

From Metapopulation Dynamics to Community Structure

Some Consequences of Spatial Heterogeneity

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I. INTRODUCTION

The most fundamental structural properties of a local community are the number and relative abundances of its member species and the pattern of their dynamical interactions (Roughgarden and Diamond, 1986). The history of community ecology largely revolves around variations on a small number of perennial themes, including: (1) the relationship between species diversity and environmental heterogeneity (e.g., resource diversity or disturbance regimes; Chesson, 1986; Huston, 1994), (2) the implications of direct and indirect interactions for community structure (e.g., dynamical constraints on food chain length; Pimm, 1982; Schoener, 1993; Wootton, 1994), and (3) historical contingency, such as multiple stable states (e.g., priority effects in competition).

A consideration of spatial dynamics can enrich all these traditional themes in community ecology. The insight that local colonizations and extinctions determine local community structure was first articulated in the 1960s in the theory of island biogeography (MacArthur and Wilson, 1967). This seminal work was soon complemented by analyses of the effects on species interactions of patch dynamics and spatial fluxes in mosaic landscapes (e.g., Levins and Culver, 1971; Horn and MacArthur, 1972; Levin, 1974; Whittaker and Levin, 1977; Holt, 1985),

a line of thinking which in recent years has crystallized into a rich body of theory under the rubric of "metapopulation dynamics" (Gilpin and Hanski, 1991).

If a "metapopulation" is defined to be a set of local populations coupled by dispersal (Hanski, 1991), a "metacommunity" may be defined simply as a set of local communities in different locations, coupled by dispersal of one or more of their constituent members (Gilpin and Hanski, 1991, p. 9). At present, there is an explosion of interest in the consequences of spatial dynamics for single-species dynamics (Hanski, this volume), interactions between species (e.g., Bengtsson, 1991; Hassell *et al.*, 1994; Kareiva and Wennergren, 1995; Nee *et al.*, this volume), and, more broadly, the structure of entire ecological communities (e.g., Case, 1991; Nee and May, 1992; Tilman, 1994; Caswell and Cohen, 1993; Holt, 1993).

My aim in this chapter is not to provide a synoptic overview of all pertinent work on the implications of metapopulation dynamics for community structure. Instead, I use variants of standard metapopulation model to examine several interlinked questions in community ecology which have not to date been examined in depth, but deserve further attention: (1) How does landscape heterogeneity influence the composition of local communities? (2) Can metapopulation dynamics constrain food web structure, for instance the average length of food chains? (3) When do indirect interactions constrain community membership at the level of entire landscapes? In this chapter, I use straightforward extensions of standard metapopulation models (e.g., Hanski, 1991) to examine these questions. My focus is on theory development and the articulation of hypotheses which warrant empirical scrutiny.

II. EFFECTS OF LANDSCAPE HETEROGENEITY ON LOCAL COMMUNITY COMPOSITION

Imagine a landscape that has been colonized over an evolutionary time scale from a larger species pool. For simplicity, I consider first a noninteractive community (i.e., no interspecific competition or predation) and examine the influence of heterogeneity at the landscape level on local community structure. Most metapopulation models to date have assumed that the patches comprising the metapopulation are physically homogeneous [though Horn and MacArthur (1972) and Hanski (1992b, 1995) do consider habitat heterogeneity in the context of interspecific competition]. Yet, in practice, large areas almost always encompass spatially heterogeneous local conditions (Williamson, 1981; Holt, 1992). Such regional heterogeneity can influence local community structure in a variety of ways, particularly if rarer species are considered.

Species abundance distributions typically reveal that a substantial fraction of species in local communities consists of rare species (Gaston, 1994). Surveys conducted at multiple sites, replicated over time, often show that many rare species display a pattern of local extinctions and recolonizations. For instance, in the Eastern Wood study of a bird community discussed by Williamson (1981, pp. 93–100), 28 of 44 recorded species went locally extinct at least once in the 26

years of the study. For some of these species, "extinctions" may be recorded because the site provided only a small sample drawn from populations experiencing the landscape at a coarser spatial scale (J. Bengtsson, personal communication). For other species, the Eastern Wood population may be part of a classical metapopulation, in which a balance between colonization and extinction across the landscape permits regional persistence, despite the ephemeral occurrence of populations in local communities (Hanski, this volume).

