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LETTER

Habitat loss and the structure of plant–animal mutualistic networks

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Abstract

Recent papers have described the structure of plant–animal mutualistic networks. However, no study has yet explored the dynamical implications of network structure for the persistence of such mutualistic communities. Here, we develop a patch-model of a whole plant–animal community and explore its persistence. To assess the role of network structure, we build three versions of the model. In the first version, we use the exact network of interactions of two real mutualistic communities. In the other versions, we randomize the observed network of interactions using two different null models. We show that the community response to habitat loss is affected by network structure. Real communities start to decay sooner than random communities, but persist for higher destruction levels. There is a destruction threshold at which the community collapses. Our model is the first attempt to describe the dynamics of whole mutualistic metacommunities interacting in realistic ways.

Keywords

Community structure, complex networks, habitat fragmentation, metacommunity, nestedness, pollination, seed dispersal.

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INTRODUCTION

Although most mutualistic studies have focused on a single plant–single animal interaction, there is now a long history of community-level studies of mutualisms (e.g. Feinsinger 1978; Petanidou & Ellis 1993; Bronstein 1995; Waser *et al.* 1996). More recently, this community-level approach has benefited from a network perspective (Bascompte *et al.* 2003; Jordano *et al.* 2003; Vázquez & Aizen 2004). Mutualistic networks can be described by two properties. First, they are very heterogeneous; i.e. the bulk of species have a few interactions, but a few species are much more connected than expected by chance (Jordano *et al.* 2003). Second, mutualistic networks are highly nested, that is, specialists interact with proper subsets of the species interacting with generalists (Bascompte *et al.* 2003). Given the structure described in these papers, an enduring question is to decipher what consequences this structure has for the dynamics and persistence of mutualistic communities. Recent work has started to answer this question by exploring the topological consequences of species removal in abiotic networks (Albert *et al.* 2000), food webs (Solé & Montoya 2001; Dunne *et al.* 2002) and, more recently, mutualistic networks (Memmott *et al.* 2004; Jordano *et al.* 2005). In this paper, we focus on the role of network structure for the response of a mutualistic community to habitat loss, one of the major threats to biodiversity and an important cause of mutualism disruption (Bond 1994; Kearns *et al.* 1998; Renner 1998; Ashworth *et al.* 2004). In contrast with previous work on network structure and species removal, we use a dynamic model describing changes in species abundance. Previous models of mutualistic interactions mainly describe the dynamics of a plant and an animal (Armstrong 1987; Nee *et al.* 1997; Amarasekare 2004). Only a few modelling exercises have addressed the concept of diffuse coevolution (Janzen 1980) by considering sets of interacting species (Levin *et al.* 1990; Iwao & Rausher 1997). However, in the latter case one assumes that species interact randomly, without any type of structure. Models of habitat loss, in turn have either described single species (e.g. Lande 1987; Bascompte & Solé 1996) or several species from the same trophic level (Armstrong 1987; Tilman *et al.* 1994; Stone 1995; however, see Levin *et al.* 1990; Ringel *et al.* 1996; Iwao & Rausher 1997; Melián & Bascompte 2002).

Here, we develop a spatially implicit metacommunity model describing an entire mutualistic network. As a starting point, we consider the network of interactions of two real communities, one corresponding to plant pollination and the other to plant seed dispersal. The exact pattern of

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interactions of these two networks and randomizations by means of two different null models are used as templates to build three sets of the metacommunity model. Null models are pattern-generating models that deliberately exclude a mechanism of interest, and allow for randomization tests of ecological and biogeographical data (Gotelli 2001). We first explore the parameter space compatible with the persistence of the dynamical model for the real communities. Second, we explore the response of an otherwise persistent community to habitat destruction. By comparing the response of the real community with the two randomizations, we can assess to what extent network structure affects the response of the metacommunity to habitat loss.

