

Habitat destruction and extinction in competitive and mutualistic metacommunities

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Abstract

Because habitat loss is a leading cause of extinction, it is important to identify what kind of species is most vulnerable. Here, I use algebraic and graphical techniques to study metacommunity models of weak competition or locally facultative mutualism in which species may coexist within patches. Because a competition–colonization trade-off is not required for regional coexistence of competitors, poor competitors are often regionally rare and most prone to extinction, in contrast to results from previous models of strongly competitive metapopulations. Metacommunities of mutualists can suffer the abrupt extinction of both species as habitat destruction is increased. These highlight the importance of identifying the mechanisms by which species coexist to predict their response to habitat loss.

Keywords

Habitat destruction, extinction, competition, mutualism, metapopulation, model.

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INTRODUCTION

Soon after the metapopulation concept was introduced for a single species (Levins 1969, 1970), it was extended to cover interspecific competition (Levins & Culver 1971). In general, species competing in a patchy environment can affect each other in three ways:

- (1) by increasing the extinction rate of the other species in patches where they co-occur,
- (2) by decreasing the chance a propagule will successfully colonize a patch occupied by the other species and
- (3) by decreasing the rate at which propagules are produced in jointly occupied patches. The first form of competition is called *extinction competition*, while the second and third have not been clearly distinguished and both have been called *migration competition* (Levins & Culver 1971; Slatkin 1974; Hanski 1983). I will call the second form of competition *establishment competition* and the third form of competition *propagule production competition*. In their analysis, Levins and Culver (1971) tacitly assumed that the species are independently distributed. This simplifies the mathematics by reducing the number of equations, but in general the assumption of independence is incorrect (Slatkin 1974). Here, I will show that independence holds under pure propagule production competition when dispersal is global.

In the last decade, metacommunity models have been used to examine the effect of habitat destruction on

extinction in competitive metacommunities (Nee & May 1992; Tilman *et al.* 1994, 1997; Neuhauser 1997; Klausmeier 1998). Competition is strong in these models; they assume severe extinction and colonization competition so that species cannot coexist within local patches and form a competitive hierarchy. Regional coexistence is possible between species that show a competition–colonization trade-off; inferior competitors survive because their greater colonization ability allows them to colonize empty patches before a superior competitor arrives (Skellam 1951; Hutchinson 1951; Hastings 1980; Tilman 1994). Habitat destruction effectively lowers the colonization rate of all species. Thus, these models predict that the first species driven extinct is usually the best competitor/poorest colonist (Nee & May 1992; Tilman *et al.* 1994, 1997; see Klausmeier 1998 for exceptions in communities of three or more species).

To complement these results, in this paper I develop and analyse a model of weakly competing metapopulations in which species can coexist within patches. By changing parameter values so that species benefit each other, the same equations can be used to model metapopulation dynamics of locally facultative mutualists. As in previous models, species with low colonization ability are most prone to extinction due to habitat loss. However, because the competition–colonization trade-off is not required to allow regional coexistence, this model does not predict the biased extinction of superior

competitors. In fact, I argue that if all else is equal, locally rare competitors will be regionally rare and most prone to extinction. Among mutualists, either the poorer colonist goes extinct first or both species go extinct simultaneously as habitat destruction is increased.

