

Robustness of mutualistic networks under phenological change and habitat destruction

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Abstract: Global changes, such as climate change and habitat destruction, threaten bio-
8 diversity and ecosystem functioning. On the one hand, climate change can alter species
phenologies and therefore disrupt species interactions. On the other hand, habitat destruc-
10 tion can damage biodiversity and population viability. The effects of these factors have been
studied separately in mutualistic networks and other ecological networks. However, we still
12 know very little about their potential effects on the diversity and structure of mutualistic
networks when both factors act simultaneously. Here, we developed a mutualistic metacom-
14 munity model to explore the effects of habitat destruction and phenological changes on the
diversity and structure of plant–pollinator networks. Interestingly, we find that the effects
16 of habitat destruction and phenological changes act synergistically, largely damaging local
and global diversity and network structure (i.e. connectance and nestedness). Therefore,
18 these effects do not act in an additive fashion and can produce a sudden collapse of the
metacommunity. We conclude that the synergistic effects of climate change and habitat
20 destruction can be more damaging than expected, as some empirical studies have shown.

Keywords: mutualistic metacommunities, phenological shifts, habitat loss

22 1 Introduction

Climate change is known to cause important alterations in species phenologies (Parmesan and Yohe,
24 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
26 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
28 they are not a serious threat due to functional redundancies in the case of large communities (Benadi
et al., 2013).

30 Not all possible mutualistic interactions between species are observed. Some links are indeed *forbid-*
den by phenological mismatch, or by other reasons, e.g. large size differences between insect proboscis
32 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
34 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.
36 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.

38 This redundancy of interactions at the regional scale could provide resilience against multiple in-
teractions losses triggered by climate change, and ensure the long term persistence of diversity and
40 functioning of whole metacommunities. But in order for this to happen, a large enough number of lo-
calities (e.g. sites or patches) have to exist, and their separation must enable dispersal, such that local
42 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),
44 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
46 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
48 (Fortuna and Bascompte, 2006; Fortuna et al., 2012).

However, to our knowledge, there are no studies investigating the joint effect of habitat destruction
50 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
52 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
54 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
56 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
58 Beaubien, 2001) and local adaptation (Phillimore et al., 2012).

In this contribution we study the changes on diversity and network properties, as mutualistic meta-
60 communities are subject to phenological changes and habitat destruction. This paper aims to un-
derstand the robustness of mutualistic metacommunities against the detrimental effect of changes in
62 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 deter-
64 mine 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.
66 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,
68 we find that the interaction between phenological mismatch and habitat destruction makes mutualistic
metacommunities much more vulnerable than considering their separated effects.

70 2 Spatially explicit model

We consider a metacommunity of $i = 1, \dots, N_P$ flowering plants and $j = 1, \dots, N_A$ pollinators dis-
72 tributed over several sites, see Figure 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
74 $S_j(x, t)$. 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
76 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
78 site, and the structure of the network can differ from one site to another, and from one year to the
next.

80 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
82 of the plants. For the pollinators, the corresponding equations describing survival and dispersal will
be symmetrical, i.e. j and i are interchangeable.

84 **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:

$$Q_i(x, t) = \sum_j S_j(x, t) O_{ij} \quad (1)$$

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

$$Q_i^0 = \sum_j O_{ij} \quad (2)$$

which is a site-independent, species-specific property. Q_i^0 will be considered as a baseline for interaction-
 90 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.
 92 We formulate the probability of local survival as:

$$P_i(x, t) = (1 - \epsilon(x)) \left(\frac{Q_i(x, t)}{Q_i^0} \right)^{\frac{1}{\theta_i}} \quad (3)$$

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
 94 if all its pollinators are present then $Q_i(x, t) = Q_i^0$ and $P_i(x, t) = 1 - \epsilon(x)$, where $\epsilon(x)$ is a small
 extinction probability that is site-specific, but not species-specific. The pace at which survival drops
 96 due to local interaction losses depends on a *tolerance* parameter θ_i . Supplementary Figure 1 shows
 a sketch of (3) when $\theta > 1$. The limit $\theta_i \rightarrow \infty$ parallels the assumption of many studies of network
 98 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
 100 collapse too easily under these condition, even in the absence of the perturbations considered in the
 Methods (Supplementary Figure 2).