MATERIALS AND METHODS

Data set

The first mutualistic community corresponds to the plant–pollinator network of Zackenberg in Greenland. It is composed of $P = 31$ plant species, $A = 76$ insect species and $L = 456$ interactions (J. M. Olesen and H. Elberling, unpublished data; Fig. 1a). The second community corresponds to the plant–seed disperser network of a high-elevation Mediterranean forest (Nava de las Correhuelas, Sierra de Cazorla, south-eastern Spain). It is composed of $P = 25$ plant species, $A = 33$ bird species and $L = 154$ interactions (P. Jordano, unpublished data; Fig. 1d). Our metacommunity model has two variants. The first describes the exact wiring of these two networks (i.e. it exactly reproduces which animal interacts with each plant). The second type of metacommunity model describes a randomization of the observed network of interactions. This randomization is achieved by means of two different null models.

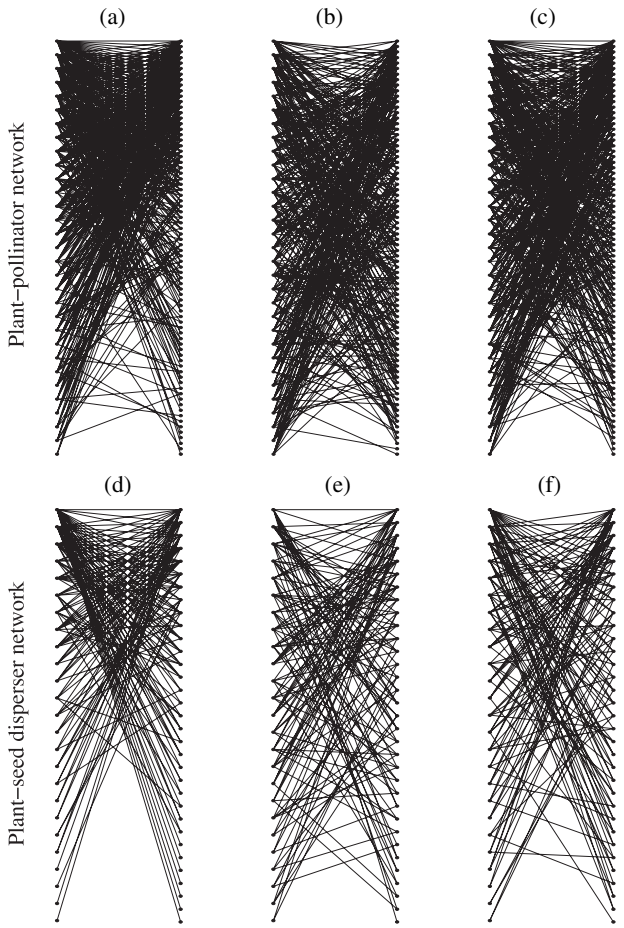

Figure 1 Bipartite graphs depicting real plant–animal mutualistic networks (a, d), and networks built using null model 1 (b, e), and null model 2 (c, f). Species in each set are represented by nodes arranged along the vertical lines (plants on the left and animals on the right) and shown in decreasing number of interactions per species. A plant and an animal interact if they are linked by a line.

Null models

Null model 1 (lacks degree and nestedness)

This model probabilistically maintains the observed number of interactions, but these are completely reshuffled among all animal–plant pairs; i.e. each animal–plant pair has the same probability to interact. This probability is estimated as the number of interactions in the original network (L) divided by the number of possible pairs ($P \times A$, i.e. the network connectance Fonseca & John 1996). This model neither maintains the number of interactions per species (degree hereafter) nor nestedness. A replicate of this null model for each mutualistic network is shown in Fig. 1b,e.

Null model 2 (lacks nestedness)

This model probabilistically maintains the observed total number of interactions (as before) and approximately maintains the number of interactions per species (degree), but it does not maintain nestedness. Now, the probability of drawing an interaction between plant i and animal j is the arithmetic mean of the interaction probability of plant i (i.e. fraction of ones in row i) and animal j (i.e. fraction of ones in column j). Thus, the probability of drawing an interaction is proportional to the degree of both the animal and the plant species. Figure 1(c, f) shows a replicate of this null model for each mutualistic network. For additional details on null models 1 and 2, see Bascompte *et al.* (2003).

