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LETTER

Phenology drives mutualistic network structure and diversity

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Abstract

Several network properties have been identified as determinants of the stability and complexity of mutualistic networks. However, it is unclear which mechanisms give rise to these network properties. Phenology seems important, because it shapes the topology of mutualistic networks, but its effects on the dynamics of mutualistic networks have scarcely been studied. Here, we study these effects with a general dynamical model of mutualistic and competitive interactions where the interaction strength depends on the temporal overlap between species resulting from their phenologies. We find a negative complexity–stability relationship, where phenologies maximising mutualistic interactions and minimising intraguild competitive interactions generate speciose, nested and poorly connected networks with moderate asymmetry and low resilience. Moreover, lengthening the season increases diversity and resilience. This highlights the fragility of real mutualistic communities with short seasons (e.g. Arctic environments) to drastic environmental changes.

Keywords

Asymmetry, connectance, diversity-stability debate, intraguild competition, mutualistic networks, nestedness, phenology, resilience, season length.

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INTRODUCTION

Mutualism has been suggested to be the mainstay of ecological communities (Bronstein *et al.* 2006). Mutualistic interactions are ubiquitous in nature and many ecosystems depend on the presence of mutualist services (e.g. pollination) (Bawa 1980; Janos 1980). The structure and dynamics of plant–animal mutualistic communities (e.g. plant-pollinators, plant-seed dispersers) have been extensively studied (Bascompte & Jordano 2007; Vázquez *et al.* 2009b). The topological description of these networks of interactions has revealed very interesting patterns of how these webs are structured. Mutualistic webs are highly asymmetric (Bascompte *et al.* 2006; Bascompte & Jordano 2007) in terms of degree (i.e number of interactions) and also in terms of interaction strength between mutualist partners (Vázquez & Aizen 2004; Bascompte *et al.* 2006; Vázquez *et al.* 2007). They are also highly nested, nestedness describing how 'specialists interact with species that form perfect subsets of the species with which generalists interact' (Bascompte *et al.* 2003). Nested topologies seem to be temporally invariant (Alarcon *et al.* 2008; Petanidou *et al.* 2008), and recent theoretical work indicates that nestedness begets stability and biodiversity (Bastolla *et al.* 2009). However, it is still not clear what the main mechanisms are that give rise to these topological properties. It has been suggested that there is a combination of niche and neutral processes governing the topology of mutualistic webs (Jordano *et al.* 2003; Krishna *et al.* 2008; Vázquez *et al.* 2009a). Neutral processes driven by random interactions and dispersal are important factors explaining the observed patterns, but niche processes based on biological trait differences are undoubtedly also dominant forces in the evolution and ecology of mutualistic webs (Vázquez *et al.* 2009a).

Recent studies suggest that these networks are shaped mainly by biological constraints (Vázquez *et al.* 2009b; Olesen *et al.*, 2010), also called forbidden links. Forbidden links are potential interactions that are not observed due to biological constraints, such as morphological differences, body size or phenological uncoupling (Jordano *et al.* 2003; Olesen *et al.*, 2010). Phenological uncoupling has been considered one of the most important constraints shaping these webs, explaining around one-third of all non-observed interactions (Olesen *et al.*, 2010). Furthermore, Vázquez *et al.* (2009b) found that species abundance and phenological and spatial overlaps seem to better explain and predict the structure of mutualistic webs than phenotypic traits and phylogenetic relationships do. Abundance and phenology are clearly related because species phenologies (i.e. length of activity during the season) determine: (1) who potentially interacts with whom (and therefore the number of interactions) and (2) relative species abundance in a specific time of the season. Studies of phenology have a long history in the ecological literature (Rathcke & Lacey 1985), mostly dedicated to describe and quantify the effect of phenological overlaps to explain community composition (Flemming & Partridge 1984; Feinsinger 1987), and how species phenologies are affected by abiotic factors (Inouye *et al.* 2000). More recently, several studies have reported dramatic changes in species phenology by global warming (Peñuelas & Filella 2001; Post & Forchhammer 2001). Phenological shifts potentially have disastrous consequences for mutualistic community composition (Memmott *et al.* 2007; Hegland *et al.* 2009). However, we are still far from making good predictions about the fate of mutualistic communities under global warming, because we do not yet know the general effects of phenology in the dynamics of mutualistic communities.

Thus, it is crucial to obtain thorough understanding of the role of phenology on mutualistic communities, not only because it is a key factor in the assembly of these webs, but also for the conservation of ecological communities threatened by rapid global changes. Phenology has been poorly studied in theoretical models of mutualistic networks. Theoretical work has focused on studying the effect of phenological shifts in a static network (Memmott *et al.* 2007) or the network build-up mechanism (Kallimanis *et al.* 2009; Pradal *et al.* 2009). Some results suggest that mutualistic network properties can be produced stochastically (Kallimanis *et al.* 2009). However, there is ample empirical evidence indicating that the assembly of mutualistic webs is not a fundamentally stochastic phenomenon (Jordano *et al.* 2003; Olesen *et al.* 2007, 2010). Moreover, some basic questions remain to be answered: to what extent can phenological coupling explain the observed topological patterns? And more importantly how relevant is phenology for the stability of mutualistic webs?

Here, we develop a discrete multispecies population dynamics model based on mutualism and competition that considers the phenology distribution of the species (i.e. their distribution of starting and final dates of activity). We (1) build the network of interactions, (2) determine interaction strengths from the phenological couplings and (3) study their dynamics. We use phenological coupling (i.e. how much temporal overlap exists between two species) as a proxy for species interaction strength, because this simple measure give us a potential estimate of the interaction frequency between species and it allows making intercommunity comparisons. Phenological coupling between mutualists give us an indication of how much exchange of resources (e.g. nectar, pollen) and/or services (e.g. pollination) potentially occurs between a plant and animal species (Memmott *et al.* 2007; Miller-Rushing *et al.* 2010). It can also indirectly give insight into how much competition for resources or services potentially occurs among species of the same guild (e.g. plants or animals) (Feinsinger 1987; Aizen & Rovere 2010). Our model allows us to study the effect of phenological distributions on the topology and dynamics of mutualistic webs and, to our knowledge, is the first one to use a biological proxy for interaction strength. In particular, we find that phenology distributions maximising mutualistic couplings and minimising competition promote coexistence and generate topological properties observed in real plant–animal mutualistic communities.