102 **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
 104 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 Figure 1), and whether
 106 or not site y hosts plant i in the first place. The colonization probability of site x is:

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

i.e. the complement of the event that all sites different than x hosting plant i fail to colonize x .
 108 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
110 decays $\sim 63\%$ (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.

112 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
114 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
116 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 $c < C_i(x, t)$
118 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.

120 3 Methods

3.1 Data source and parameter settings

122 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
124 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
126 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
128 much larger database (Memmott et al., 2007). In addition to the past phenologies and interactions
(from little more than a century ago), Burkle et al. dataset also includes the phenologies of the same
130 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.) with realistic ones (as in Burkle et al.),
132 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
134 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
136 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
138 though they overlap in time; this is done using the binary interaction matrix from Burkle et al. (2013)
supplementary material (Figure S9 part A).

140 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
142 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 (see
144 Supplementary Figure 2). After that time, phenological changes and/or habitat loss occurs (see section
on simulation scenarios). Table 1 shows the parameter values.

146 3.2 Simulation scenarios

We will study the joint effect of phenological shifts and habitat destruction under two different simu-
148 lation scenarios:

Projected changes: start and end dates at the time of Robertson (1929) are shifted by a number
150 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
152 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,
154 and starting 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
156 (2009–2010) dates, recorded by 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
158 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
160 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).
162

Phenological shifts change the matrix of phenological overlaps O_{ij} . As a consequence, the strengths
164 of existing interactions can increase/decrease (i.e. more/less days of overlap), as shown by Figure
1B; or even disappear (complete loss of overlap). Novel interactions (new O_{ij} entries) could happen
166 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
168 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
170 have higher rewiring probabilities than specialist species. The new probabilities of local survival are

172 computed using equation (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
174 $Q_i(x, t)$ 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. $P_i(x, t) = 1 - \epsilon(x)$.

176 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 $\epsilon(x)$ from 0.05
178 (Table 1) to 1 (i.e. the site becomes lethal). Thus, for the scenario of projected changes we combine
4 levels of phenological shift $\mu = 0, -10, -20, -30$ with 10 levels of site destruction $\phi = 0, 0.1, \dots, 0.9$.
180 Combinations with $\mu = 0$ or $\phi = 0$ correspond to site destruction only, or phenological shift only,
respectively. For the historical scenario we only have 2 levels of phenological shift $\mu = past$ which
182 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
184 destruction alone can lead to local interaction loss, but not to strengthening or weakening of existing
interactions, as shown by Figure 1C.

186 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
188 (see Supplementary Figure 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
190 sites end populated, even though 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
192 diversity and network structure indicators. Figure 1D indicates that both perturbations can happen
simultaneously.

194 3.3 Metacommunity diversity

For each combination of levels of phenological shift and site destruction, we measure changes in global
196 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
198 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
200 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
202 changes (absolute value), the less robust the metacommunity. Distributions of these differences (there

are 100 replicates) are graphically represented using boxplots and scatterplots.

204 Estimation of interactive effects

To inquire if phenological shifts and site destruction have interactive effects on diversity, we compare
206 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
208 alpha diversity 200 years after a simultaneous phenological shift μ (e.g. -10 days or *present* phenologies)
and site destruction ϕ is:

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

210 where the factors in the right-hand side are the fractions assuming that only phenology changed $(\mu, 0)$,
or only site destruction took place $(0, \phi)$. We generated 100 products like (5) using the 100 replicates
212 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 com-
214 puted 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 $\sim 95\%$ quantile of the standard normal distribution
216 (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
218 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).

220 3.4 Network structure indicators

For every non-empty site (i.e. with at least one plant and one pollinator) among the non-destroyed
222 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
224 (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.
226 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.,
228 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
230 which in turn help many specialized mutualists survive (Bascompte and Jordano, 2013), which helps
in preventing cascading extinctions.

232 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
234 (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
236 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
238 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
240 when there are no shared interactions between pairs of species, to 100 when the matrix of interactions
is fully nested.

242 4 Results

4.1 Projected change scenario

244 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
246 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
248 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
250 (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.

252 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
254 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
256 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
258 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
260 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
262 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.

264 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
266 independently (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
268 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
270 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
272 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-
274 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
276 $\mu = -10$). 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
278 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
280 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
282 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
284 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
286 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.