THE MODEL

Consider an infinite number of identical patches, each capable of supporting viable populations. Each patch may be empty (proportion P_0), occupied by a population of either species 1 or species 2 alone (proportions P_1 and P_2), occupied by populations of both species (proportion P_{12}), or permanently destroyed (proportion D). I assume that species can stably coexist within a patch, so that extinction and establishment are not affected by the presence of the other species. This is pure propagule production interaction. Patches occupied by species i alone produce propagules at rate c_i . Assuming that propagule production is proportional to the number of individuals in a patch, locally abundant species will have a higher c than locally rare species if all else is equal. Patches occupied by both species produce species i propagules at rate $f_{ij}c_i$. Thus f_{ij} measures how much species j changes species i 's propagule production where they locally co-occur. For example, suppose species 1 has a density of 1000 individuals per patch when alone and 800 individuals per patch when co-occurring with species 2, and species 2 has a density of 100 individuals per patch when alone and 60 individuals per patch when co-occurring with species 1. Then $f_{12} = 0.8$ and $f_{21} = 0.6$, and if individuals of both species create propagules at the same rate, then $c_1 = 10c_2$. Propagules are dispersed globally. A propagule of species i which lands on a patch without species i already present successfully colonizes that patch. Species i goes extinct within patches at rate m_i . Figure 1 summarizes the transitions between states.

These assumptions result in the following equations:

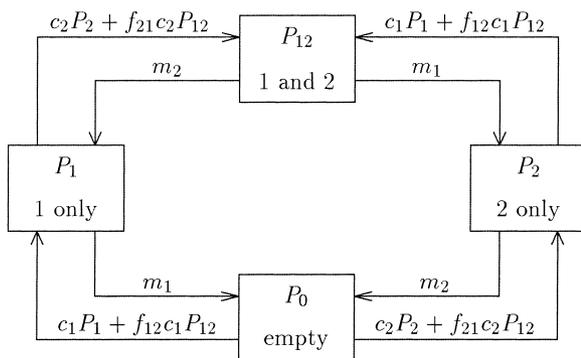


Figure 1 State transition rates.

$$\begin{aligned} \frac{dP_1}{dt} &= c_1(P_1 + f_{12}P_{12})P_0 - m_1P_1 - c_2(P_2 + f_{21}P_{12})P_1 \\ &\quad + m_2P_{12} \\ \frac{dP_2}{dt} &= c_2(P_2 + f_{21}P_{12})P_0 - m_2P_2 - c_1(P_1 + f_{12}P_{12})P_2 \\ &\quad + m_1P_{12} \end{aligned} \quad (1)$$

$$\begin{aligned} \frac{dP_{12}}{dt} &= c_1(P_1 + f_{12}P_{12})P_2 + c_2(P_2 + f_{21}P_{12})P_1 \\ &\quad - (m_1 + m_2)P_{12} \\ P_0 &= 1 - D - P_1 - P_2 - P_{12} \end{aligned}$$

It is useful to consider the occupancy of non-destroyed patches; let P' be occupancy proportions conditioned on the site not being destroyed ($P' = P/(1-D)$). Then

$$\begin{aligned} \frac{dP'_1}{dt} &= c_1(1-D)(P'_1 + f_{12}P'_{12})P'_0 - m_1P'_1 - c_2(1-D) \\ &\quad (P'_2 + f_{21}P'_{12})P'_1 + m_2P'_{12} \\ \frac{dP'_2}{dt} &= c_2(1-D)(P'_2 + f_{21}P'_{12})P'_0 - m_2P'_2 - c_1(1-D) \\ &\quad (P'_1 + f_{12}P'_{12})P'_2 + m_1P'_{12} \end{aligned} \quad (2)$$

$$\begin{aligned} \frac{dP'_{12}}{dt} &= c_1(1-D)(P'_1 + f_{12}P'_{12})P'_2 + c_2(1-D) \\ &\quad (P'_2 + f_{21}P'_{12})P'_1 - (m_1 + m_2)P'_{12} \end{aligned}$$

$$P'_0 = 1 - P'_1 - P'_2 - P'_{12}$$

If $D = 0$, (1) and (2) are identical and $P = P'$. Let $p'_1 = P_1 + P'_{12}$ and $p'_2 = P_2 + P'_{12}$ so that p'_i represents the total proportion of non-destroyed patches occupied by species i :

$$\begin{aligned} \frac{dp'_1}{dt} &= c_1(1-D)(P'_1 + f_{12}P'_{12})(1 - p'_1) - m_2p'_1 \\ \frac{dp'_2}{dt} &= c_2(1-D)(P'_2 + f_{21}P'_{12})(1 - p'_2) - m_1p'_2 \end{aligned} \quad (3)$$