MUTUALISTIC COMMUNITY MODEL

Model formulation

Our mutualistic community is composed of two guilds: annual plant and animal species, forming a bipartite network of interactions of n_P ($i = 1,\ldots, n_P$) plants and n_A ($j = 1,\ldots, n_A$) animals. We split the dynamics of the community into: (1) *density-independent dynamics*: in which background mortality takes place and (2) *density-dependent dynamics*: in which reproduction occurs resulting from the phenological overlaps that determine the strength of mutualisms between species of different guilds and competition between species of the same guild

Density-independent dynamics

A single cohort of P_i (A_j) individuals of plant i (animal j) emerges at day d_i (δ_j). The probability that a plant (animal) survives from 1 day to the next is S_P (S_A). On day e_i (ε_j) all survivors leave seeds (eggs) and die. Thus, the population dynamics of plant and animal cohorts are given by

$$P_{id} = \begin{cases} P_i S_P^{d-d_i} & d_i < d < e_i \\ 0 & \text{otherwise} \end{cases}$$
$$A_{jd} = \begin{cases} A_j S_A^{d-\delta_j} & \delta_j < d < \epsilon_j \\ 0 & \text{otherwise} \end{cases} \tag{1}$$

where d is a day of season with season length (SL) ($1 \leq d \leq SL$). This accounts for the fact that abundances are not constant, but decline during the activity season (Pradal *et al.* 2009).

Density-dependent dynamics

The relative strengths of mutualistic and competitive interactions are proportional to the amount of phenological overlap between species. To illustrate this, we consider the case of mutualism. If a plant and an animal coincide on the same day, a mutualistic interaction exists and each individual receives one 'profit token'. Thus, the number of tokens collected by a single plant at day d is the number of animals it meets that day, $\sum_j A_{jd}$. Integrating along the period of activity SL, the profit tokens collected by an individual of plant i will be $\sum_{d=1}^{SL} \sum_{j=1}^{n_A} O_{ijd} A_{jd}$, where O_{ijd} is 1 if i and j coincide on day d, and 0 otherwise. By substituting A_{jd} from (eqn 1) in this double sum, we can rewrite it as $\sum_{j=1}^{n_A} m_{ij} A_j$, where $m_{ij} = \sum_{d=1}^{SL} O_{ijd} S_A^{d-\delta_j}$ is a mutualistic coefficient, i.e. the annual per capita positive effect of animal j on plant i. In a similar fashion we can define the mutualistic coefficient μ_{ji}, the annual per capita positive effect of plant i on animal j. With respect to intraguild competition, the coincidence of two plants (animals) in the same day penalises each species with a 'cost token', and the corresponding competition coefficient $x_{ik}(y_{jk})$ [i.e. the annual per capita negative effect of plant (animal) k on plant i (animal j)] is calculated as $x_{ik} = \sum_{d=1}^{SL} O_{ikd} S_P^{d-d_k}$ (see Appendix B for details). Summarising, the interaction coefficients between two species are the sums of their daily coincidences, weighted by their ever decreasing frequencies due to mortality. Note that in the case of $i = k$ ($j = k$), x_{ii} (y_{jj}) is an intraspecific competition coefficient. In contrast with interspecific competition coefficients that can be zero if two species never coincide, intraspecific coefficients are never zero, because a species always coincides temporally with itself. Furthermore, the phenophase of a species cannot be shorter than its overlap with other species, which implies that intraspecific competition coefficients can never be smaller than interspecific competition coefficients.

The number of seeds (eggs) produced by a plant (animal) depends on the balance of positive (mutualisms) versus negative (competition) effects experienced during the season. According to eqn 1 the number of reproducing plants (animals) of species i (j) at the ending day d_i (δ_j) is $P_i S_P^{e_i-d_i}$ ($A_j S_A^{\epsilon_j-\delta_j}$). We model reproduction as a multispecies version of the Ricker map, such that, when combined with eqn 1, the plant and animal population sizes at year t+1 are related to the sizes at year t as:

$$P_i' = P_i S_P^{e_i-d_i} r \exp\left(\frac{\sum_j m_{ij} A_j}{h_P + \sum_j m_{ij} A_j} - b \sum_k x_{ik} P_k\right) \tag{2}$$
$$A_j' = A_j S_A^{\epsilon_j-\delta_j} \rho \exp\left(\frac{\sum_i \mu_{ji} P_i}{h_A + \sum_i \mu_{ji} P_i} - \beta \sum_k y_{jk} A_k\right)$$

where r (ρ) is a growth rate scaling factor. The per capita reproduction rates are increasing but saturating functions of the strength of the mutualistic interactions [this ensures that population dynamics are bounded (Vandermeer & Boucher 1978)]; h_P (h_A) is a half-saturation constant. The negative effects of competition are simply additive (Bastolla *et al.* 2009). Longer phenophases are expected to produce larger overlaps and thus higher mutualistic (m_{ij}, μ_{ji}) and intraguild competitive (x_{ik}, y_{jk}) effects. The relative strength of competition against mutualism depends on the scaling factor b (β).

In this model mutualism can be *obligate* or *facultative*. Obligate mutualists have baseline growth rates smaller than one ($rS^{e_i - d_i} < 1$, $\rho S^{\varepsilon_j - \delta_j} < 1$, $S < 1$), and in the absence of mutualistic interactions they always go extinct (even when competitors are absent). Facultative mutualists have baseline growth rates larger than one ($rS^{e_i - d_i} > 1$, $\rho S^{\varepsilon_j - \delta_j} > 1$, $S < 1$). Facultative species can grow in isolation (i.e. in the absence of mutualism and competition), but in the presence of other species their fate depends on the balance between mutualism and competition. In the absence of mutualism, facultative species may coexist or not with other species or the same guild; this depends on the matrix of competition coefficients and the other model parameters (Strobeck 1973). Facultative species may need mutualistic partners to avoid competitive exclusion or to increase their dominance. The proportion of obligate and facultative species in the model depends on the *SL*. This is because a shorter season entails shorter phenophases whereas shorter phenophases are associated with higher average baseline growth rates ($rS^{e_i - d_i} > 1$, $\rho S^{\varepsilon_j - \delta_j} > 1$, $S < 1$) and higher average baseline growth rates allow a higher proportion of facultative to obligate mutualists. Most of the model analysis was done with facultative species (see subsection: Phenology distributions and parameter settings for details).

MODEL ANALYSIS

We employed numerical simulations to study the effect of phenology on network topology, community stability and biodiversity.

