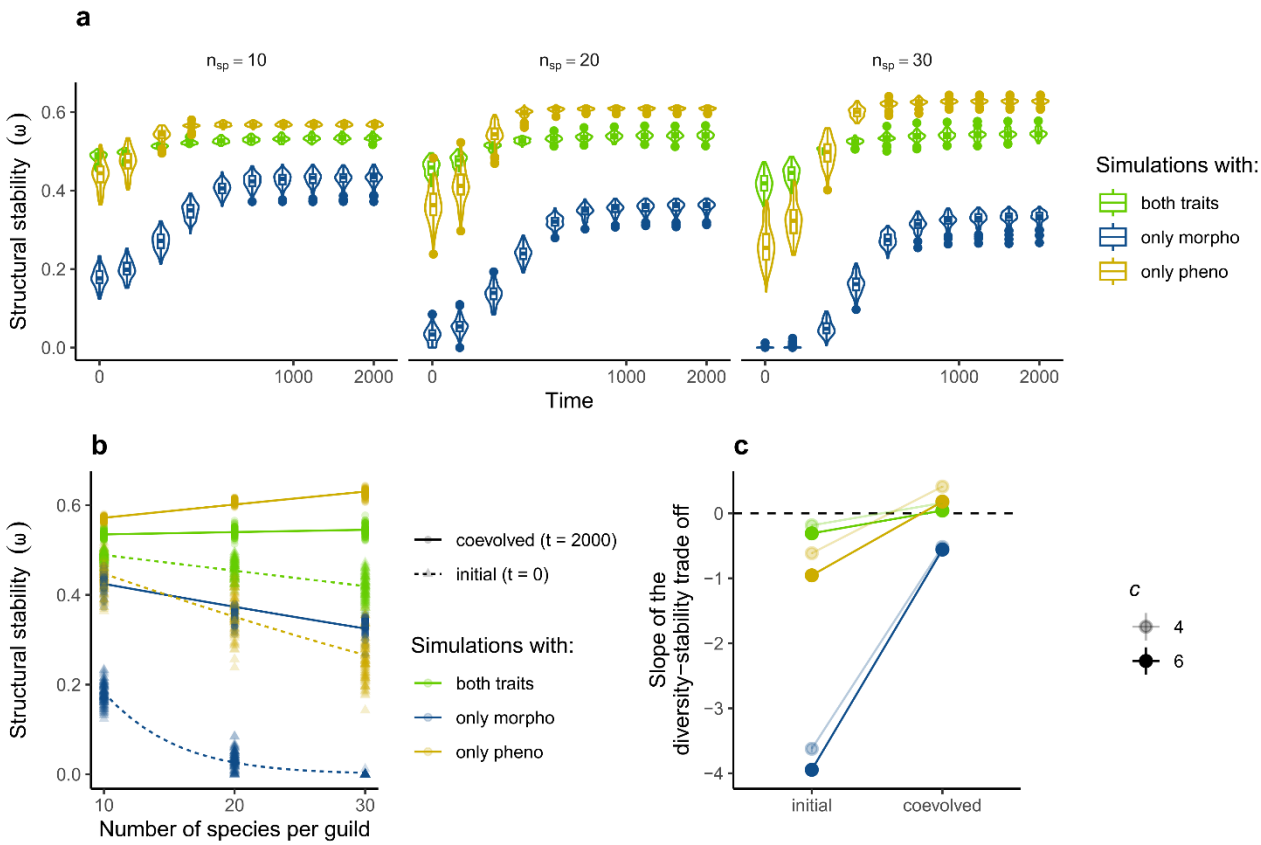

Fig. 4: phenological coevolution increased structural stability and dampened the diversity-stability trade-off. *Changes in structural stability (average species persistent probability) over time, for the three coevolution scenarios and number of species per guild, when competition was moderate (c = 4). See Fig. S6 for simulations with c = 2 & c=6. The x-axis is square-root transformed. (b) structural stability as a function of the number of species per guild (i.e. diversity), for interspecific competition strength c=4. Lines show the predictions of a Generalized Linear Model (GLM, cf. Methods). (c) Slopes of the diversity-stability relationships extracted from the GLM. Error bars (±$CI_{95\%}$) are too small to be visible.*

Finally, to assess the stabilizing role of phenology on real-world communities, we analyzed the phenological organization of 17 empirical plant-pollinator networks. We found evidence for a high proportion of the "V+" motifs (Fig. 5a), described in Fig. 1c, which suggests that coevolution of species phenologies have shaped the seasonal structure of plant-pollinator interactions. Our results show that the proportion of motifs promoting facilitation were relatively consistent with what was predicted by mixed coevolution and higher than what would be found in random initial networks (Fig. 5a).

