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Robustness of mutualistic networks under phenological change and habitat destruction

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Climate change can alter species phenologies and therefore disrupt species interactions. Habitat destruction can damage biodiversity and population viability. However, we still know very little about the potential effects of these two factors on the diversity and structure of interaction networks when both act simultaneously. Here we developed a mutualistic metacommunity model to explore the effects of habitat destruction and phenological changes on the diversity and structure of plant–pollinator networks. Using an empirical data set of plant and pollinator interactions and their duration in days, we simulated increasing levels of habitat destruction, under projected scenarios of phenological shifts as well for historically recorded changes in phenologies. On one hand, we found that habitat destruction causes catastrophic collapse in global diversity, as well as inducing alternative states. On the other hand, phenological shifts tend to make interactions weaker, increasing local extinction rates. Together, habitat destruction and phenological changes act synergistically, making metacommunities even more vulnerable to global collapse. Metacommunities are also more vulnerable to collapses under scenarios of historical change, in which phenologies are shortened, not just shifted. Furthermore, connectance and nestedness tends to decrease gradually with habitat destruction before the global collapse. Small phenological shifts can raise connectance slightly, due novel interactions appearing in a few generalist species, but larger shifts always reduce connectance. We conclude that the robustness of mutualistic metacommunities against habitat destruction can be greatly impaired by the weakening of positive interactions that results from the loss of phenological overlap.

Climate change is known to cause important alterations in species phenologies (Parmesan and Yohe 2003), leading to temporal mismatches in mutualistic interactions (Memmott et al. 2007) and other ecological interactions (Edwards and Richardson 2004). Several studies suggest that these mismatches can have serious consequences for species diversity and ecological functions in mutualistic networks (Bartomeus et al. 2011, Memmott et al. 2007, Encinas-Viso et al. 2012), while others suggest that they are not a serious threat due to functional redundancies in the case of large communities (Benadi et al. 2014) or because many other factors can obscure the direct influence of phenology (Forrest 2015).

Not all possible mutualistic interactions between species are observed. Some links are indeed 'forbidden' by phenological mismatch, or by other reasons, e.g. large size differences between insect proboscis and flower pistil. But other links are simply 'missing', because the spatial scale of a study was not large enough, or because traditional analysis sample static snapshots of the communities, without taking temporal dynamics into account (Olesen et al. 2011). Thus, missing links can be in principle accounted for, if we treat large communities as 'metacommunities' (Leibold et al. 2004, Holyoak et al. 2005), i.e. sets of local communities distributed in space, linked by the dispersal of multiple interacting species. It is then conceivable that not all possible links between mutualists have to exist at all localities.

This redundancy of interactions at the regional scale could provide resilience against multiple interactions losses triggered by climate change, and ensure the long term persistence of diversity and functioning of whole metacommunities. But in order for this to happen, a large enough number of localities (e.g. sites or patches) have to exist, and their separation must enable dispersal, such that local diversity and network connectivity can be continuously repaired. This bring us to consider another important threat, namely habitat destruction or fragmentation (Rathcke 1993, Holyoak et al. 2005), in addition to climate change. Habitat fragmentation is known to threaten diversity and population viability (e.g. gene flow), and some studies indicate that mutualisms can be destroyed by habitat fragmentation (Fortuna and Bascompte 2006, Fortuna et al. 2012). More specifically, those studies have found that beyond a critical value of habitat destruction, species interactions are lost very rapidly (Fortuna and Bascompte 2006, Fortuna et al. 2012).

However, to our knowledge, there are no studies investigating the joint effect of habitat destruction and phenological changes. Investigating the simultaneous effects of phenological changes and habitat destruction in mutualistic

networks is important to understand how global changes affect biodiversity and network structure (Tylianakis et al. 2008). Furthermore, it remains unclear how phenological changes themselves can affect mutualistic metacommunities, because so far most theoretical studies investigating the effects of phenological changes in mutualistic communities (Memmott et al. 2007, Encinas-Viso et al. 2012) have not incorporated spatial effects and processes in their models. The joint study of phenology and spatial structure is very important, as shown by some empirical studies, which have found that changes in phenology by temperature can affect species ranges (Chuine and Beaubien 2001) and local adaptation (Phillimore et al. 2012).

In this contribution we study the changes on diversity and network properties, as mutualistic metacommunities are subject to phenological changes and habitat destruction. This paper aims to understand the robustness of mutualistic metacommunities against the detrimental effect of changes in species phenology and habitat fragmentation. For this purpose, we have developed a model in which the local presence of the species in a metacommunity and their periods of activity, respectively determine the distribution and relative weights of their mutualistic interactions. Alterations took place by destroying different amounts of localities or sites, and by causing mismatches in the species phenologies. Our simulations use phenological data that was originally recorded by Robertson (1929) a century ago, and phenological data recorded in the same region in present times by Burkle et al. (2013). In general, we find that the interaction between phenological mismatch and habitat destruction makes mutualistic metacommunities much more vulnerable than considering their separated effects.

Spatially explicit model

We consider a metacommunity of $i = 1,\ldots,N_P$ flowering plants and $j = 1,\ldots,N_A$ pollinators distributed over several sites (Fig. 1a). We use a binary state variable to indicate if a plant i is present $S_i(x,t) = 1$ or absent $S_i(x,t) = 0$ in site x in the year t, and similarly for the pollinators $S_j(x,t)$. A weighted interaction matrix O_{ij} indicates if there is a mutualistic interaction between a plant and an animal or not ($O_{ij} > 0$ or $O_{ij} = 0$); it also indicates the number of days during which the plant and the animal phenologies overlap (e.g. $O_{ij} = 10$ days). This matrix describes the structure of the network, provided that all species are present. However, some species can be absent in a particular site, and the structure of the network can differ from one site to another, and from one year to the next.

The presence or absence of a species in a site in the next year depends on two stochastic events occurring in this order: survival and colonization. We will explain these events from the point of view of the plants. For the pollinators, the corresponding equations describing survival and dispersal will be symmetrical, i.e. j and i are interchangeable.