Phenology distributions and parameter settings

Previous work indicates that the distribution of phenologies or phenophases in mutualistic communities is right skewed (Rathcke & Lacey 1985; Kallimanis *et al.* 2009), and particularly that the phenology of flowering plants is log-normally distributed (Bawa 1980; Kallimanis *et al.* 2009). We tested various distributions and decided to use a log-normal distribution for the generation of phenology distributions (see Appendix B for details): the starting dates (d_i, δ_j) are log-normally distributed variables with mean μ_d and variance σ_d^2 of the corresponding normal distribution of the logarithm of starting dates [$\log(d)$] and the phenology lengths (p_i, p_j) are log-normally distributed variables with mean μ_p and variance σ_p^2 of the normal distribution of the logarithm of phenology lengths [$\log(p)$]. The ending dates (e_i, ε_j) are calculated by summing the values of the starting date (d_i) and phenology length (p_i), such that: $e_i = d_i + p_i$. The mean starting date was set to $\mu_d = 1$ and the mean phenology length is $\mu_p = 1$. The different season lengths $SL = 6$, 18, 60, 300 set the maximum value of phenology length (p_i) possible for any species. The variances were varied in the range [0, 6]. As we explained before, in our model, we can have facultative and/or obligatory mutualistic species depending on the *SL* and parameter settings chosen. For example, using the parameter values: $r = \rho = 1.5$, $b = \beta = 1.5$, $h_A = h_P = 1$ and $S_P = S_A = 0.99$, we have 100% facultative species for $SL \leq 40$ days and facultative as well as obligatory species for $SL > 40$ days. We did most of the analysis with 100% facultative mutualists ($SL = 18$).

We set $r = \rho = 1.5$, $b = \beta = 1.5$, $h_A = h_P = 1$ and $S_P = S_A = 0.99$ based on our sensitivity analysis to assure persistence and stability. We simulated the community dynamics 120 times for each combination of variances of starting dates and phenology lengths ($\sigma_{d,i}^2$, $\sigma_{p,j}^2$). The initial community diversity consisted of 60 plant and 60 animal species densities randomly chosen from an uniform distribution. We checked for different community diversities n_A,$n_P = 50$, 60, 70, 100, 120 and different ratios of plants to animals 1:1, 1:2, 1:3, but we did not find qualitatively important differences. The running time of the simulations was 3500 years, which is more than enough to ensure the convergence to an attractor. A species was removed and considered extinct if its density fell below 10^{-8}. The model was fully implemented in MATLAB 7.7 (The Mathworks Inc., Natick, MA, USA).

Stability, resilience and community diversity

We determined community stability by means of the variance of all population dynamics over the last 500 time steps of the simulation. We declared a community as stable if this variance was less than 10^{-6}. For stable communities we determined the leading Eigenvalue λ_1 of the Jacobian matrix of the dynamical system (eqn 2), and computed resilience as the return rate to a stable equilibrium after a small perturbation: $-\log(\lambda_1)$ (DeAngelis 1980). Because communities also change due to extinctions, we recorded initial and final values for community statistics (size, diversity) and network properties.

Network properties: nestedness, connectance and asymmetry

Nestedness in mutualistic networks is defined as the degree to which specialists interact with proper subsets of the species interacting with generalists (Bascompte *et al.* 2003). We calculated nestedness in two ways: (1) the temperature of the interaction matrix (Atmar & Patterson 1993) and (2) the NODF algorithm (Almeida-Neto *et al.* 2008). We then calculated relative nestedness (N^*) as a measure of how nested a network is compared to the mean expected value from a null model (N_r): $N^* = (N - N_r)/N_r$ (see Appendix B for details). We only reported nestedness values using the NODF algorithm because both metrics gave very similar results and NODF is less prone to Type I errors (Almeida-Neto *et al.* 2008). Mutualistic and competitive connectance was also calculated for each network. Connectance is a measure of the proportion of realised interactions among all possible interactions in a network. Mutualistic connectance occurs between animals and plants and competitive connectance only between plants (animals). The asymmetry of the interaction strength between plants and animals was calculated using relative dependence values as in Bascompte *et al.* (2006) (see Appendix B for details).

Statistical analyses

We performed statistical analyses in R 2.10.1 (R Development Core Team 2010) to test the effect of network structure (nestedness, asymmetry and connectance) on the final community diversity and resilience. We used generalised linear models (GLM) because our data had non-normally distributed errors. We used Gamma GLM models with identity-link (Bolker 2008) to test the effect of network structure on community resilience and Poisson regressions to test the effect on final community diversity. We assessed the significance of the most adequate model by an analysis of deviance (Likelihood ratio tests) on a nested sequence of models using a forward elimination process, going from a full model with two-way interactions to a minimal adequate model; *P* values were used to evaluate the elimination process. Furthermore, we studied the effect of *SL* on network structure, diversity and resilience of final communities using Kruskal–Wallis one-way ANOVA.

RESULTS

Community diversity

Each sampled phenology distribution generates a specific network structure of interactions, depending only on the variances of starting dates (σ_d^2) and phenology lengths (σ_p^2) and on the SL. Network properties change drastically from their initial values to various equilibrium values. Species extinctions often occur during the dynamical process, creating different community diversities depending on the variation of starting and ending dates. Highest community diversity is reached when both variances were low and equal $(\sigma_d^2 = \sigma_p^2 < 3)$ (LEV) (see Fig. 1b). Furthermore, the variance of starting dates (σ_d^2) seems to be more important for increasing coexistence of species than the variance of phenology lengths (σ_p^2). This is because the variance of starting dates determines the spread of species phenologies across the season. Summarising, smaller variances in starting dates and phenology lengths lead to higher diversity.