As predicted by the simulations, considering the seasonal structure in interactions led to an increase in the structural stability of the empirical communities (Fig. 5b-c). This shows that the stabilizing role of the coevolved seasonal structures that we found *in silico* is likely to be important in stabilizing natural mutualistic communities. In addition, the negative relationship between stability and diversity that we observed in empirical communities was dampened when seasonal structure was considered (Fig. 5b).

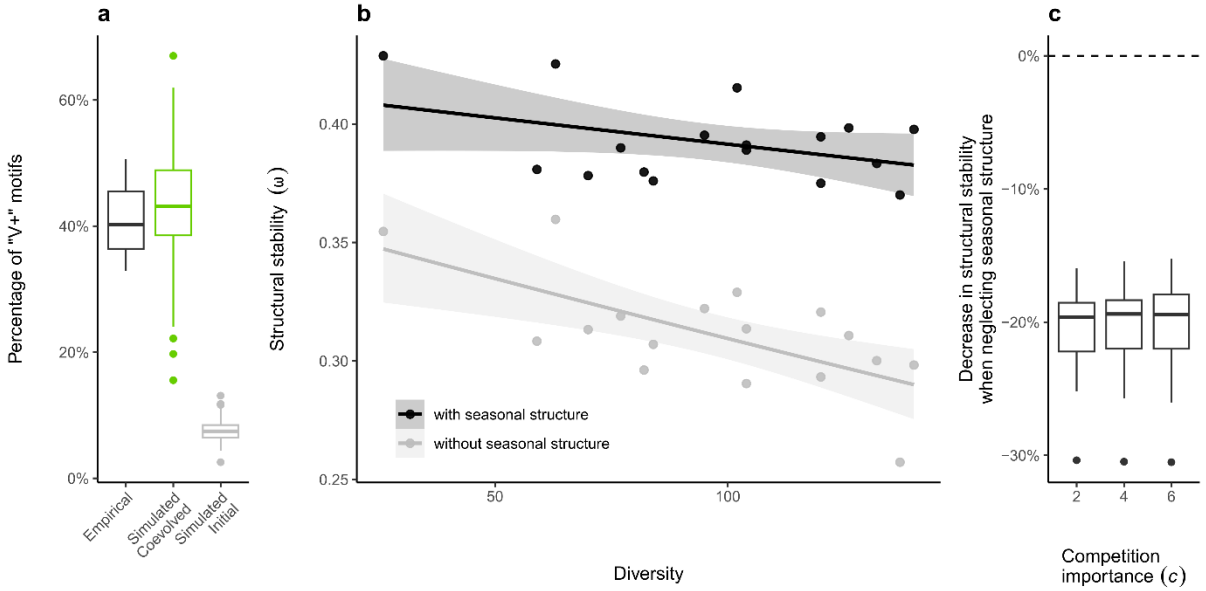

Fig. 5: Seasonal structure in interactions stabilize natural communities. *(a) Distribution of the percentage of "V+" motifs, relative to the total number of V motifs, in the 17 empirical networks, and in simulated networks with similar dimensions (cf. methods), before (i.e. random, grey) and after mixed coevolution (green). (b) Structural stability, average probability of persistence, as a function of community diversity (number of pollinator and plant species), when accounting for seasonal structure in competitive interactions or when neglecting this seasonal structure, for a given competition importance (c = 4). The lines and ribbon show the estimated values and their 95% confidence interval, respectively, obtained by generalized linear model with a quasi-binomial error structure. (c) The decrease in percentage of the structural stability observed when neglecting seasonal structure, relative to the measure when considering it, as a function of the overall competition importance (c parameter). n = 17 for each boxplot. Dots represent outliers.*

Discussion

Our results show that explicitly modelling the linkage rules defining species interactions is important to understand the community level outcomes of coevolutionary dynamics. We show that, in theory, a positive relationship between diversity and stability could be achieved by the coevolution of phenological traits but not by the coevolution of morphological traits. Consistently with our theoretical results, we show that the seasonal structure of empirical plant-pollinator communities strongly dampened the diversity-stability trade-off observed when neglecting that seasonal structure. Our results highlight that a frequently neglected ecological mechanism, the temporal organization of species interactions that emerges when phenological traits are considered, is key to understand coevolutionary dynamics and the stability of diverse mutualistic communities.

