# Habitat loss and the disassembly of mutalistic networks

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Recent studies have described the architecture of plant–animal mutalistic networks, but little is known on how such networks disassemble as a consequence of global change. This is a relevant question because 1) species interactions seem to be very susceptible to habitat loss, and 2) the loss of a critical fraction of interactions can abruptly change the topology of the entire network with potential consequences for its functioning. Here we develop a spatially explicit metacommunity model based on the structure of 30 real mutalistic networks. We find that there is a critical value of habitat destruction beyond which interactions are lost very fast. Second, there is a homogeneous distribution of the number of interactions per patch when the habitat is pristine, while this becomes very skewed at the brink of extinction. This increase in skewness is discussed in the context of potential indicators of network collapse.

The consequences of global change have mainly been assessed at the level of individual species. There is now ample evidence that global change affects the distribution, abundance, and physiology of species (Sala et al. 2000, Parmesan 2003). Less attention has been given to the consequences for species interactions, but a recent review has concluded that pairwise interactions are very sensitive to several drivers of global change (Tylianakis et al. 2008). The next step is to scale from such pairwise effects to entire networks of interactions.

Recently, several papers have shown that plant–animal mutalistic networks such as those describing pollination and seed dispersal have a well-defined architecture (Bascompte and Jordano 2007). As a preliminary assessment of the implications of network architecture for their robustness to habitat loss, Fortuna and Bascompte (2006) analyzed a spatially implicit meta-community model based on the structure of interactions of real mutalistic networks. This paper found that the number of species collapses after a critical fraction of habitat has been destroyed. However, this implicit approach can not inform on how interactions are lost since two previously interacting species can be found on separate habitat patches and therefore their interaction is lost despite both partners are regionally present. As Janzen (Janzen 1974) already noted it, there is a 'much more insidious kind of extinction: the extinction of ecological interactions'. To tackle the extinction of interactions we need a spatially explicit framework. This spatially explicit approach could ultimately inform us on how to scale from local to regional networks.

Previous studies have already considered spatially explicit models of seed dispersal. These papers have emphasized that

since the spatial distribution of individuals in a community may influence species interaction probabilities – which in turn will determine network patterns – bird density, landscape structure, and neighborhood effects will affect fruit-removal rates and seed dispersal (Carlo et al. 2007, Morales and Vázquez 2008, Morales et al. 2012). None of these papers, however, has focused on the disassembly of mutalistic interactions as a consequence of habitat transformation.

Here, we analyze a spatially explicit meta-community model with local interactions and dispersal to nearest patches to address how the mutalistic network disassembles as habitat is progressively destroyed (Fig. 1a). We also explore how the extant interactions are distributed across the landscape and how this distribution changes as more habitat is randomly destroyed. Although modeling spatially explicit mutalistic networks by using lattices ignores local heterogeneity in how interacting individuals encounter each other, this is the first theoretical attempt to explicitly tackle the problem in a synthetic way.

## Material and methods

The model landscape is a $100 \times 100$ square lattice with identical habitat patches (Fig. 1a). We assume that the patch size is large enough to harbor the entire network of mutalistic interactions when the habitat is pristine. Thus, initially all patches contain the whole network, i.e. each patch has all plants, all animals, and all realized interactions of a real mutalistic network. We used 30 real mutalistic networks as the skeleton for the network model (10 pollination networks and 20 seed-dispersal networks). These
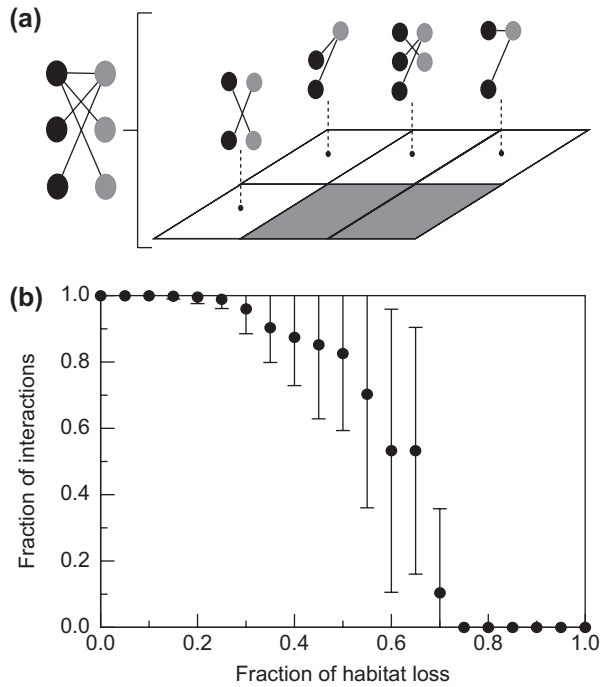
**(a)**