Survival

Let us assume that the survival of plant species i at site x depends on the number and weight of the mutualistic interactions with their pollinators in that site:

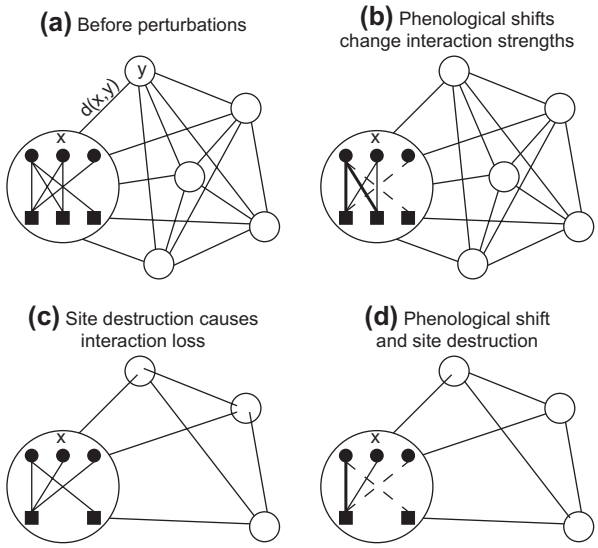

Figure 1. Spatially explicit metacommunity model. (a) randomly positioned sites (e.g. x) are separated from other sites (e.g. y) by a certain distance (e.g. $d(x, y)$). Site x is enlarged to show the local bipartite network of plants (circles) and pollinators (squares). The survival probability of a species at x, depends on the number and strength of its interactions (Eq. 3); colonization of x by a species depends on its distance from the other sites (Eq. 4). (b) phenological shifts cause interactions to strengthen (thick links) or to weaken (dashed links). (c) site destruction reduce colonization rates, causing interaction loss. (d) phenological shifts and site destruction can occur simultaneously.

$$Q_i(x,t) = \Sigma_j S_j(x,t) O_{ij} \tag{1}$$

which is the total number of interaction-days experienced locally. The best chances of survival at site x are when all the pollinators of species i (i.e. those j for which $O_{ij} > 0$) are present, i.e. when $Q_i(x, t)$ is equal to:

$$Q_i^0 = \Sigma_j O_{ij} \tag{2}$$

which is a site-independent, species-specific property. Q_i^0 will be considered as a baseline for interaction-days. Since some pollinators will be locally absent at x, the number of interaction-days will be generally smaller than this baseline. Local survival increases as $Q_i(x,t)$ gets closer to Q_i^0, and decreases otherwise. We formulate the probability of local survival as:

$$P_i(x,t) = (1 - \varepsilon(x)) \left[\frac{Q_i(x,t)}{Q_i^0} \right]^{\left(\frac{1}{\theta_i}\right)} \tag{3}$$

In this way, if all the pollinators of i are absent in x then $Q_i(x,t) = 0$ and $P_i(x,t) = 0$, whereas if all its pollinators are present then $Q_i(x,t) = Q_i^0$ and $P_i(x, t) = 1 - \varepsilon(x)$, where $\varepsilon(x)$ is a small extinction probability that is site-specific, but not species-specific. The pace at which survival drops due to local interaction losses depends on a *tolerance* parameter θ_i. Supplementary material Appendix 1 Fig. S.1 shows a sketch of Eq. 3 when $\theta > 1$. The limit $\theta_i \to \infty$ parallels the assumption of many studies of network structural stability, whereby a species or node is removed only when it becomes totally

disconnected from the network (Memmott et al. 2004). We do not consider $\theta < 1$, because metacommunities collapse too easily under these condition, even in the absence of the perturbations considered in the Methods (Supplementary material Appendix 1 Fig. S.2).

Colonization

The colonization of site x by species i depends on the number and distances to the other sites, and their states of occupancy following the survival event. More explicitly, we assume that the probability of colonization of x from a site y is independent of the other sites, that it decreases exponentially with the euclidean distance between them $d(x,y)$ (Supplementary material Appendix 1 Fig. S.1), and whether or not site y hosts plant i in the first place. The colonization probability of site x is:

$$C_i(x,t) = 1 - \Pi_{y \neq x}\left[1 - S_i(y,t)e^{-d(x,y)/\delta_i}\right] \quad (4)$$

i.e. the complement of the event that all sites different than x hosting plant i fail to colonize x. Equation 4 assumes that one successful colonization ensures the presence of species i at x in the next year. The parameter δ_i is the *dispersal range,* i.e. the distance at which colonization probability decays ~63% (e^{-1}). Notice that the occupancy $S_i(y, t)$ of a source site y may have changed from 1 to 0 as a result of species i failing at the survival event.

During the simulation from year t to year $t+1$, the sites are first scanned to determine their occupancies. If site x contains species i, a number p from a random uniform distribution between 0 and 1 is compared with the survival probability $P_i(x,t)$: if $p < P_i(x,t)$ then $S_i(x,t) = 1$; if not then $S_i(x,t) = 0$. If the species was not present in that site, nothing is done. After this is done for all species at all sites, we consider colonization. If species i is absent at site x, a number c from a random uniform distribution between 0 and 1 is compared with the colonization rate $C_i(x, t)$: if $c < C_i(x, t)$ then we set $S_i(x, t+1) = 1$; if not then $S_i(x, t+1) = 0$. If the species was present in that site, nothing is done, colonization is not going to alter its presence.

Methods

Data source and parameter settings

In order to simulate our model we need a source of phenological overlap matrices O_{ij}. These data could be artificially sampled (Encinas-Viso et al. 2012) using information about empirically known distributions of activity dates (Kallimanis et al. 2009) and mutualistic links (Bascompte and Jordano 2007). However, in this paper we are going to use the dataset of Burkle et al. (2013) (available at <http://dx.doi.org/10.5061/dryad.rp321>). This dataset comprises 26 plants (forbs) and 109 pollinator (bees) species, with phenologies and interactions as recorded by Robertson (1929) in a much larger database (Memmott et al. 2007). In addition to the past phenologies and interactions (from little more than a century ago), the dataset of Burkle et al. also includes the phenologies of the same species recorded in the present (2009–2010), making it particularly useful for comparing the effects of artificially generated phenological shifts (as in Memmott et al. 2007) with realistic ones (as in Burkle et al. 2013), as described in the section on simulation scenarios.