288 4.2 Historical change scenario

The diversity indices display similar decreasing trends as in the scenario where the phenologies were
290 projected, but there are important quantitative differences. The results are presented again graphically,
in Figure 5 (note again: condition *past* in the figures corresponds to $\mu = 0$ in projected scenarios, thus
292 no differences are expected here). In general, declines in local diversity are more pronounced and
metacommunity collapse requires lower fractions of destroyed sites. The response of global diversity is
294 very variable, but the region of bi-stability is not as sharply defined as in the scenarios with projected

changes. Pollinator extinctions are proportionally more frequent than plant extinctions.

296 Like in the scenario of projected phenologies, Figure 6 indicates that decreases in local and global
diversity are significantly higher for the simulated data, compared with the prediction that phenolog-
298 ical shifts and site destruction act independently (5). The discrepancy is actually much larger than
the discrepancy under the projected scenario when the phenological shift is the largest. This again
300 strongly supports the hypothesis, that perturbations in phenology and site destruction act synergisti-
cally. Figure 6 only considers the plants (but the outcome for animal diversity is similar).

302 Local network connectances and nestedness (averages over non-destroyed, non-empty sites) are vis-
ibly reduced as a consequence of phenological shift, as shown by Figure 7. For large amounts of sites
304 destroyed, average reductions in connectance and nestedness are less pronounced. Like in the former
simulation scenarios, this may reflect the robustness of a very few non-destroyed sites, which manage
306 to keep a core of well connected generalists, making them viable.

5 Discussion

308 5.1 Metacommunity collapse

In general we found that the loss of global diversity in response to habitat destruction is catastrophic
310 (Scheffer et al., 2001), i.e. there are critical levels of habitat destruction above which all plants and
pollinators go extinct together, in all the remaining sites (Fortuna and Bascompte, 2006; Fortuna et al.,
312 2012).

When phenological shifts occur, metacommunities collapse with lower fractions of sites destroyed.
314 This is because temporal shifts tend to make interaction strengths weaker. 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
316 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
318 invariant (equation 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
320 a way such that missing a few interaction-days due to local partner absences do not cause extinctions
before the perturbations take place (see Supplementary Figure 2). When phenologies are altered, some
322 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
324 new conditions they are closer to match their interaction-day baselines (Q_i^o). However, for species that
lose interaction-days, local survival can decrease very fast. This difference in response is because the

326 survival probability function (3) shows diminishing returns ($\theta > 1$ in Table 1, see also Supplementary
Figure 1), this is the “ratchet analogy”. As phenologies advance towards earlier dates and become more
328 variable, local survival rates will mainly decrease, sites will become poorer as species sources, and less
sites have to be destroyed in order to cause the collapse of the metacommunity.

330 The metacommunity displays bi-stability in response to habitat destruction, i.e. alternative steady-
states (Scheffer et al., 2001). This is expected in obligatory mutualisms, where minimum partner
332 abundances are required for survival. Bi-stability can have important consequences for the recovery
of metacommunities from perturbations. This can be illustrated by the following reasoning. We have
334 seen that a metacommunity can tolerate the destruction of a large number of sites, but only as long
as local diversities (α) remain large enough to compensate for the decrease in colonization rates. Once
336 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
338 happen in at least two ways: (i) by populating non-destroyed and re-created sites with the complete
set of species, which is typically a planned but costly endeavor; (ii) or by letting nature determine
340 which species end up in which sites, i.e. an unguided and likely inefficient process. Under the first
(i) option, high local diversities would make recovery easier. It is like “running the film backwards”
342 until the point of collapse. Under the second (ii) option however, chance does not ensure high local
diversities, even if each species exists at least in one site. Under these circumstances (ii), only increased
344 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 (i). This behavior, where the response of the system
346 (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
348 hysteresis in large plant–pollinator networks, when pollinators are affected by a mortality stressor.

In contrast with global diversity, the decrease in local diversity caused by site destruction tends to
350 be gradual instead of critical. Local diversity averages decay monotonically as long as no extinctions
occur at the global scale. A simple explanation for this is that each remaining site ends farther
352 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
354 in species composition, are too far away to send or receive migrants, a sudden global collapse occurs.
With the introduction of phenological shifts, the declines in local diversity become not only larger, but
356 also more variable. In some few cases, when the phenological changes are not too large, local diversity
can increase thanks to interaction rewiring (i.e. species drawing new links with other species), mostly
358 by generalist species which happen to be critical for the integrity of the whole network.