**(b)**

Figure 1. A spatially explicit approach to mutualistic networks (a). Each patch contains a local network, and the composite of all patches constitutes the regional network. Black and gray nodes represent plant and animal species, respectively. Destroyed sites are indicated by the gray lattice sites. The disassembly of mutualistic networks is represented as the fraction of remaining interactions as habitat is progressively destroyed (b). The figure summarizes the result for 20 metacommunities, and represents the average ($\pm$ SD) fraction of initial interactions for a specific fraction of randomly destroyed patches across 10 replicates and all networks.

networks show a broad variation in the number of interactions, ranging from 22 to 234 ($81.6 \pm 50.3$, mean and standard deviation, respectively; Supplementary Material Appendix Table 1).

On this landscape we simulated a cellular automata of the real network which evolves through discrete time steps exhibiting local species extinction and dispersal to the nearest patches. We use a Moore's neighborhood with reflecting boundary conditions. Essentially, this is a spatially explicit stochastic version of the implicit deterministic model studied by Fortuna and Bascompte (2006).

All plant and animal species are assigned an extinction probability drawn from a uniform distribution within the range [0.14–0.16]. Similarly for intrinsic colonization probabilities mediated by the partners (range [0.04–0.06]). Although the asymmetric network structure should make generalist species more regionally abundant and difficult to eliminate than specialist species, we did not want to impose the consequences of network structure on species life history traits. The distribution of extinction and colonization probabilities is the same across species and networks and it allows the coexistence of all species and interactions regionally in the absence of habitat destruction for the entire set of communities considered. That is, before starting destroying any habitat patch, we must ensure that none species nor interactions go extinct regionally (from the entire landscape). At each time step, extinction and

colonization events are simultaneous for both animals and plants. Thus, a plant species present in a site has a given probability to become extinct. Similarly, an empty site can become colonized from each one of its 8 nearest neighbors in which both the plant and at least one of its animal partners are present. Specifically, the probability that plant $l$ colonizes a non-destroyed, empty patch $m$, $p(i, m)$, was modeled using the following saturating function:

$$p(i, m) = 1 - \left[ \prod_{n=1}^{N} \prod_{j=1}^{J} \left( 1 - \frac{c_{ij}}{j} \right) \right]$$

where $N$ is the number of nearest neighbor patches in which both the plant and at least one of its animal partners are present, $J$ is the total number of animals $j$ interacting with plant $i$ that are present in patch $n$, and $c_{ij}$ is the intrinsic colonization probability of plant $i$ mediated by animal $j$. In this way, colonization events from each of the animal partners are not treated as independent events, so the larger the number of animal partners within a source site, the smaller the increase in the probability of colonizing from such a patch. This non-linearity in the colonization probabilities for the plants induced by the animals and for the animals induced by the plants is intended to limit the colonization abilities since, for the sake of simplicity, we have neither considered competitive interactions between plants for resources (light, water, …) nor between animals for the plant resources. Similarly, an animal $j$ has a probability of becoming extinct from an occupied patch; likewise, a site $m$, in which at least one of the $I$ plant partners are present, can become occupied by an animal $j$ from those neighboring sites $N$ in which it is present, with a probability $p(j, m)$ that depends asymptotically on the number of mutualistic plant partners $i$ that the empty site (recipient site) harbors:

$$p(j, m) = 1 - \left[ \prod_{n=1}^{N} \prod_{i=1}^{I} \left( 1 - \frac{c_{ji}}{i} \right) \right]$$

where $c_{ji}$ is the intrinsic colonization probability of animal $j$ mediated by the presence of the plant $i$.