The phenological data comprises a pair of dates per species that indicates the start and the end of the activity period, i.e. the phenology. These two dates define a calendar vector of size 365, filled with 1s for days of presence (between start and end dates, inclusive) and 0s for days of absence. An entry O_{ij} in the phenological overlap matrix is the scalar product of the calendar vectors of species i and j. Some of the O_{ij} must be turned to zero because the species concerned did not actually interact even though they overlap in time; this is done using the binary interaction matrix from Burkle et al. (2013) supplementary material (Supplementary material Appendix 1 Fig. S9 part A).

Metacommunity dynamics is simulated over 100 sites, randomly distributed over a unit square (thus all inter-site distances are $d(x, y) < \sqrt{2}$). Each species initially occupies 50 randomly chosen sites. Each site has a common baseline extinction rate ε. Tolerance and dispersal range is species-independent ($\theta_i = \theta$ $\delta_i = \delta$), with values chosen such that no species goes extinct during the first 200 years (Supplementary material Appendix 1 Fig. S.2). After that time, phenological changes and/or habitat loss occurs (see section on simulation scenarios). Table 1 shows the parameter values.

Simulation scenarios

We will study the joint effect of phenological shifts and habitat destruction under two different simulation scenarios:

Projected changes

Start and end dates at the time of Robertson (1929) are shifted by a number of days sampled from a normal distribution with mean $\mu = -10, -20, -30$ days with standard deviation $\sigma = |\mu|$. The negative value of the means is because most phenologies are predicted to advance as a consequence of warming (Parmesan and Yohe 2003). In this scenario the duration of the phenologies are not changed. The sampled shifts are rounded to the closest integer value, and staring and ending dates are cutoff whenever they fall outside of the 1–365 range. This approach is similar to Memmott et al. (2007).

Historical changes

Start and end dates at the time of Robertson (1929) are replaced by the present (2009–2010) dates, recorded by

Table 1. Parameter values used in the simulations. The values of θ and δ where chosen such that all plants and animals can survive globally before the change in the phenologies and/or habitat destruction (Supplementary material Appendix 1 Fig. S.2).

Parameter	Value
Number of sites	100
Years	400
Year of change	200
Replicas	100
Site extinction rate (ε)	0.05
Initial occupancy	50%
Replicas	100
Tolerance (θ)	3
Dispersal range (δ)	0.05

Burkle et al. (2013). For pollinators that went extinct, the present dates are sampled with replacement from the dates of surviving species. This is done on the assumption that, had these species survived, their phenologies would have changed in a similar manner than the survivors. In this scenario the advance of the phenologies (e.g. the starting dates) is between 10 and 20 days for the majority of the species, and their durations are generally shortened, especially in the pollinators (Burkle et al. 2013).

Phenological shifts change the matrix of phenological overlaps O_{ij}. As a consequence, the strengths of existing interactions can increase/decrease (i.e. more/less days of overlap), as shown by Fig. 1b; or even disappear (complete loss of overlap). Novel interactions (new O_{ij} entries) could happen between species that overlap after the shift but did not before, following the 'rewiring' rule devised by Burkle et al. (2013): plant i and pollinator j will interact O_{ij} days with a probability that is the product of their generalisms. The 'generalism' of a species is the number of its interactions divided by the potential number of interactions permitted by the phenology, before the shift. Thus, generalists have higher rewiring probabilities than specialist species. The new probabilities of local survival are computed using Eq. 3, but the Q_i^0 used in the denominators are those before the change took place. This allows to compare interaction loss/gain against historical, species-specific baselines. This means that following a shift, a species could end up with more interaction days than before, and $Q_i(x,t)$ can be larger than Q_i^0 in some sites. In these cases we set $Q_i(x, t) = Q_i^0$, and the probability of local extinction becomes site-specific, i.e. $P_i(x,t) = 1 - \varepsilon(x)$.

For each simulation scenario we perform habitat fragmentation by destroying a randomly selected fraction ϕ of the sites. Destruction consists of changing the site extinction probability $\varepsilon(x)$ from 0.05 (Table 1) to 1 (i.e. the site becomes lethal). Thus, for the scenario of projected changes we combine four levels of phenological shift $\mu = 0, -10, -20, -30$ with 10 levels of site destruction $\phi = 0, 0.1, \ldots, 0.9$. Combinations with $\mu = 0$ or $\phi = 0$ correspond to site destruction only, or phenological shift only, respectively. For the historical scenario we only have two levels of phenological shift $\mu = past$ which is equivalent to $\mu = 0$ of the first scenario, and $\mu = present$ corresponding to the historical change; these are combined with the 10 destruction levels. Because it reduces colonization opportunities, site destruction alone can lead to local interaction loss, but not to strengthening or weakening of existing interactions, as shown by Fig. 1c.

Alterations of phenology, and site destruction, are introduced after the first 200 years of simulation – time by which the metacommunity has reached an attractor in which no extinctions have yet occurred (Supplementary material Appendix 1 Fig. S.2) – and the simulation is continued for 200 years. Notice that due to the order of events of the dynamics (survival followed by colonization), it is possible that some destroyed sites end populated, even tough they do not spread any migrants in the next year. These sites are 'black hole sinks' (Loreau et al. 2013), and they are not accounted for in the calculation of species diversity and network structure indicators. Figure 1d indicates that both perturbations can happen simultaneously.

Metacommunity diversity

For each combination of levels of phenological shift and site destruction, we measure changes in global and local species diversity or richness. Global richness or 'gamma diversity' γ, counts the number of species by aggregation of all non-destroyed sites. Local species richness or 'alpha diversity', on the other hand, is the number of species surviving in a particular non-destroyed site. Since there is a very large number of sites (Table 1) we average local diversities across (non-destroyed) sites and denote it with α. Changes in alpha $\Delta\alpha = \alpha_{400} - \alpha_{200}$ and gamma $\Delta\gamma = \gamma_{400} - \gamma_{200}$ diversity are taken between the time just before the perturbation (year = 200), and 200 years after (year = 400). The larger the changes (absolute value), the less robust the metacommunity. Distributions of these differences (there are 100 replicates) are graphically represented using boxplots and scatterplots.