Our model predicts that the joint effects of changes in phenology and the destruction of sites can be larger than the combination of their independent effects, a interaction called *synergy*. We can hypothesize why does this synergy between phenology and space exists. If we pay attention to the local survival probability function (3), we can see that phenological shifts and habitat destruction together determine the sum of the numerator (1). 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 one successful colonization by a mutualistic partner ensures a contribution in the sum (1). However, if phenological mismatches occur, many interactions will become weaker (recall the ratchet analogy), and the rescuing effect of colonization is reduced, as if site destruction were larger than it really is. In this way, phenological mismatches (having a global scope), re-enforce the detrimental consequences of interaction loss (local scope) caused by site destruction, and thus we have a synergy. In addition, consider that the survival function (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 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.

5.2 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 occur 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 (see Supplementary Figures 3, 4). 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 (Figures 4,7). 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.

5.3 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.

424 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 phe-
426 nologies (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 net-
428 work. As Figure 7 shows, this can result in loss of network connectance and nestedness when the
fraction of sites destroyed is relatively small (between 0 and 0.2). These differences between the sce-
430 narios illustrate the importance of considering not just the phenological shifts, but also the changes in
the duration of activity seasons.

432 5.4 Plant and pollinator vulnerability

In our simulations, the pollinators tend to lose a larger fraction of species than the plants as consequence
434 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
436 plants by a little more than 4 to 1 (109 vs 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
438 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
440 species that goes extinct, a plant species loses 1/109 th of its total number of interaction-days, whereas
for each plant that goes extinct, an animal loses 1/26 th; in other words, the vulnerability against
442 interaction loss would rise faster for the animals than for the plants. This difference in vulnerability
between plants and pollinators is larger in the scenario where phenologies change following historical
444 patterns, because the pollinators have their phenologies greatly reduced in duration in comparison
with the plants (Burkle et al., 2013).

446 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
448 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
450 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.
452 Thus, diet flexibility may be more frequent than our model assumes, helping more specialist species to
better deal with interaction loss.

454 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
456 interactions are being lost. For example, perenniality is common in angiosperm plants and they would
allow them to skip interactions for several years, whereas in our model the total absence of interactions
458 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
460 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
462 of the web of interactions.

5.5 Conclusion

464 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
466 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
468 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
470 sites) will turn more challenging in the face of phenological mismatches caused by climate change.

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Tables

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

Table 1: Parameter values used in the simulations. The values of θ and δ were chosen such that all plants and animals can survive globally before the change in the phenologies and/or habitat destruction (see Supplementary Figure 2).

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.

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 ($\Delta\alpha$) comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations, and the mean value (asterisk). Scatterplots of global diversity change ($\Delta\gamma$) 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 and nestedness (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.

Figure 5. Changes in (a) plant and (b) animal diversities as a function of the fraction of sites destroyed, under past and present day phenologies (scenario of historical change). The boxplots for local diversity decline ($\Delta\alpha$) comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations, and the mean value (asterisk). Scatterplots of global diversity change ($\Delta\gamma$) are overlaid by the average trend (line).

Figure 6. 95% confidence intervals for predicted ('*', independent effects) and observed ('o', simulation results) fractions of plant alpha and gamma diversities, 200 years after a given fraction of sites destroyed under the scenario of historical phenological shifts.

Figure 7. Changes in local connectance and nestedness (averages over non-destroyed, non-empty sites) against the fraction of sites destroyed, under past and present day phenologies (scenario of historical change). The boxplots comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations.