Equations (3) are not a closed system since P'_1 , P'_2 , and P'_{12} still appear. To close (3), we note that the distributions of species 1 and 2 become independent as t tends to infinity (see Appendix). Independence means that the probability of finding species 1 in a patch is not affected by the presence or absence of species 2. Species become independent because competition occurs only through the globally-dispersed propagule pool. Since species become independent asymptotically, I assume that

they begin independent. By independence, $P_1 = p'_1(1 - p'_2)$, $P_2 = p'_2(1 - p'_1)$, and $P_{12} = p'_1 p'_2$. Substituting into (3),

$$\begin{aligned} \frac{dp'_1}{dt} &= c_1(1 - D)(p'_1(1 - p'_2) + f_{12}p'_1 p'_2)(1 - p'_1) - m_1 p'_1 \\ \frac{dp'_2}{dt} &= c_2(1 - D)(p'_2(1 - p'_1) + f_{21}p'_1 p'_2)(1 - p'_2) - m_2 p'_2 \end{aligned} \quad (4)$$

Equations (4) will be the model I investigate.

MODEL ANALYSIS

No interaction

When species do not interact $f_{12} = f_{21} = 1$. In this trivial case, (4) reduces to two separate single-species Levins' equations:

$$\begin{aligned} \frac{dp'_1}{dt} &= c_1(1 - D)p'_1(1 - p'_1) - m_1 p'_1 \\ \frac{dp'_2}{dt} &= c_2(1 - D)p'_2(1 - p'_2) - m_2 p'_2 \end{aligned} \quad (5)$$

The equilibrium density of species i is

$$\hat{p}'_i = 1 - \frac{m_i}{c_i(1 - D)}, \quad (6)$$

so species i persists when

$$D < 1 - \frac{m_i}{c_i} \quad (7)$$

Competition

In competitive metapopulations, species densities are lower in patches where they coexist, so $f_{ij} < 1$. It can be shown that there is only one feasible two-species equilibrium (see isoclines in Fig 2). The algebraic expression for this equilibrium is unwieldy. Invasion criteria can be used to determine the outcome of metapopulation competition: when species i can invade a monoculture of species j , but not vice-versa, species i outcompetes species j ; when both species can invade monocultures of the other, the two species coexist.

The monoculture equilibrium of species j is

$$\hat{p}'_j = 1 - \frac{m_j}{c_j(1 - D)}. \quad (8)$$

The growth rate of species i when rare is

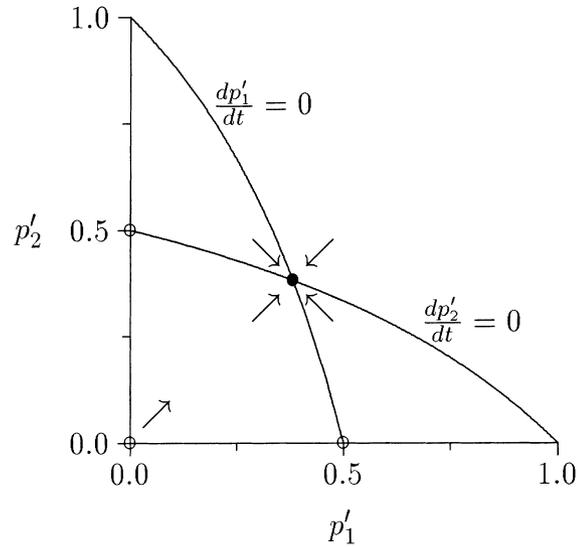


Figure 2 Phase plane diagram with isoclines for two equal competitors. Parameter values are: $c_1/m_1 = 2$, $c_2/m_2 = 2$, $f_{12} = 0.5$, $f_{21} = 0.5$, $D = 0$. Closed (open) circles denote stable (unstable) equilibria.