In contrast to morphological traits, phenological traits can decouple interactions in time, rendering an asymmetric partition between the mutualistic interactions and the competition for

mutualistic partners (10, 39). Surprisingly, this key mechanism explaining species coexistence has only recently been integrated to ecological models, but is now well recognized as an important ecological mechanism (5, 10, 11, 28, 29, 39, 40). Here we show that seasonal structures fostering stability can emerge from coevolutionary dynamics. Importantly, our model did not include any abiotic constrain on phenologies other than physiological bounds. Thus, in our simulations, the emergence of seasonal structure was only driven by species interactions. This suggests that the mechanism we describe could be universal: seasonal structures in interactions are expected to be present in every mutualistic system where interspecific competition for mutualistic partners is high enough, regardless the abiotic seasonality. Since, interspecific competition for mutualistic partners has been reported to be strong in many different mutualistic systems, such as pollination (38), seed-dispersal (36, 41), mycorrhizae (42) and cleaner-client fishes (43) , we expect that these systems would exhibit stabilizing seasonal structures. Our results could explain why even tropical mutualistic systems with relatively constant abiotic conditions, such as plant-hummingbird interactions, exhibit a stabilizing seasonal structure (11, 15).

Here, we also highlight that different kinds of traits led to interaction networks with different structures. Coevolution of morphological traits led to a collection of sub-communities, each comprised of a few specialist species, corresponding to a modular network. In contrast, the coevolution of phenological traits led to a more permissive resource partitioning, with networks containing some generalist species and a nested structure where more specialized species interact with the core of generalist species. Our results thus suggest that coevolution of species phenology might be one of the main structuring factors of mutualistic networks, explaining how they can be diverse and stable at the same time.

Using a set of 17 empirical networks, we found a high proportion of "V+" motifs indicating that in many plants or pollinators that share common partners do not fully overlap in their phenology. These phenological motifs promoting facilitation were present in the empirical networks in a higher proportion than what would be expected if phenologies would be distributed randomly. This support the fact that these motifs have emerged in nature due to phenological coevolution, consistently with our theoretical predictions. Neglecting the seasonal structure in the empirical interaction networks caused an underestimation of the structural stability of the communities of ~20%, with variation depending on the community diversity.

Our findings linking phenological coevolution and increased community stability can be generalized to other kinds of traits, provided that they allow to decouple the interactions with a common partner in time or space. For example, one can consider traits associated with thinner temporal dynamics, such as pollinator's daytime activity and flower opening times (e.g. diurnal *vs*. night) or morphological traits with inter- or intra-individual variation, such as flower heights. These kinds of traits can also create "V+" motifs, maintaining mutualistic interaction with two different partners while removing direct competition between them. For instance, differences in flower heights in a tree could allow two pollinator species that fly at different heights to avoid competition while still interacting with the same tree population. This can happen both if different individuals display different heights, or within the same individual tree when it has flowers at different heights. This vertical stratification exists for example in plant-hummingbird interactions (44). Thus what we call here phenological and morphological trait could be also generalized as traits with and without inter-individual variation, respectively, which is

consistent with recent results highlighting intraspecific variability as a key mechanism promoting the stability of plant-pollinator communities (45).

By showing that complex interaction structures fostering stability can emerge from species' fitness driven evolution, we effectively link coevolutionary mechanisms and community ecology. Most importantly, the emergence of these stabilizing structures depends on which kind of traits coevolve. For example, the well-studied nested structure emerged when including phenological traits but not when considering only morphological traits. Overall, our results suggest that coevolutionary dynamics enhance the positive effect of seasonal structures on community stability (5, 10, 11, 28, 29), which is probably a key mechanism to understand how natural communities can be both diverse and stable.

Acknowledgements

We thank Nerea Montes for the help while collecting data. We also thank the taxonomists L. O. Aguado and T. Wood for their help with some bee identifications. FD was funded by *postdoc Mobility* grant from the SNF (project number: P500PB_217801), and VDG by a Marie Skłodowska-Curie grant (N°101064340) from the European Union's Horizon 2021 research. Data collection was funded by a Marie-Curie Career Integration from the European Union's Horizon 2020, the BeeFUN project (PCIG 14-GA-2013-631653), granted to IB.

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