Estimation of interactive effects

To inquire if phenological shifts and site destruction have interactive effects on diversity, we compare the changes that occurred in the simulations, with changes predicted as if phenological shifts and site destruction were having independent effects. Under the prediction of independence, the fraction of alpha diversity 200 years after a simultaneous phenological shift μ (e.g. -10 days or 'present' phenologies) and site destruction ϕ is:

$$F(\mu,\phi)_{pre} = \frac{\alpha_{400}(\mu,0)}{\alpha_{200}(\mu,0)} \times \frac{\alpha_{400}(0,\phi)}{\alpha_{200}(0,\phi)} \tag{5}$$

where the factors in the right-hand side are the fractions assuming that only phenology changed (μ, 0), or only site destruction took place (0, ϕ). We generated 100 products like Eq. 5 using the 100 replicates available for each factor. We calculate a 95% confidence interval for $F(\mu, \phi)_{pre}$, and for the fractions actually observed in the simulations $F(\mu, \phi)_{obs} = \alpha_{400}(\mu, \phi)/\alpha_{200}(\mu, \phi)$. Confidence intervals are computed as $\bar{F} \pm 1.96(\sigma_F/\sqrt{n})$, where $\bar{F}$ and σ_F are the average and standard deviation of $F(\mu, \phi)_{pre}$ or $F(\mu, \phi)_{obs}$ upon $n = 100$ replicates, and ± 1.96 is the ~95% quantile of the standard normal distribution (Sokal and Rohlf 1987). If the confidence intervals of predicted and observed outcomes overlap, we cannot rule out the independence of effects between phenological shifts and site destruction. If they do not overlap, then we have reasons to believe that an interaction of effects has taken place. The same comparison is performed for the changes in gamma diversities (γ).

Network structure indicators

For every non-empty site (i.e. with at least one plant and one pollinator) among the non-destroyed sites, we calculate the changes in two network structure indicators, connectance and nestedness, just before phenological changes and habitat destruction take place (year = 200), and 200 years later (year = 400). The differences between these two times are averaged across the sites (non-destroyed, non-empty). This is done for every combination of phenological shift and fraction of sites destroyed. Connectance and nestedness are considered as two of the most important factors giving

robustness to ecological networks against interaction loss, in particular for mutualistic networks (Bascompte et al. 2003, Bascompte and Jordano 2007, Bastolla et al. 2009, Vázquez et al. 2009, Allesina and Tang 2012). Higher connectance and nestedness facilitate the permanence of a core of generalists species which in turn help many specialized mutualists survive (Bascompte and Jordano 2013), which helps in preventing cascading extinctions.

Connectance is defined as the proportion of links observed in a site divided by the potential number of links (Olesen and Jordano 2002) that could occur if all plants and pollinators were present there (i.e. 26 plants $\times$ 109 pollinators = 2834 links). Nestedness is defined as a network pattern where the more specialist species interact only with proper subsets of those species interacting with the more generalists ones (Bascompte et al. 2003). To estimate nestedness we used the 'nested' metric based on 'overlap' and 'decreasing fill' (NODF), developed by Almeida-Neto et al. (2008), which is commonly used to estimate nestedness, and is statistically robust regarding changes in sample size (which decreases due to site destruction). NODF runs from zero, when all species interact with the same partners or when there are no shared interactions between pairs of species, to 100 when the matrix of interactions is fully nested.

Results

Projected change scenario

Figure 2 shows how diversities change among the different combinations of phenological shift and site destruction levels. Local diversity decreases monotonically with respect to the fraction of sites destroyed. Local diversity also tends to decrease with the amount and the variability of the phenological shifts (μ), although there are exceptions when the shift is small ($\mu = -10$), most likely because some generalist species have net gains of interaction-days due to rewiring. It is important to remind that decays in local diversities can never be equal to the original numbers of plants (26 species) or pollinators (109 species), simply because local diversities before the perturbations were already (a bit) lower than these numbers, due to the stochastic nature of the survival and dispersal events.

If phenologies are not altered ($\mu = 0$), global plant and pollinator diversities are generally preserved ($|\Delta\gamma| \approx 0$) for up to 50% of the sites destroyed. As the destroyed fraction increases, there is a sharp transition where the entire metacommunity collapses, all plants and pollinators go extinct together ($|\Delta\gamma| = 26$ plants or 109 pollinators). On average, global diversity follows a sigmoid decrease, but this average is misleading: the transition towards the collapse displays strong bimodality. There is a relatively wide region of site destruction levels, e.g. from 0.6 to 0.8 when $\mu = 0$, where the outcome is (with very few exceptions) either the total collapse, or the survival of almost all the species in the metacommunity, depending on the conditions at the time of the perturbation. When phenologies are shifted, this region of bimodality, or alternative outcomes, shifts towards lower fractions of destroyed sites. For example if $\mu = -20$, bimodality occurs when the fraction of destroyed sites ranges from approx. 0.5 to approx. 0.7. Also note that in the region of bimodality, non-collapsed metacommunities become less rich under phenological alterations, i.e. they persist but some species go extinct globally.

Figure 3 shows the confidence intervals for local and global fractions of diversity 200 years after the perturbations; for the simulations, and for the prediction that phenological shift and site destruction act independently (Eq. 5). When the phenological shift is small ($\mu = -10$), simulations and prediction match (confidence intervals overlap), and we shouldn't rule out that phenological perturbations and habitat destruction act independently. In contrast, for larger amounts of phenological shift ($\mu = -20, -30$) the decrease in the simulated data is significantly larger than the decrease in the predictions. These results give us a good reason to say that phenological shifts and habitat destruction act synergistically, in the sense that their combined effects are higher than their effects separately. The same patterns for local and global diversities also occur in the pollinator guild (not shown).