Metacommunity model

Models addressing pair-wise interactions on a patchy landscape have been described by a set of differential

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equations representing the fractions of empty patches, patches occupied only by the plant, and patches occupied by both the plant and the animal (Nee *et al.* 1997; Amarasekare 2004). This is a suitable approach when considering a pair-wise interaction. But the number of equations needed to describe the system increases exponentially with the number of species involved (the number of equations in networks with the same number of plant and animal species is equal to $2^n - 1$, where n is the total number of species). Thus, we need a simpler framework to describe the spatial dynamics of mutualistic interactions in species-rich communities.

We consider mutualists inhabiting a landscape consisting of an infinite number of identical, well-mixed patches. The interaction is obligate for the animal (i.e. the animal cannot survive in a patch in the absence of all the plant species it interacts with), while the plant is able to survive in the absence of the animal but cannot reproduce without it. Following the patch occupancy model by Armstrong (1987), see also Amarasekare (2004), $c_{p_i a_j}$ is the per capita colonization rate of plant i when pollinated or dispersed by animal j. Similarly, c_{a_j} is the per capita colonization rate of animal j (it may only colonize patches occupied by the plants it interacts with).

The above parameters encapsulate both reproduction and subsequent establishment of offspring via random dispersal. Plant species i becomes extinct in patches at a per capita rate e_{p_i} (e_{a_j} for animal species j). These extinction rates summarize all forms of density-independent mortality experienced by adult plants and animals. It is assumed that the extinction of plants from a patch causes the subsequent extinction of the animal depending exclusively on that plant (Armstrong 1987).

We have developed a set of differential equations describing the fraction of the total available patches occupied by plant i (p_i) and animal j (a_j) reproducing the pattern of species interactions described above. d represents the fraction of patches permanently lost throughout habitat loss. To illustrate the structure of the model, next we consider some simple scenarios (see Fig. 2 for a schematic representation): (i) one specialist plant and one specialist animal (Fig. 2a)

$$\frac{\mathrm{d}p}{\mathrm{d}t} = c_{pa}a(1 - d - p) - e_p p, \tag{1}$$

$$\frac{\mathrm{d}a}{\mathrm{d}t} = c_a a(p - a) - e_a a. \tag{2}$$

Because the animal can only occupy patches occupied by the plant, the fraction of patches occupied by the animal (a) is a subset of the patches occupied by the plant (p). Equation 1 has two terms, a colonization (positive) term and an extinction (negative) term. For the plant, the colonization term is equal to the colonization rate mediated by the animal (e.g. seed dispersal) (c_{pa}) times the fraction of source patches, i.e. patches occupied by the animal (and the plant) a, times the fraction of sites available for colonization, i.e. empty, non-destroyed sites ($1 - d - p$). The extinction term in eqn 1 is the extinction rate times the fraction of sites occupied. This assumes that the extinction rate of the plant is the same regardless of whether animals are present or absent. Similarly, the animal can colonize non-destroyed sites occupied by the plant and free of itself ($p - a$) (see Bascompte & Solé 1998, for a full derivation of a similar one predator–prey model). This set of equations builds from the pioneering metapopulation model by Levins (1969) and its extension by Lande (1987) introducing a fraction of patches destroyed.