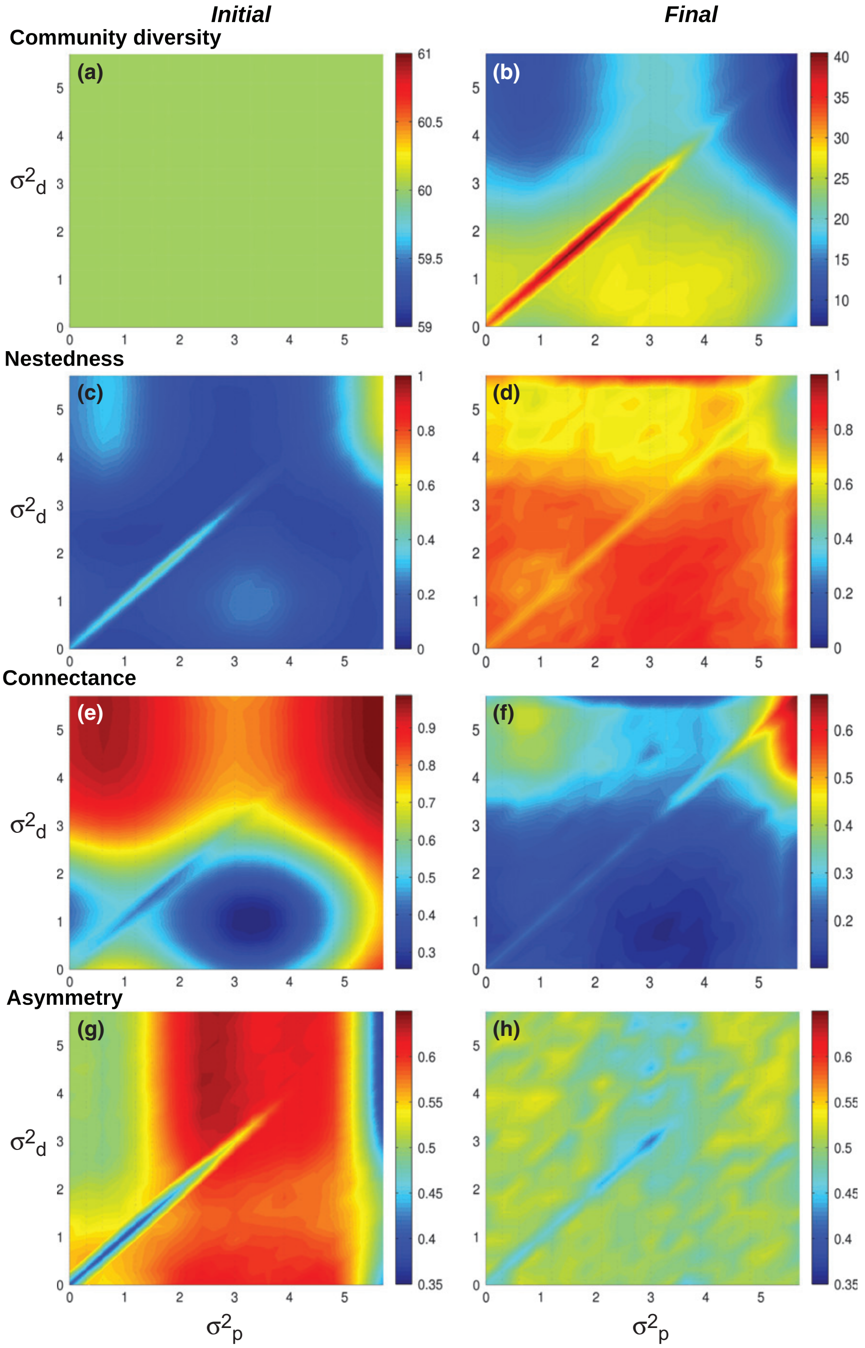

Figure 1 Network structure changes. The left column (panels a, c, e, g) represents initial values and the right column (panels b, d, f, h) represents final values of different network properties and community diversity. All network properties (nestedness, connectance and asymmetry) have profound changes. Results are averaged over 150 simulations for each phenology distribution combination (σ_d^2, σ_p^2). The season length is $SL = 18$. Initial community diversity was $P = 60$ and $A = 60$, for plants and animals, respectively. Demographical parameter values used: $r_i, \rho_j = 1.5$, $b_i, \beta_j = 1.5$ and $S_A, S_P = 0.99$. Nestedness values were all significantly different from null model estimates $(P < 0.05)$.

Mutualistic and competitive connectance

The connectances of mutualistic and competitive interactions are very similar (Fig. 1e,f and Figure SA2a,b), and hence highly correlated for initial ($R^2 = 0.678$, $P < 0.001$) and final values ($R^2 = 0.952$, $P < 0.001$), regardless of the phenology distribution variances. This dependence is due to the symmetry between plant and animal phenologies (Figure SA8a,b); hence changes in the connectance of mutualistic interactions are not independent of the connectance of competitive interactions. For example, a fully coupled mutualistic network in our model implies a fully coupled web of competitors and vice versa. Because of this high correlation, we report only the mutualistic connectance.

Network structure changes

Network dynamics changes several structural properties of the initial network configurations. Nestedness increases for all communities irrespective of the variance of their phenology distribution (Fig. 2a) and high variance communities have the highest initial nestedness (Fig. 1c) and nestedness increases only slightly for these communities. Connectance (mutualistic and competitive) decreases in all communities irrespective of the variance of their phenology distribution (Fig. 1f). This indicates that mostly species that are highly connected are eliminated during the dynamics. Even though nestedness increases and connectance decreases in all simulated communities, the amount of change depends on the variance of starting dates (σ_d^2) (Fig. 1).

The average asymmetry per species between plants and animals is initially different across simulated communities but very similar in final stable communities (Fig. 2b) and they reach an intermediate value of asymmetry ($\Theta \approx 0.5$) (Fig. 1h). This indicates that stable communities have many phenological couplings between species of similar phenology lengths and very few highly asymmetrical couplings between species of different phenology lengths (Fig. 3). *LEV* communities ($\sigma_d^2 = \sigma_p^2 < 3$) have the lowest average asymmetry ($\Theta \approx 0.4$) (Fig. 1g) because they have phenology distributions well spread across the season and phenological couplings between mutualists are very symmetrical. High equal variance communities ($\sigma_d^2 = \sigma_p^2 > 5$) also have low asymmetry because they have many couplings between species of similar phenology lengths (Figure SA1 and SA7) as well.

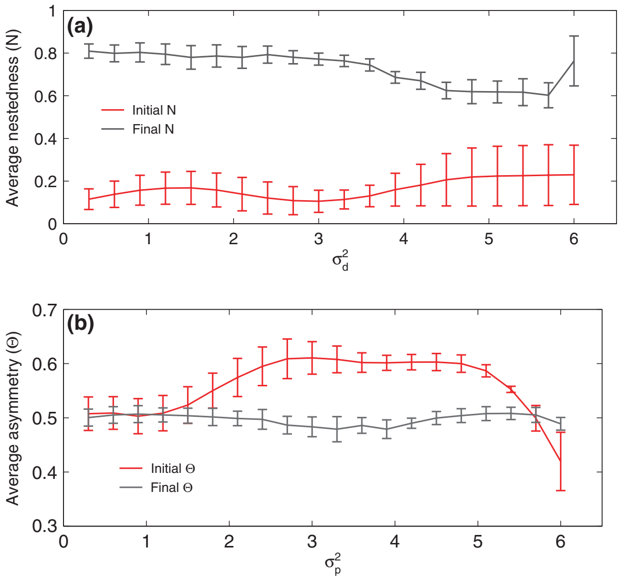

Figure 2 Changes in (a) nestedness and (b) asymmetry with variance in starting date and phenology length. Nestedness shows greater variation due to changes in the variance of starting dates and asymmetry shows higher variation due to changes in the variance of final dates. Red and grey solid lines indicate initial and final values, respectively. The size of the bars represents the standard error values for each average value ($SL = 18$).

High asymmetry is expected when $\sigma_p^2 \neq \sigma_d^2$, i.e. when there is a large number of phenological couplings between species of different phenology lengths (Fig. 1g).