Figure 4 shows the changes in the local averages of connectances and nestedness, for the non-destroyed, non-empty sites. For all conditions of phenological shift these network indicators tend to decrease with habitat loss (there is only a very small increase of nestedness at 10% of habitat loss when $\mu = -10$). Notice that this decrease tends to be larger for intermediate fractions of sites destroyed. This is most likely because at large fractions of sites destroyed, connectances and nestedness are averaged over the very few remaining sites that manage to keep enough plants and pollinators together, making them viable. When phenologies advance a few days and with low variabilities ($\mu = -10$), connectances increase a little bit, but further phenological advances and variability ($\mu = -20, -30$) only causes further decrease in connectance. The small increase may be due to the fact that small changes in phenology may not seriously impair local survival in many species, and can create new interactions for some generalist species (rewiring), which in turn can benefit less generalist mutualists. This effect disappears if phenologies change too much; large changes and variability in phenologies contribute to net losses of interactions (on average) in many simulations. Nestedness, by contrast, shows a tendency to increase with phenological shifts, but the outcomes are very variable, and in a large number of simulations averages decrease when the changes in phenology are larger.

Historical change scenario

Simulations under the historical change scenario display the same general patterns of global and local diversity decrease as in the scenario where the phenologies were projected, but there are important quantitative differences. For economy of space, the figures corresponding to these simulations (which are designed like Fig. 2, 3, 4) are presented in the online supplement of this paper.

In general, declines in local diversity are more pronounced and metacommunity collapse requires lower fractions of destroyed sites. The response of global diversity is very variable, but the region of bi-stability is not as sharply defined as in the scenarios with projected changes.

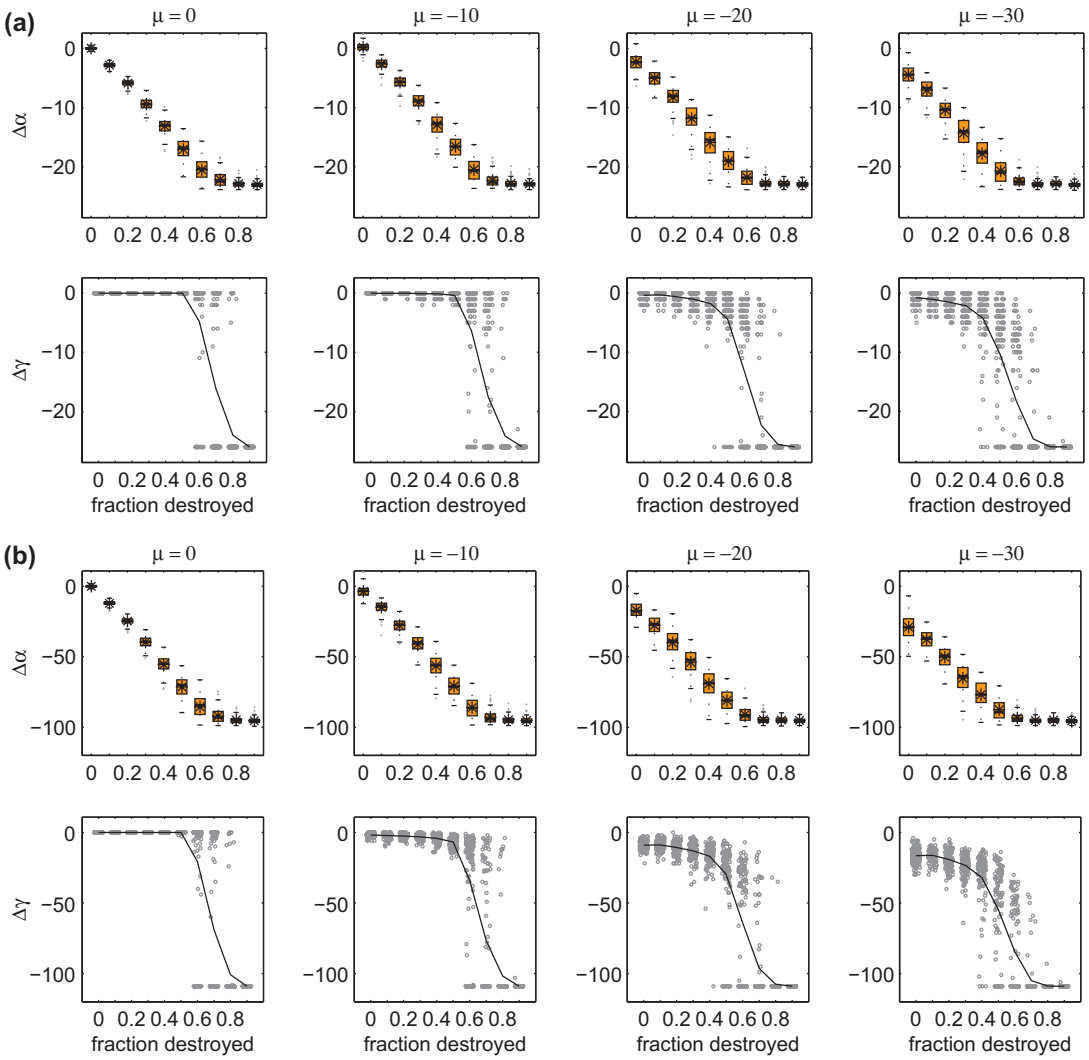

Figure 2. Changes in (a) plant and (b) animal diversities as a function of the fraction of sites destroyed, under different projected amounts of phenological shift (μ columns). The boxplots for local diversity decline (Δα) comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations, and the mean value (asterisk). Scatterplots of global diversity change (Δγ) are overlaid by the average trend (line).