However, Harrison (1994b; see also Harrison and Taylor, this volume; Schoener, 1991) has argued that species which in a particular patch network show frequent extinctions and colonizations, may actually have a few persistent populations, which permit overall persistence. Moreover, a local population that never goes extinct may nonetheless prove to be a sink population, maintained by a regular flow of individuals from self-sustaining source populations (Shmida and Ellner, 1984; Holt, 1985, 1993; Pulliam, 1988; S. Hubbell, personal communication).

Local species richness thus may be enhanced if, at the landscape scale, habitat heterogeneity provides each species with some habitat patches permitting long-term persistence. Guaranteed local survival in some habitats allows a species to be present (e.g., as rare transients or sink populations) over a much broader range of habitats. To examine this effect in more detail, it is useful to consider a metapopulation model that incorporates habitat heterogeneity in colonization and extinction rates.

A. A Metapopulation Model for a Heterogeneous Landscape

Assume that the landscape consists of a large number of habitat patches, of which a fraction H are suitable for the community. For simplicity, I will consider that just three habitat types are present: patches of two distinct habitat types, potentially occupied by species in the community, embedded in a third matrix habitat, unsuitable for any of them. Let h_i be the fraction of habitat patches of type i . Necessarily, $h_1 + h_2 = H \leq 1$. Some species in the community may be habitat specialists on just habitat 1, others specialists on habitat 2, and yet others may be habitat generalists, able to use both habitat types (possibly to different degrees).

Let p_i denote the *fraction* of habitat patches of type i occupied by a focal species. The total occupancy of this species over the entire landscape is $p = p_1 + p_2$. Let e_i be the rate of extinction of the focal species in patches of habitat type i and c_{ij} the rate of colonization of type i patches due to emigration from patches of type j ($i, j = 1, 2$). The following model describes dynamics of the total metapopulation:

$$\begin{aligned} \frac{dp_1}{dt} &= (c_{11}p_1 + c_{12}p_2)(h_1 - p_1) - e_1p_1 \\ \frac{dp_2}{dt} &= (c_{21}p_1 + c_{22}p_2)(h_2 - p_2) - e_2p_2 \end{aligned} \tag{1}$$

In a metapopulation with homogeneous habitat patches, colonization and extinction rates should be independent of patch type, so $c_{ij} = c$ and $e_i = e$. Model (1) then reduces to the usual form, $dp/dt = cp(H - p) - ep$ (Levins, 1969a; Hanski, 1991, this volume).

Let us consider first a species specialized to just habitat i . By assumption, this species cannot occupy habitat j at all, hence $p_j = 0$. When rare, the species increases at a rate (per occupied patch) of $c_{ii}h_i - e_i$ and equilibrates with a fraction $\hat{p} = h_i - e_i/c_{ii}$ of the landscape occupied. If we define the "conditional incidence" (Holt, 1993) I_i of species i to be the probability that it occupies a patch, given that the patch is suitable for it, then at equilibrium $I_i = 1 - e_i/h_i c_{ii}$. The species will persist in the landscape (without repeated invasion from an external source pool) only if $c_{ii}h_i > e_i$.

Assume that in the regional source pool, species specializing to the two habitats are equally common, and that each ensemble of habitat specialists can be described with the same bivariate frequency distribution of colonization and extinction rates. Further, assume that in the landscape habitat 1 is the commoner, i.e., $h_1 > h_2$. It follows that the rarer habitat (habitat type 2) should have fewer species that are habitat specialists. Moreover, those specialist species which are present should on average have lower overall occupancies, compared with species specialized to the commoner habitat.

If two species have equal conditional incidences, but differ in their habitat specialization, the species specializing in the rarer habitat must have a higher colonization rate or a lower extinction rate. Extinction and colonization rates reflect many aspects of individual and population ecology, such as life history responses to disturbance, temporal dynamics in local population abundance, resource specialization, resistance to resident predators, and so forth. Hence, there should be systematic differences in entire suites of ecologically relevant traits between ensembles of species specialized to rare, as opposed to common, habitats.

To go further with this line of reasoning, one would need to specify statistical distributions for the parameters e and c among specialist species in the species pool. This would be an interesting exercise, but at the present juncture premature, given the paucity of data on these parameters at the level of entire guilds or communities. The above theoretical results provide testable hypotheses for future comparative community studies of rare and common habitats. I now turn to a comparison of habitat specialists and generalists.