Network structure and survival rate

We assume in our model that species abundances decrease proportionally to their phenology length with a daily survival rate of $S = 0.99$. We checked the effect of this assumption through numerical simulations by setting $S = 1.0$ (see Appendix B for details). Our results shown in Appendix B indicate that our assumption ($S = 0.99$) does not change the network structure qualitatively. The most conspicuous quantitative change is that the final connectance increases much more ($\bar{C}_f = 0.74 \pm 0.14$) with $S = 1.0$ than with $S = 0.99$. Therefore, if we assume the unrealistic scenario that species survive throughout the season (i.e. abundances are constant), we increase the species probability to have more interactions and this is particularly true for species with longer phenologies.

Relationships between network properties

Our results show that initial communities with high nestedness and lower connectances are those associated with larger community diversities and fewer structural changes. Main network topological properties are associated with increases and decreases of community diversity. Decreasing connectance (*GLM*, $F_{1,47998} = 296702.19$, $P < 0.01$) (Fig. 4b) and increasing nestedness (*GLM*, $F_{1,47998} = 278844.87$, $P < 0.01$) are associated with higher diversity. But increasing interaction strength is negatively associated with community diversity (*GLM*, $F_{1,47998} = 218431$, $P < 0.01$). We also find that community diversity seems to reach an optimum at moderate asymmetry (*GLM*, $F_{1,47998} = 54528.61$, $P < 0.01$). This is because communities with average values of diversity (≈25), typically of phenology distributions with $\sigma_p^2 \neq \sigma_d^2$, have higher asymmetry. Thus, some level of asymmetry is needed to obtain higher coexistence of species; i.e. the presence of few species with long phenologies ('generalists') is associated with higher coexistence. These 'generalist' species allow some species with short phenologies to survive. But, having very high asymmetry will increase competition.

In summary, highly diverse communities are associated with high nestedness, low connectance and moderate asymmetric interactions.

Phenology lengths distributions

The distribution of phenology lengths become highly heterogeneous, irrespective of community diversity. Communities with many species with short phenologies and few species with long phenologies seem to be more stable (Fig. 5).

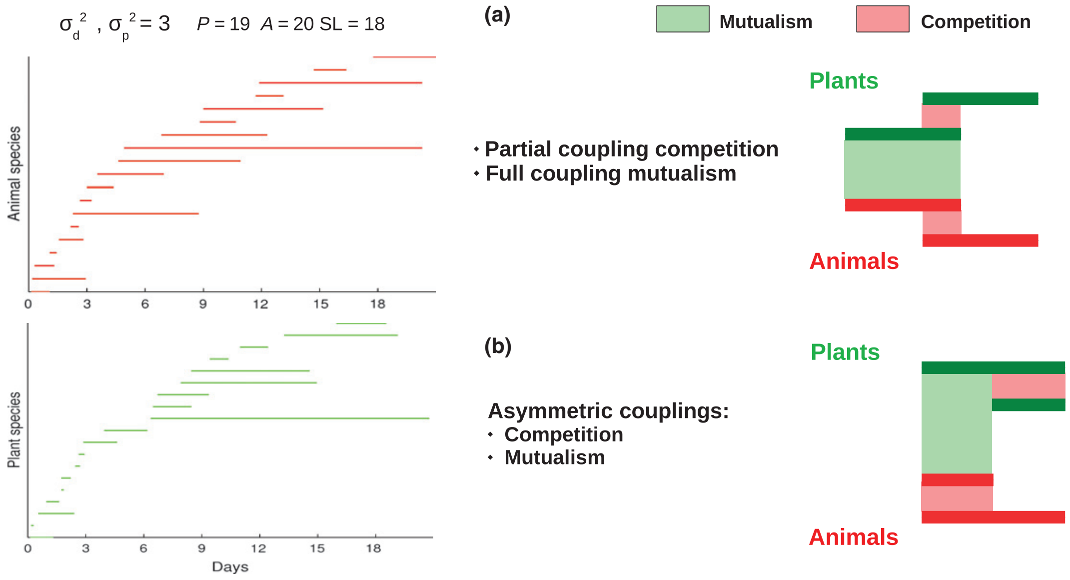

Figure 3 Phenological couplings on LEV communities. The left column shows the final distribution of phenologies of LEV communities composed of plant (green solid lines) and animal (red solid lines) species. The length of these lines represents the phenology length (p) located in a temporal scale across the season. The right column shows the different types of mutualistic (light green areas) and competitive (light red areas) phenological couplings observed in LEV communities. (a) LEV communities have a large number of fully mutualistic (highly symmetrical) and partial competitive couplings (top panel). (b) Non-LEV communities ($\sigma_d^2 \neq \sigma_p^2$) tend to have more asymmetrical couplings (bottom panel). Season length used is $SL = 18$.

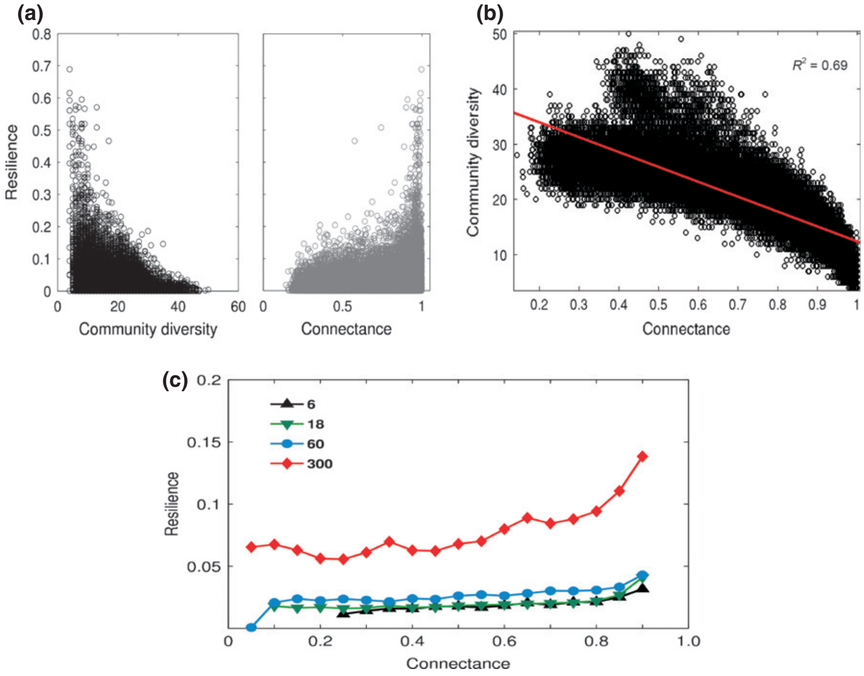

Figure 4 Relationships between connectance, resilience and community diversity. (a) Effects of community diversity and connectance on resilience. Left panel shows the resilience for different community diversities (black open circles) and the right panel shows the resilience for different initial connectance values (grey open circles). All phenology distributions were sampled from σ_d^2, σ_p^2 in the [0, 6] range and $SL = 18$ days. (b) Community diversity as a function of connectance. There is a negative correlation between diversity and connectance. Red solid line is a linear regression fit ($R^2 = 0.69$). Each open circle represents a simulated community. (c) Effect of season length on connectance and resilience. Resilience strongly increases for long SL. Each symbol represents an average value of resilience for a value of connectance (C) and SL. Data from 46 500 simulations and $SL = 6,18,60,300$.