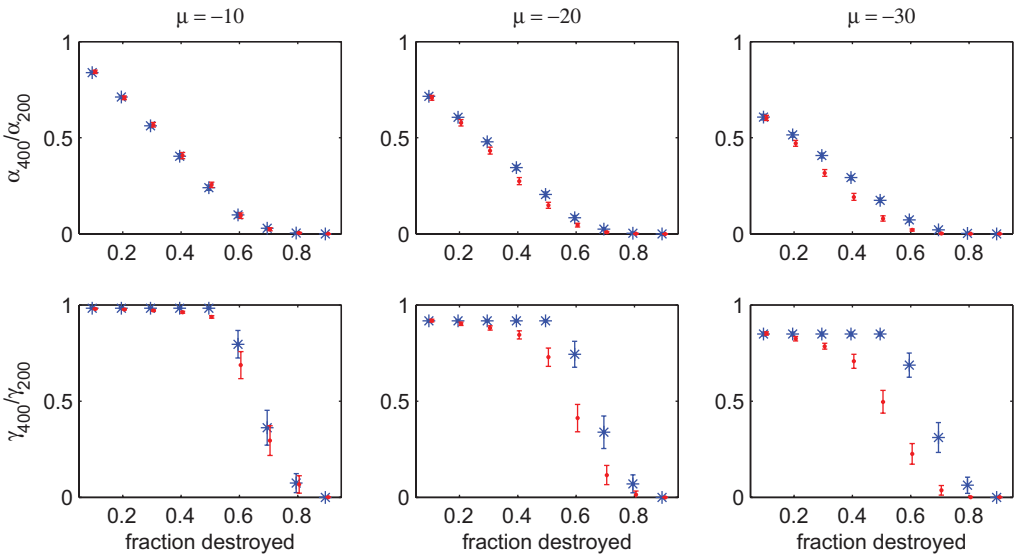

Figure 3. 95% confidence intervals for predicted ('*', independent effects) and observed ('o', simulation results) fractions of plant alpha and gamma diversities, 200 years after a given amount of projected phenological shift (μ columns) and fraction of sites destroyed.

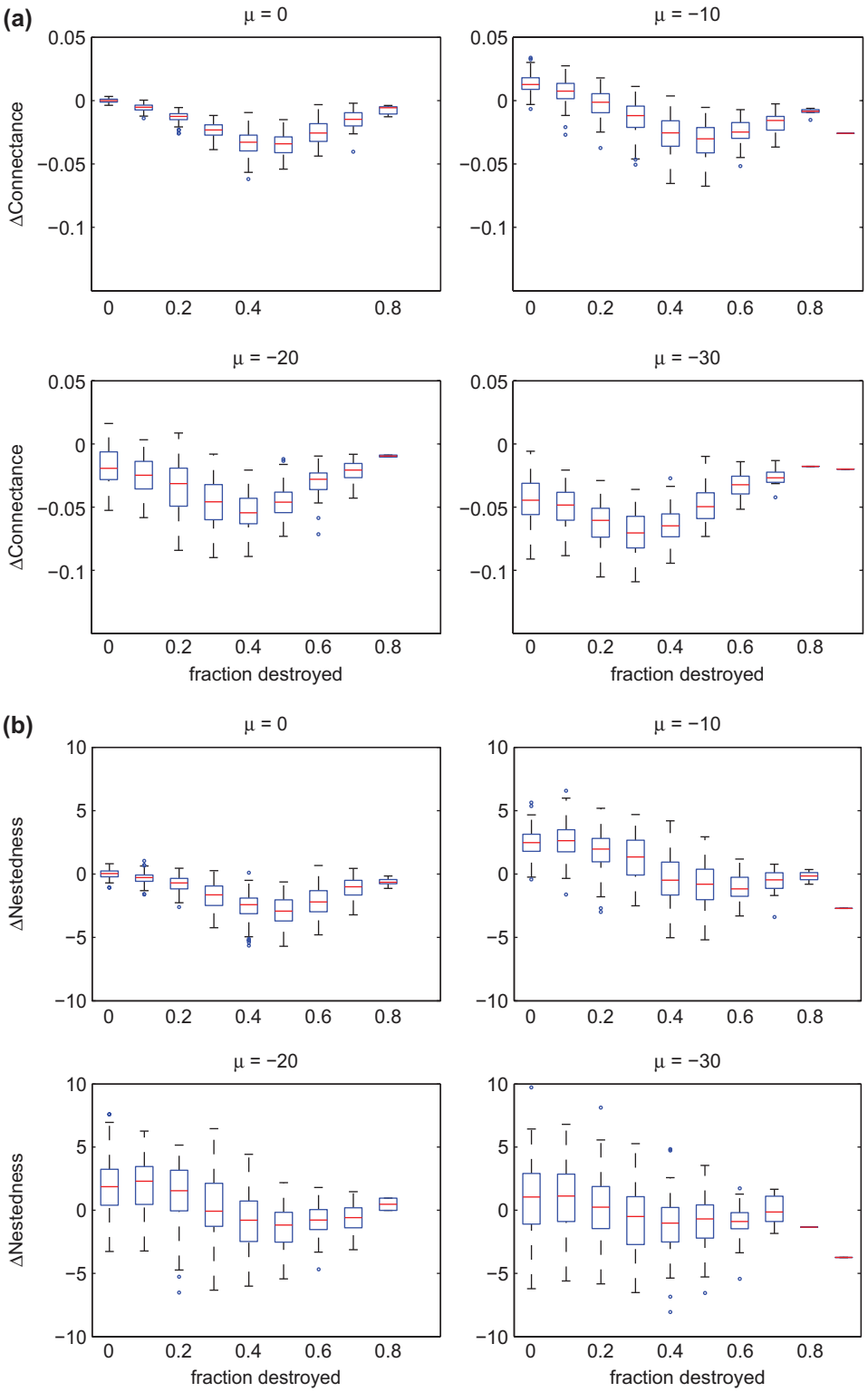

Figure 4. Changes in local connectance (a) and nestedness (b) (averages over non-destroyed, non-empty sites) against the fraction of sites destroyed, under different projections of phenological shift (μ). The boxplots comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations.

Pollinator extinctions are proportionally more frequent than plant extinctions (Supplementary material Appendix 1 Fig. S.3).