Figures

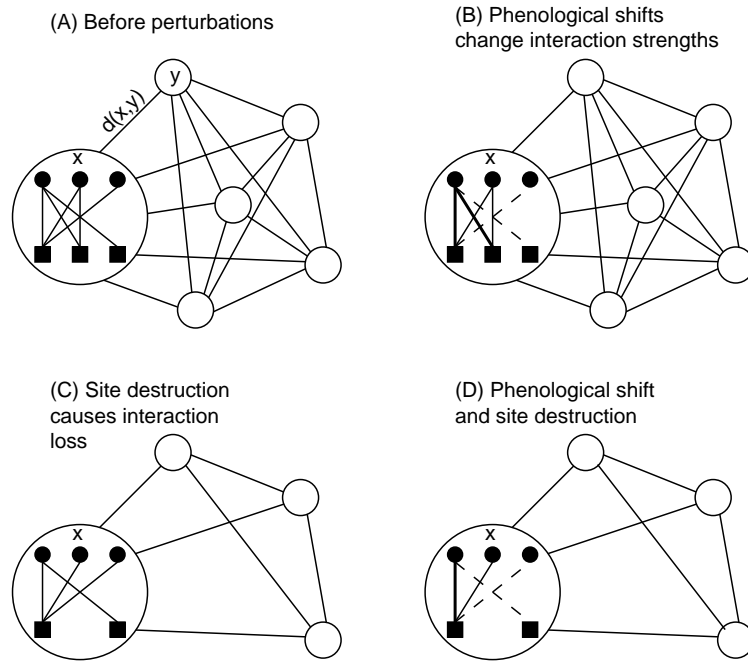
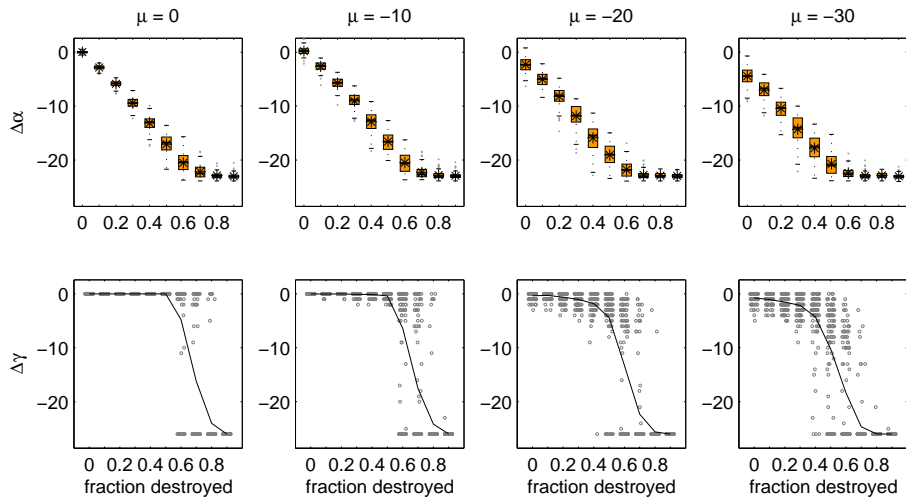
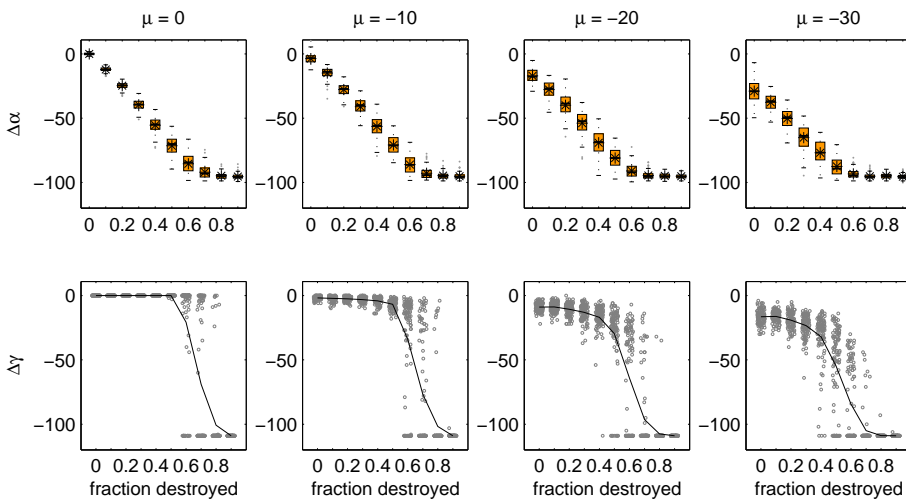


Figure 1: Spatially explicit metacommunity model. (A) Randomly positioned sites (e.g. x) are separated from other sites (e.g. y) by a certain distance (e.g. $d(x,y)$). Site x is enlarged to show the local bipartite network of plants (circles) and pollinators (squares). The survival probability of a species 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.



(a) Plants



(b) Animals

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 ($\Delta\alpha$) comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations, and the mean value (asterisk). Scatterplots of global diversity change ($\Delta\gamma$) are overlaid by the average trend (line).