On this landscape we destroy habitat patches randomly at intervals of 5%. That is, we delete 5% of randomly chosen cells at once and then we start the simulation to explore how the steady state reached regionally changes by the destroyed habitat. After that, we start again the simulation from the beginning but removing first, in this case, 10% of cells, and so on until we destroy 95% of habitat. Spatially-correlated habitat destruction does not change qualitatively the threshold for network disassembly (Supplementary material Appendix A1). The number of time steps analyzed until the new steady state is reached has been determined after exploratory tests confirming that all regional abundances converge to a stochastic steady state. We used 10 replicates for each network and value of random habitat destruction. The values plotted in Fig. 2 are the cumulative distribution of interactions across all patches across all replicates (while the values plotted in Fig. 1b are the average (and SD) across such replicates).

The present model is more appropriate for describing plant-seed dispersers than for plant-pollinators, since pollination alone does not allow plants to recolonize empty
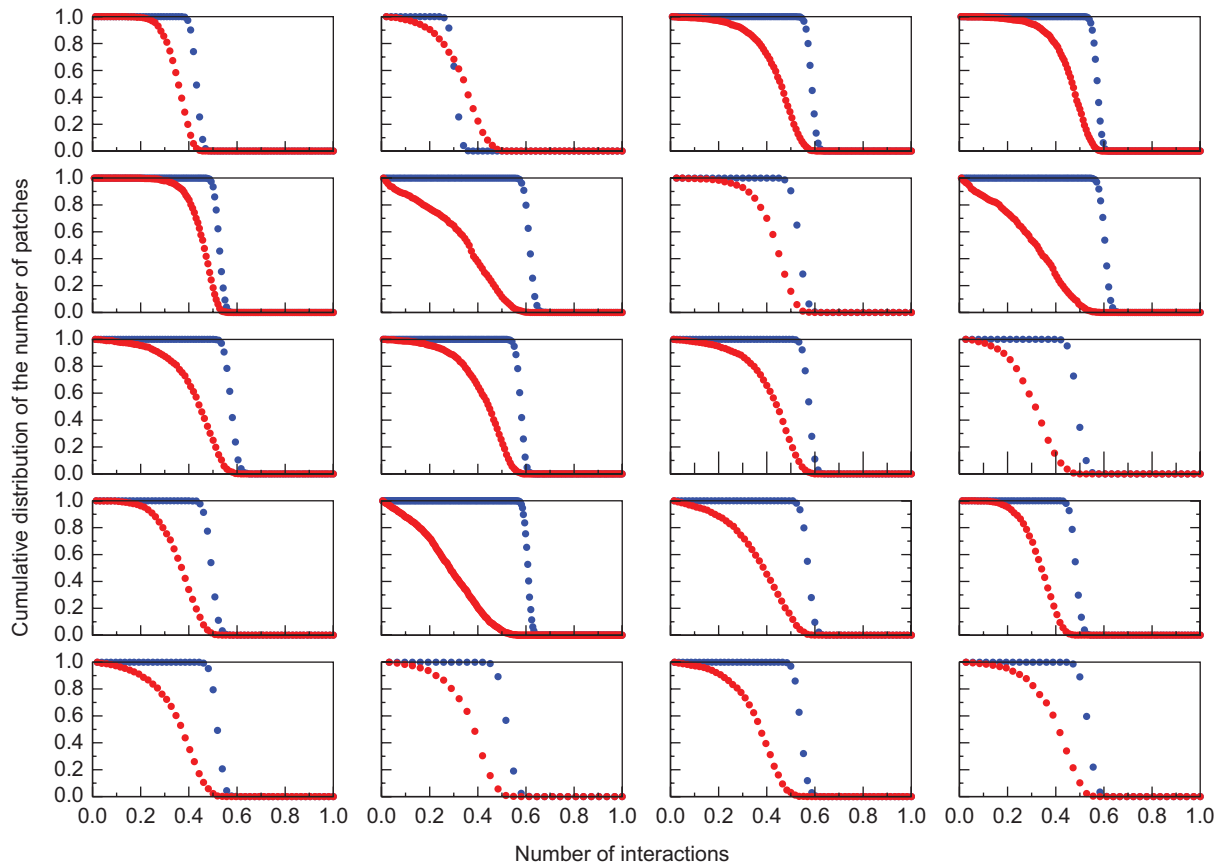
Figure 2. Spatial distribution of mutualistic interactions. Each panel represents the spatially explicit metacommunity model based on one real plant–animal mutualistic network. We used 10 replicates for each network and value of random habitat destruction (at intervals of 5%). The values plotted are the cumulative distribution of interactions across all patches across all replicates. The distribution of the number of interactions per patch is represented for two scenarios: when all habitat is pristine (blue), and at the brink of extinction, i.e., for the destruction value prior to the first global extinction of interactions (red). As noted, the distribution of interactions per patch becomes highly skewed near the extinction threshold.

patches. But because it does reduce the risk of local extinction of plant populations as a consequence of failure to reproduce, we have decided to include in our analysis plant–pollinator networks as well.