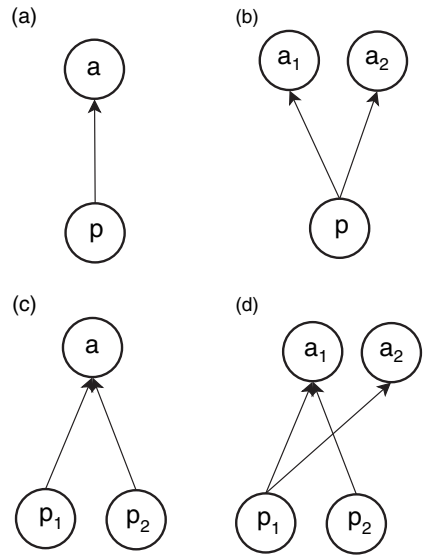

Figure 2 Mutualistic modules between plants (p_i) and animals (a_j): (a) a specialist plant and a specialist animal; (b) a generalist plant and two specialist animals; (c) two specialist plants and one generalist animal; (d) one specialist, one generalist plant and one specialist, one generalist animal.

Similarly, one can derive the next scenarios with three and four species: (ii) one generalist plant and two specialist animals (Fig. 2b)

$$\frac{\mathrm{d}p}{\mathrm{d}t} = (c_{pa_1}a_1 + c_{pa_2}a_2)(1 - d - p) - e_p p, \tag{3}$$

$$\frac{\mathrm{d}a_1}{\mathrm{d}t} = c_{a_1}a_1(p - a_1) - e_{a_1}a_1. \tag{4}$$

The dynamics of animal 2 would be described by an equation equivalent to eqn 4. (iii) Two specialist plants and one generalist animal (Fig. 2c)

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$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = c_{p_1 a}\left(\frac{p_1 a}{(p_1 + p_2) - (p_1 p_2)}\right)(1 - d - p_1) - e_{p_1} p_1 \qquad (5)$$

and similar for plant 2.

$$\frac{\mathrm{d}a}{\mathrm{d}t} = c_a a((p_1 + p_2) - (p_1 p_2) - a) - e_a a. \qquad (6)$$

In this case, because the animal can occupy patches occupied by both plants, the fraction of patches occupied by the animal a and the plant p_1 is a subset of the sum of the patches occupied by each plant ($p_1 + p_2$) minus the patches occupied by both plants ($p_1 p_2$), i.e. the total available patches for the animal. (iv) One generalist, one specialist plant and one generalist, one specialist animal (Fig. 2d)

$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = \left(c_{p_1 a_1}\frac{p_1 a_1}{(p_1 + p_2) - (p_1 p_2)} + c_{p_1 a_2}\frac{p_1 a_2}{(p_1 + p_2) - (p_1 p_2)}\right) \times (1 - d - p_1) - e_{p_1} p_1 \qquad (7)$$

$$\frac{\mathrm{d}a_1}{\mathrm{d}t} = c_{a_1} a_1((p_1 + p_2) - (p_1 p_2) - a_1) - e_{a_1} a_1. \qquad (8)$$

The other animal and plant species would be described by equations similar to eqns 4 and 5 respectively.

The above equations can be extended for the general case of i plants and j animals in species-rich mutualistic communities:

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = \sum_{j=1}^{n}\left(c_{p_i a_j}\frac{p_i a_j}{\Omega}\right)(1 - d - p_i) - e_{p_i} p_i, \qquad (9)$$

$$\frac{\mathrm{d}a_j}{\mathrm{d}t} = c_{a_j} a_j(\Omega - a_j) - e_{a_j} a_j, \qquad (10)$$

where Ω is the union of the patches occupied by n plant species interacting with the same j animal species (i.e. the total available patches for the j animal).

For each species we randomly sample an e/c rate from a uniform distribution with a chosen mean and a variance of 10%. We also randomly assign an initial abundance value. Changing the values used throughout this paper does not qualitatively change the results presented here (for a combination of e_{p_i}/c_{p_i} and e_{a_j}/c_{a_j} values allowing metacommunity persistence).

As in any other modelling exercise, the present model makes some simplifications that should be kept in mind to assess the results. For example, we assume that animals go extinct from a patch in which all the plants it interacts with go extinct. This follows previous models (e.g. see Armstrong 1987; Amarasekare 2004). Our model also assumes that plant species do not compete over mutualistic animal species and vice versa, i.e. any patch can be colonized by any species regardless of the fact that other species are present. This increases the coexistence of the system without imposing any tradeoff, and allows us to focus on the observed network of interactions as the main factor determining species richness.