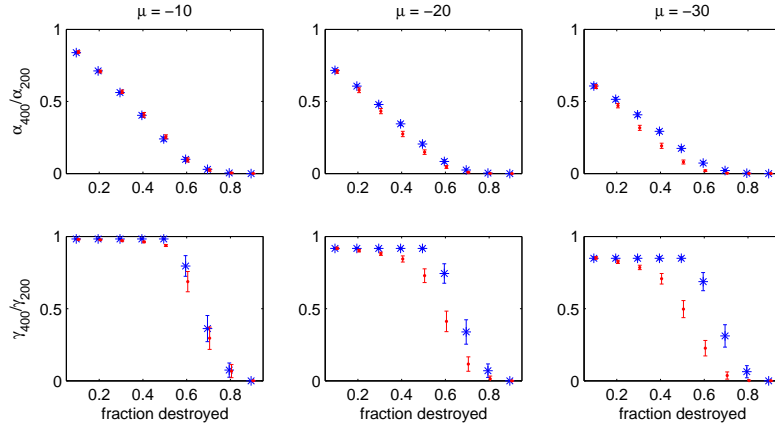
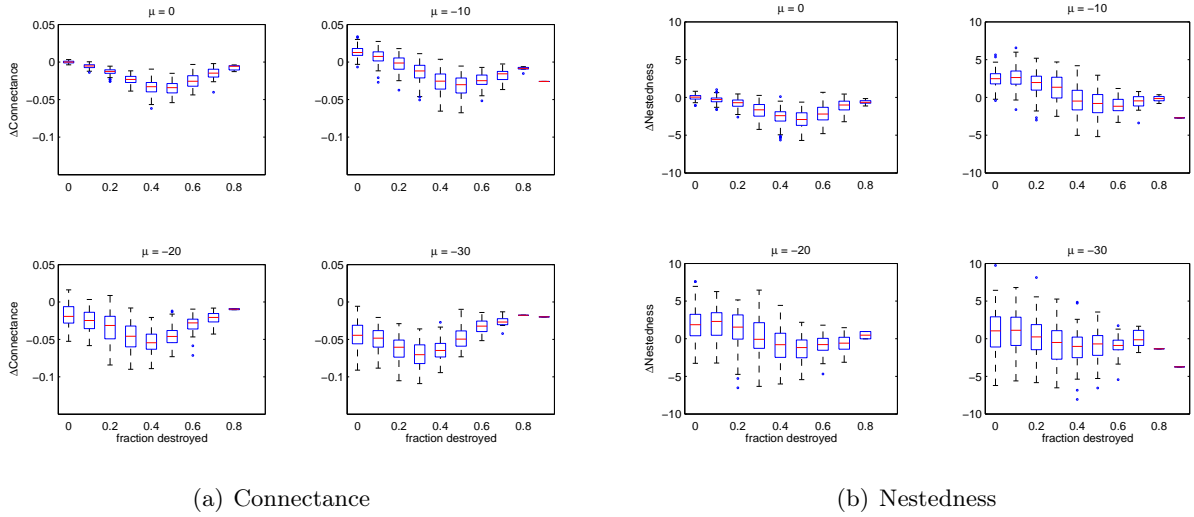


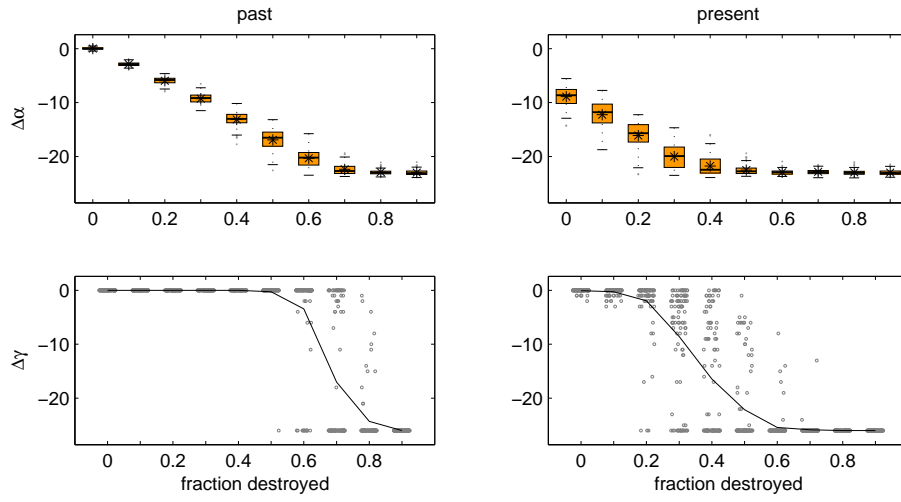
Figure 3: 95% confidence intervals for predicted (‘*’, independent effects) and observed (‘o’, simulation results) fractions of plant alpha and gamma diversities, 200 years after a given amount of projected phenological shift (μ columns) and fraction of sites destroyed.