$$\begin{aligned} \frac{1}{p'_i} \frac{dp'_i}{dt} &= c_i(1 - D)(1 - \hat{p}'_j + f_{ij}p'_j) - m_i \\ &= c_i(1 - D) \left(\frac{m_j}{c_j(1 - D)} + f_{ij} - f_{ij} \frac{m_j}{c_j(1 - D)} \right) - m_i \end{aligned} \quad (9)$$

so species i invades species j when

$$\frac{c_i}{m_i}(1 - D) > \frac{1}{f_{ij}(1 - \frac{m_j}{c_j(1 - D)}) + \frac{m_j}{c_j(1 - D)}}. \quad (10)$$

Since the right hand side of (10) approaches $1/f_{ij}$ as the effective colonization rate $(\frac{c_i}{m_i})/(1 - D)$ approaches infinity, it is impossible for species j to regionally exclude species i if

$$\frac{c_i}{m_i}(1 - D) > \frac{1}{f_{ij}}. \quad (11)$$

When (11) is met for both species, local coexistence translates directly into regional coexistence.

Figure 3(A, B) uses (10) to determine the outcome of competition between two species. Figure 3(A) shows equal competitors which halve each other's abundance in patches where they co-occur. Figure 3(B) shows the regional outcome when $f_{12} > f_{21}$ and therefore species 1 is competitively superior to species 2 within patches. In all cases, regional coexistence is assured when the colonization rates of both species are sufficiently high.

Figure 3 (A, B) can be used to graphically determine the effect of habitat destruction. Equations (4) show that as D

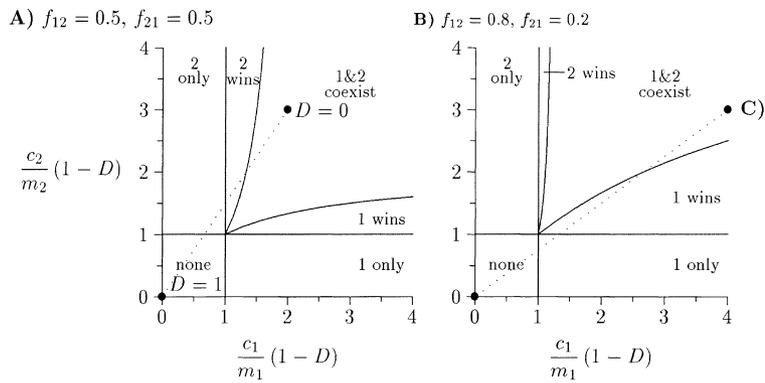
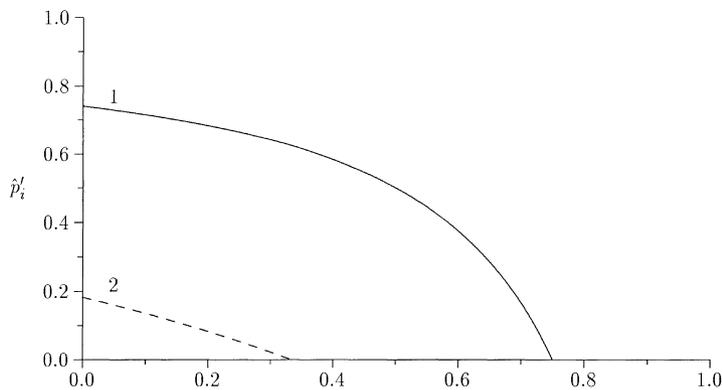


Figure 3 Species persistence and competitive outcome as determined by the ratio of colonization to mortality rates and habitat loss. (A) Competition between equal competitors; (B) competition with species 1 competitively superior to species 2; (C) patch occupancy of two competitors as a function of habitat destruction. Parameters used are: $c_1 = 4$, $c_2 = 3$, $f_{12} = 0.8$, $f_{21} = 0.2$, and correspond to the dotted path in part (B).