B. Habitat Specialists and Generalists

The cross-habitat colonization terms in model (1) represent a kind of landscape "mutualism": the incidence of a species in one habitat type may be enhanced because the species is present in another habitat as well. If a species can colonize patches of a second habitat type, without reducing its rate of colonization of patches of the first habitat type, it obviously should be able to persist better in a

heterogeneous landscape. Moreover, a habitat generalist may be a member of the local community in a particular habitat type, though this species would disappear in a homogeneous landscape consisting entirely of just that habitat type. The above model permits a closer analysis of these effects.

To determine whether or not a species can persist, one examines its rate of increase when it is rare (i.e., at low occupancy). If a species increases when rare, it will persist, whereas if it decreases when rare, it is vulnerable to extinction. When a species is rare across both habitat types, we can approximate the above model with a pair of linear differential equations. The initial growth rate of the species when rare is given by the dominant eigenvalue of this simpler model,

$$\lambda(h_1, h_2) = \frac{1}{2} [\lambda_1 + \lambda_2 + \sqrt{(\lambda_1 - \lambda_2)^2 + 4 c_{12}c_{21}h_1h_2}], \quad (2)$$

where

$$\lambda_i = c_{ii}h_i - e_i \quad (3)$$

is the rate of metapopulation growth when habitat type i alone is available in the landscape.

If h_1 is fixed and $c_{12}c_{21} > 0$, λ increases with h_2 . Thus, the ability of a species to utilize a second habitat may facilitate its persistence in a heterogeneous landscape.

Consider the special case of $c_{11}c_{22} = c_{12}c_{21}$. This constraint on parameter values could arise in two biologically distinct ways, each quite plausible in different circumstances:

1. Colonization could be determined entirely by the site of colonization (i.e., $c_{11} = c_{12}$ and $c_{22} = c_{21}$). For instance, the presence or absence of a particular mortality factor, say a natural enemy, could influence the likelihood of local colonization. If the natural enemy is found predictably in some habitats, but not others, this should lead to spatial heterogeneity in colonization rates.

2. Colonization rates of empty patches could be determined entirely by the site of origination for dispersers (i.e., $c_{11} = c_{21}$, and $c_{22} = c_{12}$). For example, the two habitat types could differ in the local average abundances achieved by a species. If individuals emigrate at a constant per capita rate, the habitat type with larger populations will exert a disproportionate effect on the colonization of empty patches.

In this special case, the combination of parameters defining the sign of the growth rate when the species is rare is given by the following expression:

$$G = \frac{c_{22}h_2}{e_2} + \frac{c_{11}h_1}{e_1}.$$

When $G < 1$, the metapopulation declines toward extinction; conversely, when $G > 1$, the metapopulation grows when it is scarce in the landscape.

If each $c_{ii}h_i/e_i > 1$, the species could persist in either habitat alone. If each $c_{ii}h_i/e_i < 1$, but $G > 1$, a species can persist in the entire landscape, even though

it cannot persist in any single habitat alone. At equilibrium in model (1), for habitat i

$$0 = [c_{ii}p_i^*(h_i - p_i^* - e_i)] + c_{ij}p_j^*(h_i - p_i^*). \quad (4)$$

If the cross-habitat parameters c_{ij} are positive, both $p_i^* > 0$. The bracketed term on the left of (4) is zero at $\hat{p}_i = h_i - e_i/c_{ii}$ and is negative for larger p_i . Because the right-hand term is positive, the bracketed term must be negative; hence $p_i^* > \hat{p}_i$. Thus, a species' incidence in one habitat type is enhanced because of spatial coupling with the second habitat type. Habitat generalization permits a species to be present with a higher than expected incidence in each habitat, given colonization and extinction rates for each habitat in isolation.

Model (1) illustrates how "spillover" between habitats can enrich local communities. Assume that habitat 2 is a "black-hole" sink (Holt and Gaines, 1992), which can be colonized but does not provide colonists for either habitat type (for concreteness, one can imagine that population densities are very low in habitat 2, so these populations provide negligible sources for colonists). Hence, c_{11} and $c_{21} > 0$, but $c_{22} = c_{12} = 0$. The incidence of the species in habitat 2 is $I_2 = p_2^*/h_2 = c_{21}p_1^*/(e_2 + c_{21}p_1^*)$, which increases with p_1^* . If H is fixed, then $p_1^* = H - h_2 - e_1/c_{11}$, which decreases linearly with h_2 . Hence, the incidence (probability of occurrence, per patch) of this spillover species increases in habitat 2, the less frequent is this habitat type, relative to the frequency of the habitat type that actually sustains a viable metapopulation.