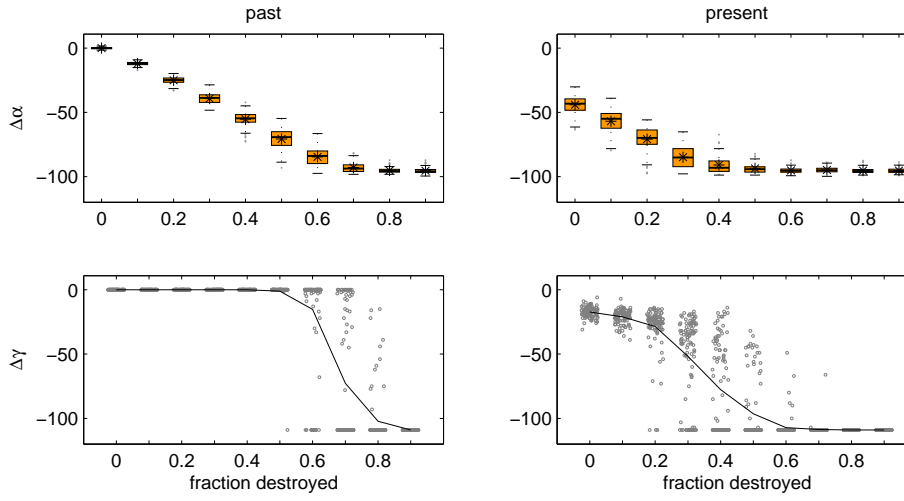
(a) Connectance

(b) Nestedness

Figure 4: Changes in local connectance and nestedness (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.



(a) Plants



(b) Animals

Figure 5: Changes in (a) plant and (b) animal diversities as a function of the fraction of sites destroyed, under past and present day phenologies (scenario of historical change). The boxplots for local diversity decline ($\Delta\alpha$) comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations, and the mean value (asterisk). Scatterplots of global diversity change ($\Delta\gamma$) are overlaid by the average trend (line).

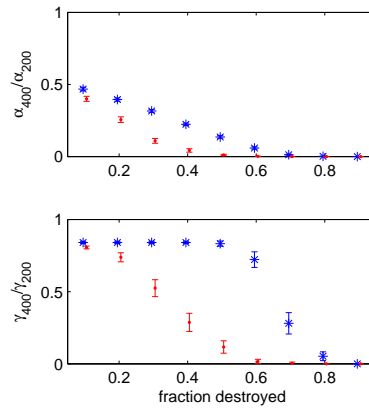
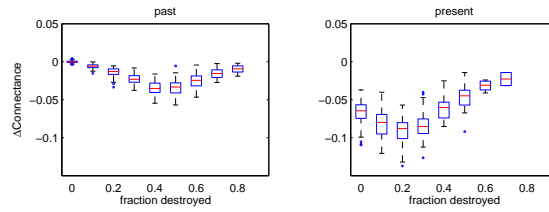
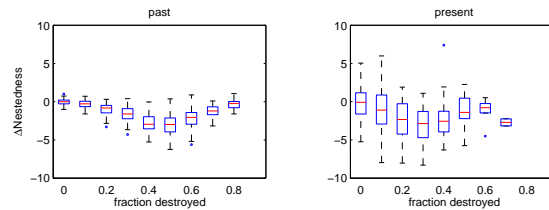


Figure 6: 95% confidence intervals for predicted (‘*’, independent effects) and observed (‘o’, simulation results) fractions of plant alpha and gamma diversities, 200 years after a given fraction of sites destroyed under the scenario of historical phenological shifts.



(a) Connectance



(b) Nestedness

Figure 7: Changes in local connectance and nestedness (averages over non-destroyed, non-empty sites) against the fraction of sites destroyed, under past and present day phenologies (scenario of historical change). The boxplots comprise the 1st, 2nd (median line) and 3rd quantile over 100 simulations.