C) $f_{12} = 0.8, f_{21} = 0.2$



increases, the effective colonization rate of both species decreases linearly, from $(c_1/m_1, c_2/m_2)$ when $D = 0$ to $(0,0)$ when $D = 1$. By plotting a line connecting $(c_1/m_1, c_2/m_2)$ with the origin, we can see how the competitive outcome changes with D (e.g. the dotted line in Fig. 3A). The first species driven extinct by habitat destruction is always the poorer colonist (the species with the lower c_i/m_i). This species goes extinct when

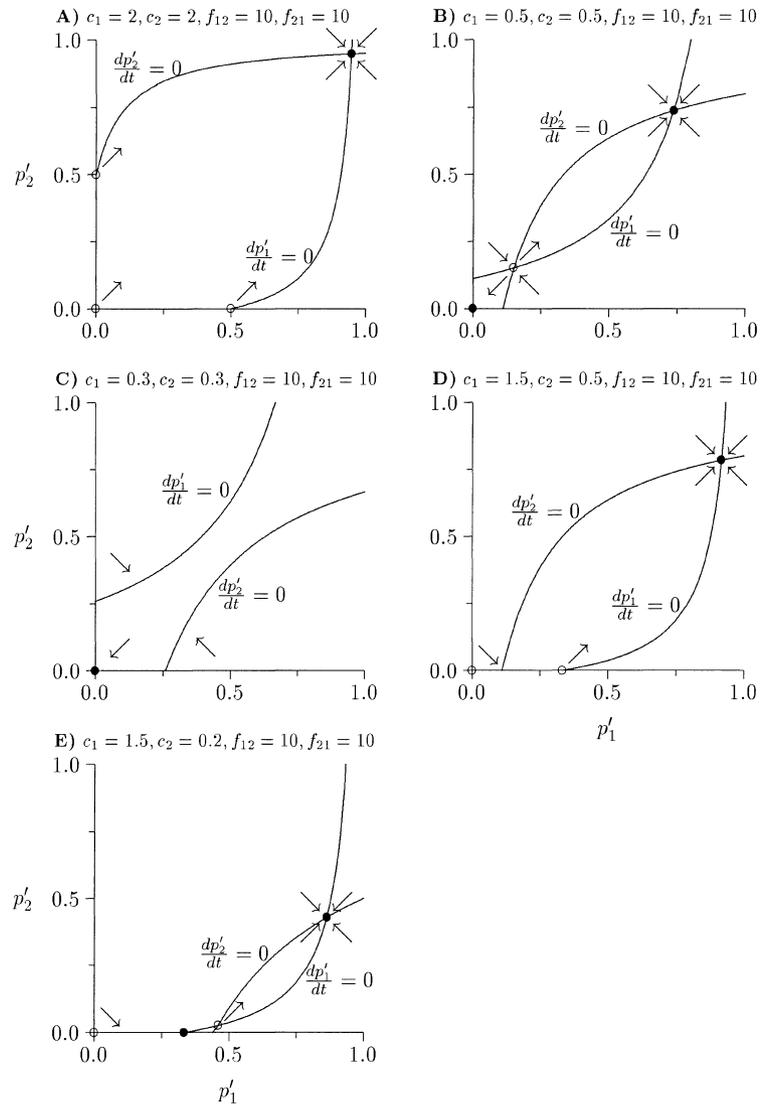
$$D \geq \frac{1}{f_{ij}} \left(\frac{m_j}{c_j} - \frac{m_i}{c_i} \right) + 1 - \frac{m_j}{c_j}. \quad (12)$$

Unlike previous models of strong competitors, the poorer colonist is not necessarily the better competitor. Figure 3(C) shows the patch occupancy of two species that do not show a competition-colonization trade-off as a function of D . In this case, the locally poor competitor, species 2, is also a poor colonist and goes extinct before the superior competitor, species 1. Species 2 appears to decline abruptly because I plot the conditional occupancy, \hat{p}'_i , which is the true occupancy divided by the proportion of remnant patches $1 - D$. The decline of both species would appear more gradual if the unconditional occupancy $\hat{p} = \hat{p}'(1 - D)$ were plotted versus D .