## Results

The cumulative network – the aggregate network across all lattice patches – retains all the original interactions until about half the landscape has been destroyed (Fig. 1b). Of course this value of habitat destruction depends on the characteristics of each community (number of species, connectance, …). Interestingly, beyond such a critical destruction value there is a fast collapse in the number of interactions (Fig. 1b), so that the network dismantles very fast. The existence of this network collapse seems insensitive to network properties but the critical value of habitat destruction at which it takes place is significantly correlated to the number of interactions of the network ($r = 0.523$, $p = 0.003$) and also to network connectance ($r = 0.417$, $p = 0.022$). The higher the number of links or network connectance, the more habitat has to be destroyed to lead all interactions extinct. So far, this is a macroscopic figure across the local

networks, so the next question is to look at how such interactions are distributed through the landscape.

When habitat is pristine, i.e. no habitat has yet been destroyed, the frequency distribution of the number of interactions per patch (blue dots in Fig. 2) is quite homogeneous, with a well-defined average local number of interactions. The landscape is composed of a series of local networks quite similar to the cumulative network (the identity of species and interactions may change through space, but the local networks are similar).

The situation is different at the brink of extinction, that is, at the value of habitat loss at which further destruction induces the first extinctions of interactions. In this case, the frequency distribution of the number of interactions per patch (red dots in Fig. 2) follows a skewed distribution. This means that the majority of patches harbor a simple local network with only a few interactions, but a few sites contain a much larger number of interactions. The disassembly of the network does not take place at a constant rate through the landscape. This result has implications for quantifying the amount of habitat that needs to be sampled in order to have a representation of the mutualistic network at a regional level: the mean number of sampled patches required to recover the complete set of links of the metacommunity is
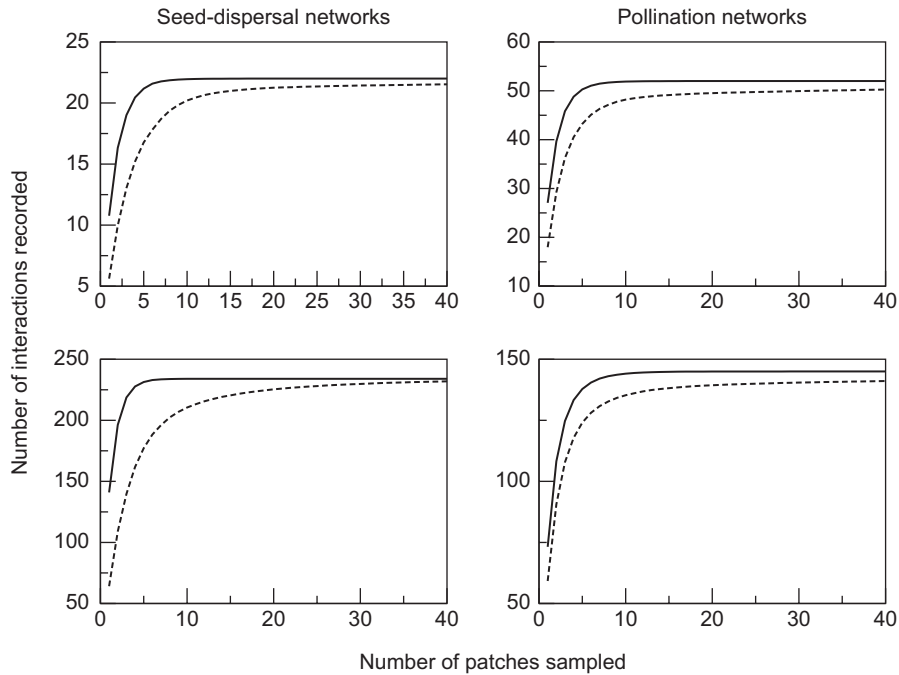
Figure 3. Capturing the structure of mutualistic networks depends on sampling effort in space and the amount of habitat progressively destroyed: the mean number of sampled patches required to recover the complete set of links of the metacommunity is significantly larger when the habitat is at the brink of extinction (dashed line) as opposed as when habitat is pristine (solid line). Patches were randomly sampled 1000 times for calculating the mean number of interactions per patch. This result is shown for the largest (at the bottom) and the smallest (on the top) seed-dispersal and pollination communities.