Stability and resilience

Ninety seven percent of the simulations achieve a stable community equilibrium at the end of the simulations. Phenology distributions with high variances ($\sigma_d^2, \sigma_p^2 > 5$) generate highly resilient communities and LEV phenology distributions generate communities with low resilience (see Figure SA3). This suggests that species poor communities have higher resilience than more diverse communities.

Indeed, resilience is inversely related to community diversity (Fig. 4a). Connectance is our best network structure predictor for community resilience (*GLM*, $F_{1,46478} = 1742.4$, $P < 0.01$). Nestedness does not show a clear relationship with resilience. However, highly nested communities were more resilient than non-nested ones (Figure SA4a).

Season length

Season length is a crucial factor for the stability and diversity of mutualistic communities in our model. Increases in *SL* produce more stable networks (Figure SA6) and higher resilience. Mean community diversity does not change with *SL*; but diversity variation and the maximum diversity reached increase (Fig. 6a). Maximum diversity increases with *SL* because of higher temporary availability of niches for networks that promote diversity, i.e. networks that maximise mutualistic couplings and minimise competitive couplings. Furthermore, community diversity variation increases with *SL* because of more variation in network configurations, in terms of connectance and interaction strength. However, nestedness is not increased by increases in *SL* (Figure SA5), which suggests that nestedness is only affected by the variances (σ_d^2, σ_p^2) of the phenology distributions.

Resilience increases with *SL* in all communities, but it increases more for highly connected communities ($C > 0.5$) than for poorly connected ones ($C < 0.5$) (Fig. 4c). Furthermore, the mean connectance of highly diverse communities (i.e. *LEV* communities) increases more in communities of longer *SL* ($C_{y=300} = 0.631 \pm 0.04$) than in communities of shorter *SL* ($C_{y=18} = 0.461 \pm 0.06$). Thus, an increase in *SL* can generate more diverse and more resilient communities, especially when they are highly connected. Average asymmetry ($\chi^2_{3,139197} = 12155, P < 0.01$) and interaction strength ($\chi^2_{3,139197} = 53858, P < 0.01$) increases with *SL* (Fig. 6b,c).

Summarising, communities living in long *SL* environments are more resilient and asymmetric than communities living in short *SL* environments. The increase in resilience with *SL* is largest for highly connected communities.

DISCUSSION

Several theoretical studies on mutualistic networks have made major progress studying the conditions for stability and coexistence of

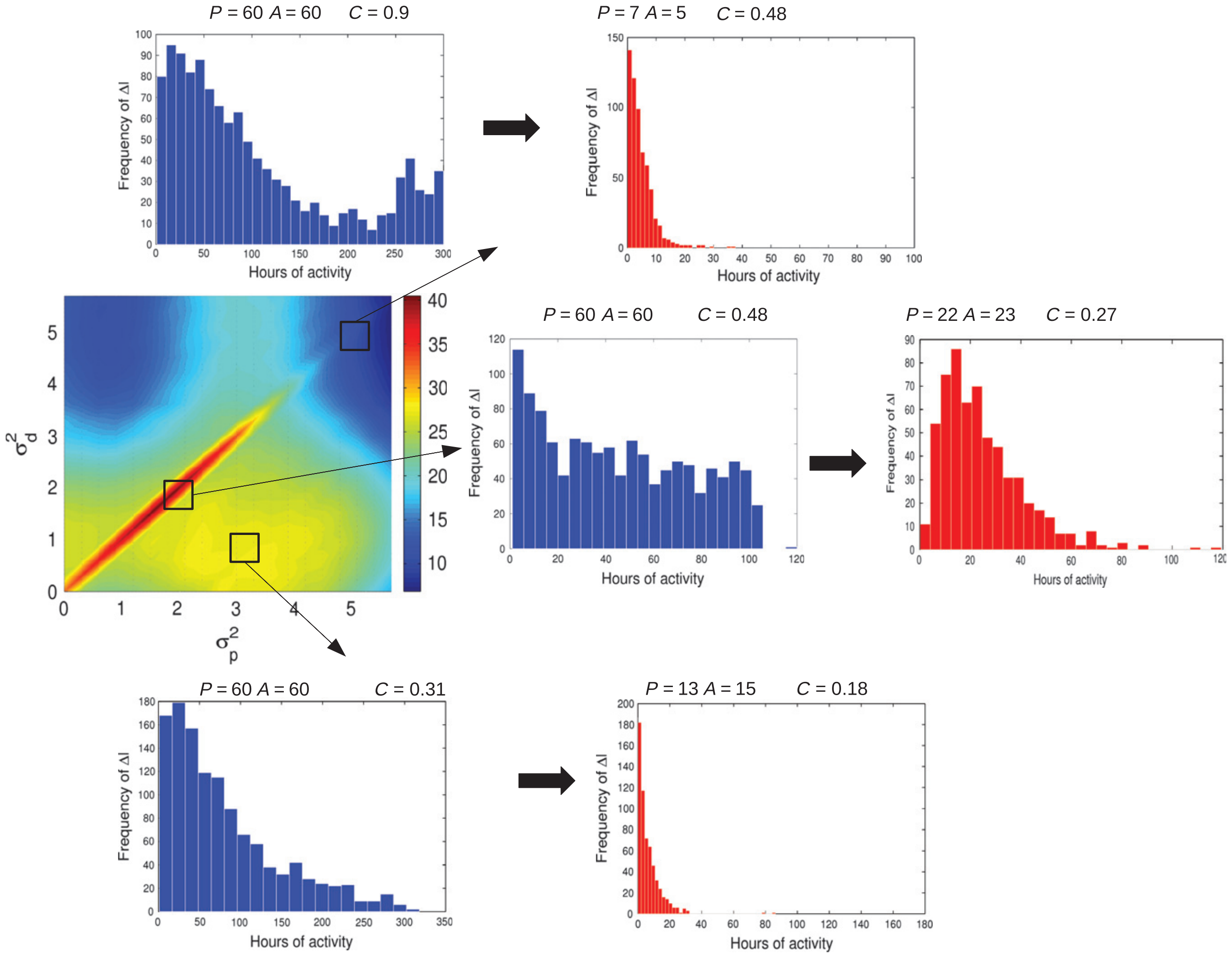

Figure 5 Change in phenophase distribution for different community diversities. Highly right-skewed phenology distributions are produced in all final communities independent of their initial phenology distribution. Blue and red bars represent initial and final phenophase distributions for the whole community, respectively. Thin black arrows indicates phenophase distributions for different final community diversities ($SL = 18$).