Mutualism

In mutualistic metapopulations, species densities are higher in patches where the two species co-occur, so $f_{ij} > 1$. When $c_1/m_1 > 1$ and $c_2/m_2 > 1$, both species can persist alone and coexist together; this is a facultative mutualism at the regional scale. The presence of both species increases the regional patch occupancy of both species (Fig. 4A). When $c_1/m_1 < 1$ and $c_2/m_2 < 1$, neither species can persist alone at the regional scale (Fig. 4B, C). For c_1/m_1 and c_2/m_2 close to 1 there are two stable equilibria: the trivial $(0,0)$ equilibrium and a positive coexistence equilibrium (Fig. 4B); this is an obligate mutualism at the metapopulation level. For smaller c_1/m_1 and c_2/m_2 there is no positive equilibrium, so coexistence is impossible (Fig. 4C). When $c_1/m_1 > 1$ and $c_2/m_2 < 1$, species 1 can persist alone but species 2 can not. If c_2/m_2 is close to 1, there may be a coexistence equilibrium regardless of whether species 2 can (Fig. 4D) or can not (Fig. 4E) invade a monoculture of species 1. If c_2/m_2 is too small however, species 2 can not persist even in the presence of species 1. These outcomes are summarized in Fig. 5(A). The boundary separating multiple stable states from non-persistence in Fig. 5(A) is determined by

Figure 4 Phase plane diagrams, with $D = 0$ and $m_i = 1$. Closed (open) circles denote stable (unstable) equilibria. (A) Regionally facultative mutualism; (B) regionally obligate mutualism showing multiple stable states; (C) regionally obligate mutualism with no positive equilibrium; (D) facultative (species 1)–obligate (species 2) mutualism without multiple stable states; (E) facultative (species 1)–obligate (species 2) mutualism with multiple stable states.



solving for the c_1/m_1 and c_2/m_2 where the two species' isoclines touch once.

The effect of habitat destruction can be seen from Fig. 5(A). Increasing D effectively reduces the colonization rate of both species. For $c_1/m_1 \gg c_2/m_2$, increasing D changes the mutualism from facultative to facultative (sp. 1)–obligate (sp. 2), then results in the extinction of species 2, then species 1. For more similar c_1/m_1 and c_2/m_2 , the mutualism changes from facultative, to facultative (sp. 1)–obligate (sp. 2), to obligate for both species, to extinction of both species simultaneously. As illustrated in Fig. 5(B), the simultaneous extinction of both species is catastrophic since the patch occupancies of both species drop from over half to zero as D is increased past the extinction threshold of $D = 0.85$.

DISCUSSION

The model studied here illustrates one way in which local processes can be scaled to explain regional patterns (Levin 1992). Just as regional coexistence is possible in metacommunity models with local competitive exclusion (Hastings 1980; Tilman 1994), local coexistence may imply regional exclusion (Fig. 3A, B). Mutualisms which are locally facultative may become obligate at the regional metapopulation scale (Fig. 5A). These disparities between local and regional outcomes occur when colonization rates are low; with high colonization rates, most patches are occupied and regional abundances mirror local abundances.