significantly larger when the habitat is at the brink of extinction as opposed to when habitat is pristine ($t_{44} = -4.820$, $p < 0.001$; Fig. 3). This result is not correlated to the number of interactions of the community ($r = 0.163$, $p = 0.456$ when the habitat is pristine, and $r = -0.056$, $p = 0.799$ at the brink of extinction; Supplementary material Appendix A1 Fig. A1). Results are robust when habitat is destroyed in a spatially-correlated way (Supplementary material Appendix A1 Fig. A2).

## Discussion

As with other interaction networks such as food webs, mutualistic networks are compiled over a spatial domain and there is no information on how their structure changes across the sampling area. To our knowledge, only a few studies have analyzed how the structure of these mutualistic networks depends on sampling effort in space (Nielsen and Bascompte 2007, Blüthgen et al. 2008, Olesen et al. 2011). These studies analyzed how network properties such as nestedness and the total number of interactions recorded scale with sampling effort. Nestedness has been found to be quite robust and stabilize quickly. Despite these papers, there is almost no information on how network structure changes, or the number of interactions is reduced, as habitat is progressively destroyed. Yet, this is the sort of question we need to address to understand the pervasive community-wide consequences of global change.

Our results show that the level of spatial sampling needed to have a good approximation of the global, composite network is quite different depending on the amount

of habitat loss. While for pristine habitats each patch provides approximately the same amount of information on the number of interactions and presumably on the structure of the network, the situation is quite different at the brink of extinction. Now sampling a few patches will not provide enough information to reconstruct the regional network. One needs a very detailed sampling to recover this regional network.

There is growing concern on the possibilities that human alteration may push ecosystems towards a critical state where an ecosystem shift can occur (Scheffer et al. 2001). In the last few years, there has been a rich body of work trying to find early-warning signals of ecosystem shifts (Scheffer et al. 2009, Carpenter et al. 2011). The bulk of such studies, however, are non-spatial, and only recently ecologists have started to explore similar indicators of spatial transitions (Guttal and Jayaprakash 2009, Dakos et al. 2009). Our results show that at the brink of extinction, the frequency distribution of the number of interactions per patch is quite skewed. Future studies should explore the generality of this result and whether it is exclusively found for abrupt transitions as opposed to smoothed ones.

The positive correlation between the extinction threshold and the connectance of the network suggests that increasing network connectance leads to global species persistence even for higher levels of habitat loss. This result echoes previous findings by Dunne et al. (2002) finding that connectance increases food-web robustness to species loss in non-spatial topological models.

One limitation of lattice models such as the one here employed is that it misses within-patch heterogeneities. Therefore, it would be useful to expand our results using

more realistic approaches such as individual-based models (Carlo et al. 2007, Morales and Vázquez 2008). Those models would allow us to quantify the effect of the neutral dynamics in spatially-explicit landscapes and to what extent our approach would be sufficient to predict phase transitions in ecological networks.

Our approach assumes that destroyed cells cannot be recolonized. This is a starting point in the investigation of the role of the spatial dimension on structuring mutualistic networks that certainly does not take into account the truly ecological complexity. For example, Carlo and Yang (2011) showed that degraded habitats can favor the presence of some species and some interaction patterns such as an increased presence of generalists.

Since species traits might be responsible for the differences in the number of links among species, and hence, could affect the susceptibility to collapse in the face of habitat destruction, futures studies should explore the role of a particular species in driving the network collapse. Neutral biodiversity theory offers an alternative approach based on differences in abundances rather than traits (Hubbell 2001). Therefore, to what extent the slope of the decay and the subsequent network collapse is driven by neutral or niche dynamics is still unclear and certainly deserves to be explored.

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Supplementary material (available as Appendix oik-O00042 at < www.oikosoffice.lu.se/appendix >). Appendix A1.