Like in the scenario of projected phenologies, decreases in local and global diversity are significantly higher for the simulated data, compared with the prediction that phenological shifts and site destruction act independently (Eq. 5). The discrepancy is actually much larger than the discrepancy under the projected scenario when the phenological shift is the largest (Supplementary material Appendix 1 Fig. S.4).

This again strongly supports the hypothesis, that perturbations in phenology and site destruction act synergistically.

Local network connectances and nestedness (averages over non-destroyed, non-empty sites) are reduced as a consequence of phenological shift. For large amounts of sites destroyed, average reductions in connectance and nestedness are less pronounced (Supplementary material Appendix 1 Fig. S.5). Like in the former simulation scenarios, this may reflect the robustness of a very few non-destroyed sites, which manage to keep a core of well connected generalists, making them viable.

Discussion

Metacommunity collapse

Habitat destruction and phenological shifts have detrimental effects on species diversity that are worth considering separately, before discussing their simultaneous effects.

Habitat destruction

Global diversity collapses catastrophically (Scheffer et al. 2001) above a critical number of sites destroyed, i.e. all plants and pollinators go extinct together, in all the remaining sites (Fortuna and Bascompte 2006, Fortuna et al. 2012). Below these critical levels, metacommunities can remain diverse or they can collapse, i.e. they can bi-stable. Bi-stability can have important consequences for the recovery of metacommunities from perturbations. This can be illustrated by the following reasoning. A metacommunity can tolerate a large number of destroyed sites as long as local diversities (α) remain large enough to compensate for the decrease in colonization rates. Once global diversity (γ) has collapsed, recovery requires the re-creation of sites, and re-introductions from an external source having the original set of species. Assuming such source exists, re-introduction can happen in at least two ways: 1) by populating non-destroyed and re-created sites with the complete set of species, which is typically a planned but costly endeavor; 2) or by letting nature determine which species end up in which sites, i.e. an unguided and likely inefficient process. Under the first 1) option, high local diversities would make recovery easier. It is like 'running the film backwards' until the point of collapse. Under the second 2) option however, chance does not ensure high local diversities, even if each species exists at least in one site. Under these circumstances 2), only increased dispersal might keep global diversity from collapsing again, but this would require to re-create a larger number of sites compared with the first option 1). This behavior, where the response of the system (i.e. global diversity) is different when the same factor (i.e. number of sites) increases or decreases, is called 'hysteresis' (Scheffer et al. 2001). A recent paper by Lever et al. (2014) highlights the role of hysteresis in large plant–pollinator networks, when pollinators are affected by a mortality stressor.

In contrast with global diversity, local diversity averages decrease gradually with site destruction. A simple explanation is that each remaining site ends farther away (on average) from a dwindling number of species sources as site destruction increases, thus recolonization becomes less likely. When these species-poor local communities, which differ greatly in species composition, are too far away to send or receive migrants, a sudden global collapse occurs.

Phenological shifts

Diversities decay with phenological shifts because interaction strengths become weaker, reducing local survival. In our model this weakening occurs in a manner that resembles a ratchet, in which a turn in one direction causes an effect, but a turn of the same magnitude in the opposite direction causes little or no effect. To understand why, let us first remember that in our model each species has a baseline number of interaction-days which is invariant (Eq. 2), and which can be taken as a proxy of its food (pollinators) or service (plants) requirements. Our simulations are set up (tolerance and dispersal conditions, number of sites, etc.) in a way such that missing a few interaction-days due to local partner absences do not cause extinctions before the perturbations take place (Supplementary material Appendix 1 Fig. S.2). When phenologies are altered, some species will gain interaction-days and some will lose interaction-days. For those species with net gains, local survival can slightly improve: they were already doing well before the changes, and under the new conditions they are closer to match their interaction-day baselines (Q_i^0). However, for species that lose interaction-days, local survival can decrease very fast. This difference in response is because the survival probability function (Eq. 3) shows diminishing returns ($\theta > 1$ in Table 1, Supplementary material Appendix 1 Fig. S.1), this is the 'ratchet analogy'. As phenologies advance towards earlier dates and become more variable, local survival rates will mainly decrease, and sites will become poorer as species sources.

Habitat destruction + phenological shifts

When habitat destruction and phenological shifts occur together, our model predicts that their joint effects on diversity can be larger than the combination of their independent effects, a interaction called 'synergy'. We think that we can explain what causes this synergy. Let us consider for example, that only site destruction takes place, but phenologies do not change. Under this scenario, a small amount of site destruction may not greatly reduce the local survival of a species, because there are still many sites acting as dispersal sources, and the strength of existing interactions (determined by phenology) has not changed yet. However, if phenological mismatches occur, many interactions will become weaker (recall the ratchet analogy), and the rescuing effect of colonization will be greatly reduced. This is because in addition to the sites lost due to habitat destruction, we must consider those non-destroyed sites that stopped being colonization sources, because interactions over there have become too weak to ensure local survival. In other words, from the point of view of any particular site, the effective number of colonization sources have decreased more than the number of sites actually destroyed. In addition, consider that the survival function (Eq. 3) is non-linear, and that mutualisms involve positive feedbacks; both factors could amplify the interaction of effects just outlined.

The synergistic effects of ecological threats or stressors (e.g. fragmentation, mortality) have been documented

for real ecosystems, but their prevalence is still a matter of debate (Crain et al. 2008, Darling and Côté 2008). There is however, abundant evidence of the role of alternative stable states, hysteresis and regime shifts in aquatic and terrestrial systems (Scheffer et al. 2001, Kéfi et al. 2007); but it is yet to be seen if such complex dynamics occur, in particular, in mutualistic metacommunities. The presence of synergies and alternative states (Scheffer et al. 2001) means that the response of a metacommunity against perturbations can be highly nonlinear, and that attempts at ecosystem restoration by reversing of existing trends (Huxel and Hastings 1999) may not suffice to yield the results expected. We also think that the spatial distribution of the sites and the pattern of site destruction, can be more complex than just random as we assumed (e.g. destruction can be more likely in the proximity of destroyed sites), and these details can have important consequences for the robustness of metacommunities against the perturbations here considered; this is a topic that deserves further study.