Previous theoretical work on extinction in competitive metapopulations has emphasized the susceptibility of

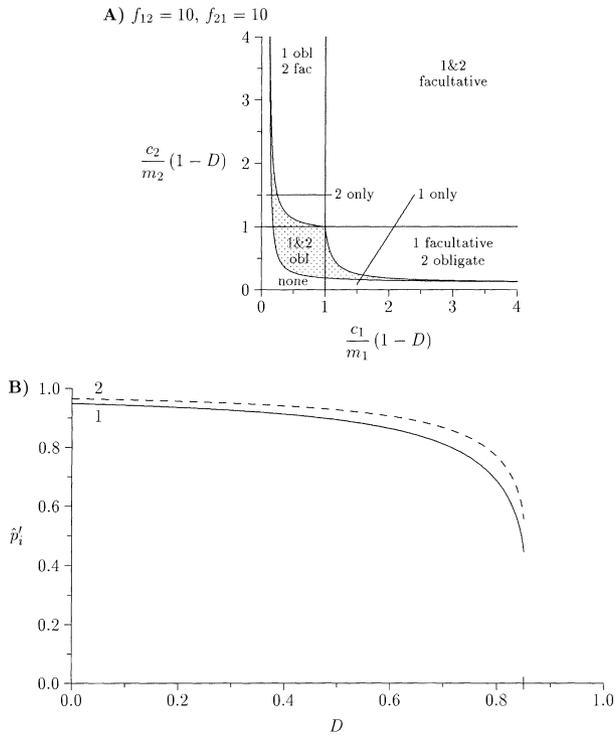


Figure 5 (A) Species persistence of locally facultative mutualists as determined by the ratio of colonization to mortality rates and habitat loss. The type of mutualism as the regional scale is given. The shaded region denotes parameter values which lead to multiple stable states. Parameter values: $f_{12} = 10$, $f_{21} = 10$. (B) Patch occupancy of two mutualists as a function of habitat loss (D). Both species go extinct simultaneously at $D = 0.85$. Parameter values: $c_1 = 2$, $c_2 = 3$, $f_{12} = 10$, $f_{21} = 10$.

superior competitors to habitat destruction (Nee & May 1992; Tilman *et al.* 1994, 1997; Neuhauser 1997; Klausmeier 1998). These studies focus entirely on strongly competing species which cannot coexist locally. Inferior competitors persist by their superior colonization rates relative to their mortality rates; it is their greater colonization ability which protects inferior competitors from extinction in these models. In contrast, in the weakly competitive metacommunities studied in this report, inferior competitors do not need to be superior colonizers in order to persist. If the *per capita* production of propagules is constant across species, then locally rare species will have lower c than locally abundant species, leading to a lower regional abundance and greater risk of extinction due to habitat destruction.

Few metapopulation models of mutualism exist, and only Nee *et al.* (1997) consider the effect of habitat destruction in a model of one locally obligate and one locally facultative mutualist. As in their model, this model of two locally facultative mutualists predicts the cata-

strophic extinction of both species as habitat destruction increases (Fig. 5). Even widespread mutualists may be at risk of sudden and unexpected extinction as habitat is lost.

The model in this report can be extended to more species; for example, for three species,

$$\begin{aligned} \frac{dp'_1}{dt} &= c_1(1-D)(p'_1(1-p'_2)(1-p'_3) + f_{12}p'_1p'_2(1-p'_3) \\ &\quad + f_{13}p'_1(1-p'_2)p'_3 + f_{123}p'_1p'_2p'_3)(1-p'_1) - m_1p'_1 \\ \frac{dp'_2}{dt} &= c_2(1-D)(p'_2(1-p'_1)(1-p'_3) + f_{21}p'_2p'_1(1-p'_3) \\ &\quad + f_{23}p'_2(1-p'_1)p'_3 + f_{213}p'_2p'_1p'_3)(1-p'_2) - m_2p'_2 \\ \frac{dp'_3}{dt} &= c_3(1-D)(p'_3(1-p'_1)(1-p'_2) + f_{31}p'_3p'_1(1-p'_2) \\ &\quad + f_{32}p'_3(1-p'_1)p'_2 + f_{312}p'_3p'_1p'_2)(1-p'_3) - m_3p'_3 \end{aligned} \quad (13)$$