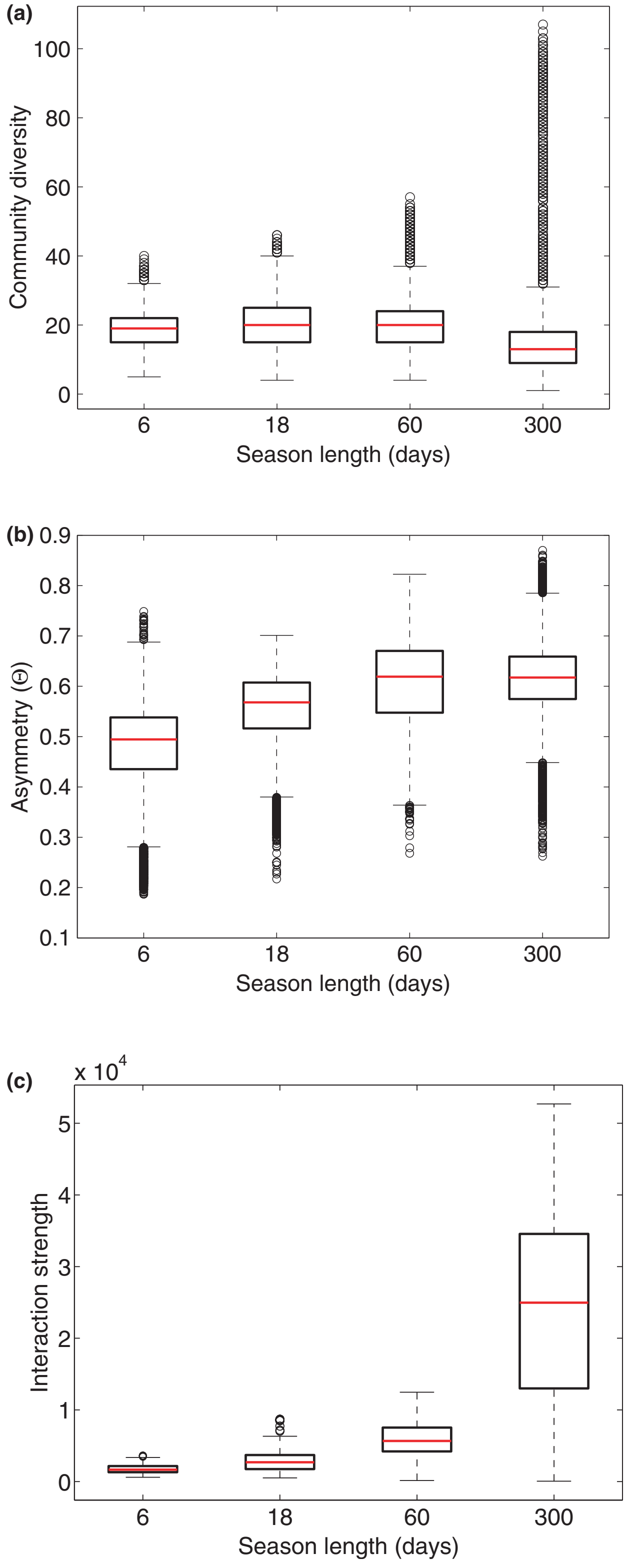

Figure 6 Effects of season length (*SL*) on community diversity, asymmetry and interaction strength. (a) Season length and community diversity. Maximum community diversity increases with *SL*. (b) Season length and asymmetry. (c) Mutualistic interaction strength and their variation strongly increase for long textitSL. The black box has lines at the lower quartile, median and upper quartile values. Red solid lines represent median values and black open circles are outliers. Data from 46 500 network simulations from different phenology distributions and four season lengths (*SL* = 6,18,60,300).

species (Bascompte *et al.* 2006; Okuyama & Holland 2008; Bastolla *et al.* 2009; Thébault & Fontaine 2010). The observations of topological properties of mutualistic webs have raised new questions about the mechanisms behind these properties (Vazquez *et al.* 2009a). Here, we have shown that using a simple biological constraint on the assembly of mutualistic communities already provides more insight into the natural emergence of network topological properties. Phenology, without invoking other biological constraints, can largely explain the main topological properties observed in real plant–animal mutualistic webs. The distribution of phenologies in our model greatly influences the stability and coexistence of species. Right-skewed phenology distributions with starting and final dates well spread across the season (i.e. *LEV* communities) maximise phenological couplings among mutualists and minimise intraguild competition, thus maximising diversity. These diverse networks are highly nested and poorly connected similar to real plant–animal mutualistic networks (Bascompte *et al.* 2003; Jordano *et al.* 2003), but they have low resilience. The diversity and stability of mutualistic webs are also highly affected by the length of the season, which emphasises the importance of abiotic factors in the assembly of these communities.

Highly diverse communities are highly nested and moreover, over time nestedness increases in all communities, regardless of their phenology distribution. This is in agreement with Bastolla *et al.* (2009), who showed that nested structures minimise interspecific competition promoting stability and species coexistence on mutualistic webs. However, in contrast to Bastolla *et al.* (2009), we do not find that fully connected networks have higher diversity. On the contrary, fully connected networks (i.e. with many of phenological couplings) in our model generate lower diversity because of high intraguild competition. This agrees with empirical evidence that minimising phenological overlaps increases the reproductive output of flowering plants (Aizen & Rovere, 2010). We argue that phenology is an important mechanism for the emergence of nested structures. However, neutral processes may also give rise to these patterns (Krishna *et al.* 2008). Thus, different processes, niche-based and neutral are acting simultaneously on the assembly of mutualistic webs (Krishna *et al.* 2008).

We found a negative relationship between complexity and stability. The long-standing debate about the diversity–stability relationship started by arguing that complexity (i.e. number of species and/or interactions) promotes ecosystem stability (MacArthur 1955). This was later questioned by May (1973), who demonstrated that randomly wired food-webs are more unstable when diversity and/or connectance are high[1]. This and subsequent studies stressed the importance of community structure for diversity–stability relationships (Yodzis 1981). In the mutualistic network literature, a positive diversity–stability relationship has been reported for two different models (Okuyama & Holland 2008; Thébault & Fontaine, 2010). In contrast, our results indicate a negative relationship: highly diverse communities have low resilience and low connectance. Furthermore, in all communities connectance decreases during the dynamical process due to intraguild competition. This indicates that extinction of highly connected species occurs frequently in all communities and more

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[1] With a fixed community diversity and average weak interaction strength. The condition for stability found by May (1973) is: $s\sqrt{mC} < 1$, s: average interaction strength, m: community diversity and C: connectance.

often in highly connected communities. On the one hand, initially highly connected communities suffer more extinctions (i.e. high phenological couplings), but their connectance remain relatively high and they are more resilient. On the other hand, poorly connected communities (e.g. LEV communities) suffer less extinction by competition hence increasing diversity, but producing communities with low resilience.