RESULTS AND DISCUSSION

By numerically solving eqns 9 and 10 we have explored the range of parameter space compatible with the persistence of the metacommunity model using the real communities (Fig. 3a–d). The community persists for a wide range of e/c rates for both plant and animal species (Fig. 3b illustrates the case of the pollination community). Before these rates are high enough for all species going extinct (Fig. 3d), there is a narrow range of the parameter space at which some

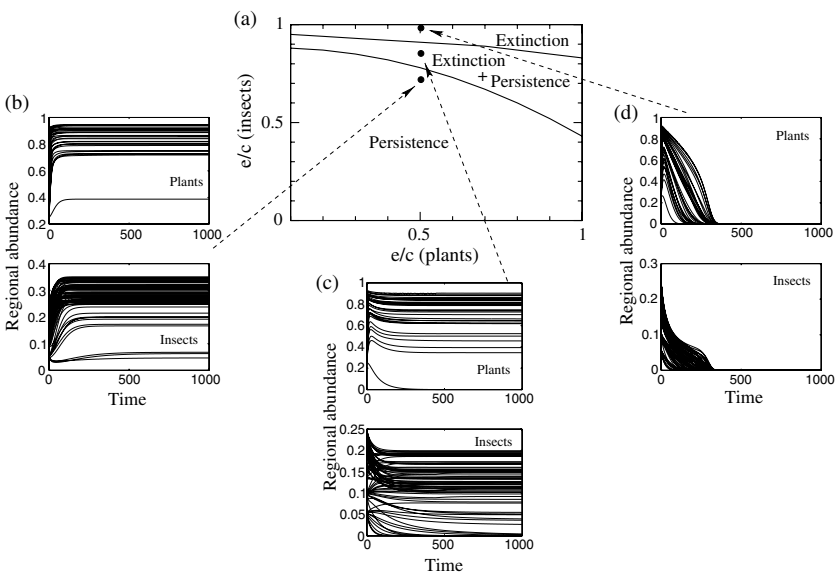

Figure 3 Dynamics of the plant pollinator metacommunity model using the real network of interactions (Fig. 1a). (a) Parameter space showing the domains of coexistence and extinction. (b–d) Dynamics for the parameter combination represented by the dot. Each species is randomly assigned a parameter value sampled from the following mean value (and a variance of 10%): (b) $e_{p_i}/c_{p_i} = 0.5$ and $e_{a_j}/c_{a_j} = 0.7$; (c) $e_{p_i}/c_{p_i} = 0.5$ and $e_{a_j}/c_{a_j} = 0.85$; (d) $e_{p_i}/c_{p_i} = 0.5$ and $e_{a_j}/c_{a_j} = 1$.

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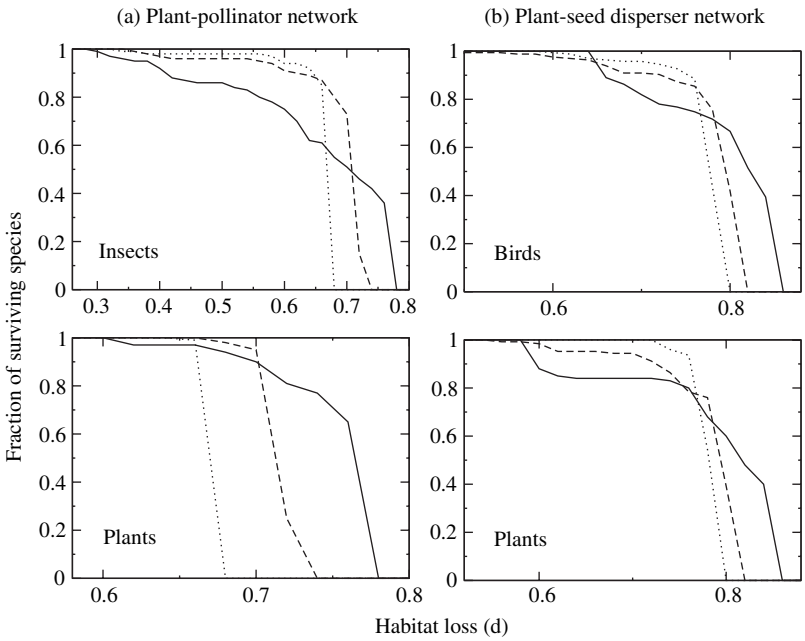