Connectance and nestedness

Habitat destruction tends to decrease connectances, but the largest decrease happens at intermediate fractions of site destruction. There is a reason for this: as long as the fraction of sites destroyed has not caused a global collapse, one would expect a landscape composed of sites with varying amounts of local richness, with species-poor sites being rescued by dispersal from richer sites; as a consequence, the averages of local connectances will be lower than before site destruction. However, if too many sites are destroyed, species-poor sites will become empty and will not be averaged; as a consequence, richer sites will cause the average values of local connectances to rise up again (but only a little bit since some species have already been lost globally). In other words, the higher connectances seen for large amounts of site destruction are due to a fewer viable, but still diverse enough localities. Altering the phenology tends to decrease connectance for all levels of site destruction, but it also introduces more variability. Indeed in a few simulations connectance can actually increase if phenologies change a little bit ($\mu = -10$ days), possibly because some mutualists advance almost in parallel, and because some generalist species are able to add new interactions (rewiring).

The pattern of change in local nestedness averages with respect to habitat destruction is somewhat similar to the pattern followed by connectance, i.e. the largest decrease occurs at intermediate fractions of sites destroyed. Simulations under projected changes of phenology tend to show increase in nestedness, but simulations following the historical pattern of change in phenology tend to show decrease in nestedness. The sub-network used in our study is known to have experienced a decrease in nestedness from the past to its present condition (Burkle et al. 2013), and this factor was implemented in the historical scenarios, but not in the projected scenarios; this can explain the difference.

Instead of averaging connectances and nestedness over the sites, we can also consider these network properties globally, like in Fortuna et al. (2012): does the interaction between plant i and pollinator j occurs at all?, disregarding in how many sites. If done in this way, connectance and nestedness tend to decrease as the fraction of sites destroyed increases (Supplementary material Appendix 1 Fig. S.6, S.7). The decrease changes from catastrophic to a more continuous decline as the phenological shift increases. This contrasts with the pattern for the local averages, where connectance and nestedness first decrease and then increase a little bit with site destruction as described before (Fig. 4). This difference in perspective reveals that the global accounting of interactions can prevent us from realizing that, even for large amounts of site destruction, some metacommunities (i.e. few replicates) can persist longer times, because a few sites can maintain high enough connectances and nestedness.

Differences between scenarios

Our simulations also show important quantitative differences between scenarios in which phenologies are projected (as in Memmott et al. 2007) and those that resembled the historical changes (as in Burkle et al. 2013). Under projected changes it takes large phenological shifts ($\mu = -30$) to lower the threshold of collapse to somewhere between 50 to 60% of sites destroyed. In contrast, the historical changes in the starting dates of the phenologies found by Burkle et al. (2013) are less than 20 days on average, but this is enough to cause collapse with much lower fractions of sites destroyed (see figures in Supplementary material Appendix 1).

The most likely cause of this difference in responses is that the historical changes not only involved phenological shifts towards earlier dates, but also the reduction in the duration of many species phenologies (always fixed when phenologies were projected). Thus, species that in the past had shorter phenologies are at great risk of losing interactions, and can end up totally disconnected from the network. This can result in loss of network connectance and nestedness when the fraction of sites destroyed is relatively small (between 0 and 0.2, see supplementary figures). These differences between the scenarios illustrate the importance of considering not just the phenological shifts, but also the changes in the duration of activity seasons.

Plant and pollinator vulnerability

In our simulations, the pollinators tend to lose a larger fraction of species than the plants as consequence of phenological alterations, a discrepancy that becomes larger when phenologies change according to the historical pattern. One factor that may explain this discrepancy is that pollinators outnumber plants by a little more than 4 to 1 (109 versus 26), making pollinators more vulnerable to the loss of plants, than plants to the loss of pollinators. This is easy to illustrate, let us imagine that all species were generalists and all interactions were equally strong in terms of interaction-days, e.g. $O_{ij} = 1$ day for all i and j (a common assumption in studies of structural robustness). Thus, for each animal species that goes extinct, a plant species loses 1/109th of its total number of interaction-days, whereas for each plant that goes extinct, an animal loses 1/26th; in other words, the vulnerability against interaction loss would rise faster for the animals than for the plants.

Certain strategies can reduce vulnerability against interaction loss. Diet flexibility in pollinators, for example, can lead

to novel interactions in many species (Burkle et al. 2013). Our simulations show that rewiring allows small increases in connectances if phenological shifts and site destruction levels are low; but rewiring favor the more generalist species, which are few and at lower risk of extinction than specialists (Rathcke 1993). Rewiring may depend on factors other than generalism, for example relative densities (Burkle et al. 2013), or competitive release following the extinction of competitors. Thus, diet flexibility may be more frequent than our model assumes, helping more specialist species to better deal with interaction loss.

A number of important plant life-history traits (e.g. perenniality, seed banks) are currently ignored in plant–pollinator network theoretical studies; however they might explain survivability in times when interactions are being lost. For example, perenniality is common among angiosperm plants and they would allow them to skip interactions for several years, whereas in our model the total absence of interactions causes extinction just after one year. Being perennial may thus delay extinction long enough for novel interactions to evolve. However, many perennials have self-incompatible mating systems and therefore they need pollination service to reproduce (Barrett 1988). It would be very interesting to consider life-history traits more explicitly in future models, to see how it would affect the robustness and stability of the web of interactions.

Conclusion

Habitat destruction or its fragmentation can lead to the local elimination of interactions. Phenological mismatches, caused mainly by global warming, can weaken existing interactions. Both threats alone contribute to the gradual erosion of interaction networks, leading to the eventual collapse of mutualistic metacommunities. The joint effects of these threats can be even more detrimental, because they can act synergistically, and because mutualisms are prone to display bi-stability. As a result, attempts at recovering metacommunities by reversing current trends of habitat fragmentation (e.g. creating new sites) will turn more challenging in the face of phenological mismatches caused by climate change.

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Supplementary material (available online as Appendix oik.01532 at <www.oikosjournal.org/readers/appendix>).
Appendix 1