Our model indicates that connectance is a key factor controlling resilience. Increases in connectance promote stability, but also increase competition. Connectance can be increased by simultaneously increasing mutualistic and competitive phenological couplings. However, to minimise competition, connectance has to decrease. This also means that mutualistic couplings decrease, but LEV communities only decrease marginally. Thus, high coexistence of species is only possible if communities have low connectance in order to minimise intraguild competition at the cost of having lower resilience. The simultaneous increase of diversity and decrease of connectance drives the communities towards an instability boundary, supporting the idea that ecosystems evolve towards a state of self-organised instability (Solé *et al.* 2002). As stated above, previous studies on mutualistic networks reporting a positive effect of connectance on stability, have found a positive diversity–stability relationship (Okuyama & Holland 2008; Thébault & Fontaine, 2010), contrary to our results. However, these studies did not consider interspecific competition in the dynamics and the importance of competition has been shown to be crucial for understanding the emergence of structural properties (Bastolla *et al.* 2009). Furthermore, we find that mutualism can be very damaging for species coexistence when competition is strong (see Appendix B for results analysing the dynamics with mutualism and competition separately). The balance between positive and negative interactions driven by phenological couplings is what finally determines the stability and coexistence of species in our model. Our results are in agreement with other studies indicating that simultaneous increases of diversity and connectance generate more instability (May 1973; Gross *et al.* 2009). However, there are other mechanisms and constraints in the assembly of mutualistic webs, such as phenotypic complementarity (Rezende *et al.* 2007), which might contribute to the stability–diversity relationship. Mutualistic communities are obviously much more complex than we modelled. For example, mutualistic communities might also have antagonistic interactions (e.g. herbivory, parasitism) (Bronstein *et al.* 2003), and including these interactions in plant–animal mutualistic dynamics can bring new insights to the complexity-stability relationship.

There is an inherent asymmetry of interaction strength between plants and animals (Vázquez & Aizen 2004; Bascompte *et al.* 2006). However, stable communities are not characterised by high levels of asymmetry. They show intermediate levels with little variation among communities. We conjecture that communities are composed of different levels of asymmetries. Highly diverse communities, in particular, show low levels of asymmetry compared to other communities, because phenological distributions maximising mutualistic couplings decrease their level of asymmetry by forming highly overlapping phenologies. Our highly diverse communities appear to be less asymmetric than empirical ones (Bascompte *et al.* 2006; Vázquez *et al.* 2007), but observed measures may be overestimating the true asymmetry (Bosch *et al.* 2009) or highly diverse communities may not be resilient enough, so they are not observed in nature. Even though highly diverse communities tend to have more symmetric interactions, we find that asymmetry is an important factor for species coexistence and stability. Moderate, but not high levels of asymmetry are necessary for species coexistence and stability.

The relationship between asymmetry and resilience is masked by the effect of SL. For short SL, we were unable to detect an effect of asymmetry on the resilience of communities. However, the positive effect of asymmetry on community resilience and diversity becomes clearer for longer SL. Short SL communities cannot produce a high proportion of asymmetrical interactions. An increase in SL boosts the proportion of communities with moderate asymmetry levels promoting coexistence and resilience.

There are conflicting studies with respect to the effect of asymmetry on the diversity and stability of mutualistic webs. The debate has centred around the questions whether weak asymmetric (Bascompte *et al.* 2006) or strong symmetric (Okuyama & Holland 2008) interaction strengths increase stability and diversity. The main difference between models is the type of functional response used to describe the mutualistic interaction. We used a saturating functional response because it better describes a consumer–resource interaction and avoids population overgrowth by large positive feedbacks (Vandermeer & Boucher 1978).

Season length clearly affects diversity and stability of mutualistic communities in our model. Empirical evidence shows that it is a limiting factor for the variation of phenological coupling (Olesen *et al.*, 2010). The rise in resilience and diversity for increases in SL seems to be generated by moderate asymmetry levels, high nestedness and connectance. Naturally, with increases in diversity, the number of interactions increase (Solé *et al.* 2002) augmenting resilience. Thus, a small window of interactions has a detrimental effect on the stability and diversity of communities, suggesting that communities living in short SL environments are vulnerable to perturbations or drastic changes driven by climatic conditions. Evidence is accumulating that high latitude communities are under severe threat of global warming (Post *et al.* 2009). Recent reports indicate that phenologies are changing quickly, but differentially depending on the species, creating phenological uncouplings at different trophic levels (Post *et al.* 2008). We cannot predict how exactly the structure of short SL communities will be affected, but we do argue that any high perturbation could produce a disruption in the network structure and eventually a cascade extinction effect, as shown previously (Memmott *et al.* 2007).

We assume facultative mutualistic interactions, following previous models (Okuyama & Holland 2008; Bastolla *et al.* 2009). However, we want to stress that regardless of the type of mutualism (obligatory or facultative), mutualism is important for the diversity and stability of the community. Under the always present competitive pressure in a guild, species without mutualistic interactions are at a serious disadvantage compared to those that are involved in mutualistic interactions. Thus, mutualism is crucial for a species persistence.

Using phenological coupling as a proxy for interaction strength we have provided insight into the emergence of network structural properties in mutualistic communities. Nevertheless, considering coevolutionary processes of different biological constraints in the dynamics of community assembly can give us even more insight. There is a phylogenetic signal in the way species interact (Rezende *et al.* 2007) and mutualistic webs are highly modular (Olesen *et al.* 2007). Thus, future research should consider the inclusion of other biological constraints and their coevolution.

We have shown that one single biological mechanism, phenology, produces the emergence of several observed patterns in mutualistic communities. The emergent patterns are not caused by a purely stochastic phenomenon, as suggested previously (Kallimanis *et al.* 2009), but interdependent network properties emerged naturally. Other ecological networks (e.g. food-webs) are also highly affected by the timing of life history events (Post *et al.* 2008). Certainly, phenological uncouplings are driving drastic changes in high latitude communities and ecosystems (Post *et al.* 2009). Thus, we believe that the role of phenology and spatio-temporal variability are pertinent to the study of community assembly, especially in communities that are highly threatened by global warming.

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AUTHOR CONTRIBUTIONS

FEV and TAR formulated the model. FEV designed and implemented the simulation model and conducted the model analyses. FEV prepared the manuscript and RSE and TAR supervised its analysis and edited the manuscript, contributing substantially to all later versions.

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