Figure 4 Effect of habitat loss (d) on the fraction of species surviving for the real network (solid line; average of 10 replicates), and the randomizations using null model 1 (dotted line; average of 10 replicates), and null model 2 (broken line; average of 10 replicates), for both the plant-pollinator network (a), and the plant seed disperser network (b). Inset names indicate the taxa represented. Parameters for each species are again sampled from a uniform distribution with mean $e_{p_i}/c_{p_i} = e_{a_j}/c_{a_j} = 0.5$ and 10% of variance for the plant pollinator network, and mean $e_{p_i}/c_{p_i} = e_{a_j}/c_{a_j} = 0.25$ and 10% of variance for the plant seed disperser network.

plant or animal species go extinct while others persist (Fig. 3c).

Once we have assessed the domain of community persistence, we can explore how an otherwise persistent community responds to habitat loss. Figure 4 shows the decay in species richness with habitat loss. The figure depicts the average of 10 replicates for both real networks of interactions and the two null models. All real and randomized communities show a nonlinear pattern in species extinction as more habitat is destroyed. The rate at which species go extinct (i.e. the slope of the curve) is higher as more habitat has been already destroyed. This result is in agreement with previous models of habitat loss for communities of a single trophic level experiencing a colonization-extinction tradeoff (Tilman *et al.* 1994; Stone 1995). However, the decay shown here is much faster, that is, mutualistic communities suddenly collapse at critical destruction values. This pattern is similar to the pattern obtained with metacommunity models emphasizing recruitment limitation and thus relaxing competitive hierarchies (Solé *et al.* 2004).

In the real communities, species start to decay sooner with habitat loss, but last longer (Fig. 4); that is, the community extinction threshold at which all species go extinct takes place for higher destruction values than for the randomized communities. Not surprisingly, null model 2 is half way between null model 1 and the real community. The structure of mutualistic networks described in previous papers (Bascompte *et al.* 2003; Jordano *et al.* 2003) seems to have implications for their responses to habitat loss. Real, structured communities go extinct for higher values of habitat destruction compared with otherwise similar, non-structured communities.

There are two properties of the real network that can explain the above differences in species decline. First, real communities show a high heterogeneity in species degree (Jordano *et al.* 2003); that is, a few species are much more connected than expected by chance. In fact, the last few species going extinct are the most generalist species. As they rely on so many species, some of the few available patches will at least contain one of the species they interact with. Similarly, for the very same reason, some species are less connected than expected by chance (specially by null model 1). These specialists go extinct first. Second, real communities are very nested (Bascompte *et al.* 2003), which implies that there is a core of generalist animals and plants interacting among themselves. This dense core is very robust to habitat loss. Network structure has also been recently adduced to explain empirical plant species decline with habitat loss in a plant pollinator community (Ashworth *et al.* 2004).

To sum up, the structure of plant–animal mutualistic networks affects the rate of species decline with habitat loss. Further work building on our approach will probably strength the relationship between network structure and community dynamics. To our knowledge, this is the first time that a model has been produced to describe the dynamics of whole mutualistic metacommunities interacting in realistic ways. Our modelling exercise may be useful in future studies focussing on the co-extinction patterns of seed dispersal or pollination disruption. These results may shed light on the multiple ways biodiversity responds to anthropogenic disturbances.

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