However, mathematical analysis of communities of three or more species is daunting. As in models of strongly competitive metapopulations (Klausmeier 1998), extinction does not necessarily proceed from the best to worst competitor; for example, Species 2 goes extinct first when $c_1/m_1 = 2$, $c_2/m_2 = 2.1$, $c_3/m_3 = 4$, $f_{12} = 0.8$, $f_{21} = 0.2$, $f_{23} = 0.8$, $f_{32} = 0.2$, $f_{13} = 0.9$, $f_{31} = 0.1$, $f_{123} = 0.8$, $f_{213} = 0.2$, $f_{312} = 0.1$. Investigation of communities of three or more species is an important area for further research.

A major assumption of this paper is that neither extinction nor establishment rates are affected by the presence of the other species, only the rate that propagule are produced. Thus, I study pure propagule production competition. This may hold for species which can persist alone and stably coexist within local patches, but may not hold for all species. Analysis of a model incorporating all forms of interaction may be enlightening.

In this report, I have analysed metacommunity models appropriate for weak competitors or locally facultative mutualists. In competing metapopulations, the species with the lowest ratio of colonization rate to mortality rate, c/m , goes extinct first; this is most likely to be a locally rare, poor competitor. In mutualistic metapopulations, either one or both species will suffer an abrupt extinction as D increases. These rather abstract results are significant because they remind those biologists who monitor and track species in the real world that the fact declines are gradual does not mean that an "extinction cliff" is not just around the corner. Of course, the details of extinction trajectories depend critically on the mechanisms that promote biodiversity in the first place. Only after we have

developed a thorough understanding of the mechanisms of coexistence in multispecies systems will we be able to effectively monitor and manage against biodiversity loss in the face of habitat destruction.

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APPENDIX: PROOF OF INDEPENDENCE

Claim The distributions of species 1 and 2, conditioned on occupying undestroyed habitat, become independent as $t \rightarrow \infty$.

Proof Independence means $P'_{12} = p'_1 p'_2$.

$$\begin{aligned} \frac{d(p'_1 p'_2 - P'_{12})}{dt} &= \frac{dp'_1}{dt} p'_2 + \frac{dp'_2}{dt} p'_1 - \frac{dP'_{12}}{dt} \\ &= c_1(1-D)(P'_1 + f_{12}P'_{12})(1-p'_1)p'_2 - m_1 p'_1 p'_2 \\ &\quad + c_2(1-D)(P'_2 + f_{21}P'_{12})(1-p'_2)p'_1 - m_2 p'_1 p'_2 \quad (A1) \end{aligned}$$

$$\begin{aligned} &-c_1(1-D)(P_1 + f_{12}P'_{12})P'_2 - c_2(1-D)(P'_2 + f_{21}P'_{12})P'_1 \\ &\quad + (m_1 + m_2)P'_{12} \end{aligned}$$

Rearranging and using $P'_{12} = p'_1 - P_1 = p'_2 - P_2$,

$$\begin{aligned} \frac{d(p'_1 p'_2 - P'_{12})}{dt} &= -(c_1(P_1 + f_{12}P'_{12}) + c_2(P'_2 + f_{21}P'_{12}) \\ &\quad + m_1 + m_2)(p'_1 p'_2 - P'_{12}). \quad (A2) \end{aligned}$$

Since $c_1(P_1 + f_{12}P'_{12}) + c_2(P'_2 + f_{21}P'_{12}) + m_1 + m_2 \geq m_1 + m_2 > 0$, (A2) shows that $p'_1 p'_2 - P'_{12}$ is bounded from above by a function which declines exponentially to zero at rate $m_1 + m_2$ and therefore $p'_1 p'_2 - P'_{12} \rightarrow 0$ as $t \rightarrow \infty$.

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BIOSKETCH

C. Klausmeier uses mathematical models to investigate the spatial and temporal dynamics of interacting populations in systems ranging from phytoplankton to plants in semi-arid regions. He is also interested in mechanistic approaches to understand community organization.

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