Species with high colonization or low extinction rates in their preferred habitat should exhibit a high occupancy in this habitat and can secondarily have a high incidence in habitats where they cannot persist. Such spillover effects should be most noticeable in rare habitats, involving in particular those species with high occupancy in frequent habitat types.

In some circumstances, utilizing a second habitat may permit a species to persist in a landscape even if there is no colonization among patches of the second habitat type. For instance, imagine that patches of habitat 2 are overdispersed, sufficiently far apart that $c_{22} = 0$, and furthermore that the species cannot persist in habitat 1 alone. The condition for such a species to persist in the entire landscape is

$$\frac{c_{11}h_1}{e_1} < 1 < \frac{c_{11}h_1}{e_1} + \frac{h_1h_2c_{12}c_{21}}{e_1e_2}. \quad (5)$$

The right-hand inequality is always met if e_2 is sufficiently small. Sparse habitats with low local extinction rates can have a large effect on the overall persistence of a species, even if the geometry of the landscape does not permit such habitats to sustain the species on their own. In effect, colonization of sparse but low-extinction habitat patches provides a kind of "spatial storage effect" (Holt, 1992), amplifying colonization rates overall in the more widespread habitat.

This two-habitat metapopulation model leads to several interesting and testable conclusions. In a heterogeneous landscape:

1. Habitat specialists will be disproportionately common in those habitats that are most common in the landscape.
2. Some generalists may persist in the landscape precisely because they can exploit a range of habitat types.
3. Species which can persist in one habitat can thereby incidentally occupy other habitats, enriching those local communities. This spillover effect should be particularly important in defining the community membership in sparser habitats and be characterized by species with high occupancies in commoner habitats.
4. Specialists on rare habitats should have unusually low extinction rates, or high colonization rates, relative to the entire ensemble of species in the landscape (including both specialists on common habitats and habitat generalists). This implies a systematic bias at the community level in entire suites of ecological factors correlated with local extinction or colonization rates.

The above model deliberately ignored species interactions. Yet, in practice, habitat suitability for a given species and its local colonization and extinction rates may be largely determined by interactions with other species. Several authors have considered metapopulation models for species interactions in homogeneous landscapes (e.g., see Nee *et al.*, this volume) and have examined competitive interactions in heterogeneous metapopulations (Horn and MacArthur, 1972; Hanski, 1992b). In the remainder of this paper, I consider some implications of trophic interactions in a heterogeneous metapopulation, using natural extensions of the above model.

III. METAPOPULATION DYNAMICS OF FOOD CHAINS

The simplest trophic interaction is the one between a specialist predator and its prey, and the simplest food web is an unbranched chain of trophic specialists. Here I first consider a metapopulation model for a three-level food chain. A food chain describes a set of tight sequential dependencies among species. In many circumstances, it is reasonable to expect that such sequential trophic dependency will lead to nested distributional patterns, in which a given species will be necessarily absent in a patch if its required prey population is absent (Holt, 1993, 1995).

Let the state of a patch be identified by the length of the food chain it contains, such that "0" denotes an empty patch, "1" a patch with just the basal prey species, "2" a patch with both the basal prey and an intermediate predator, and "3" a patch with both these plus a top predator. The fraction of patches found in state i is denoted by p_i . We assume that the basal species in the food chain is a habitat specialist and that its required habitat occupies a fraction $h < 1$ of available

patches in the landscape. The following model describes colonization–extinction dynamics in this metapopulation:

$$\begin{aligned} \frac{dp_1}{dt} &= (c_{01}p_1 + c'_{01}p_2 + c''_{01}p_3)(h - p_1 - p_2 - p_3) \\ &\quad - (c_{12}p_2 + c''_{12}p_3)p_1 + e_{31}p_3 + e_{21}p_2 - e_{10}p_1, \\ \frac{dp_2}{dt} &= (c_{12}p_2 + c''_{12}p_3)p_1 - (e_{20} + e_{21})p_2 + e_{32}p_3 - c_{23}p_3p_2, \\ \frac{dp_3}{dt} &= c_{23}p_3p_2 - (e_{30} + e_{31} + e_{32})p_3. \end{aligned} \quad (6)$$

For clarity, the order of the subscripts for the colonization and extinction coefficients indicates the direction of flow among states (read them from left to right). Thus, the c_{ij} 's denote the rate at which colonization transforms patches from state i to state j ; the e_{ij} 's likewise set the rates of extinction, changing patches from state i to state j .

In the basal prey equation, the parameter c'_{01} arises because empty patches can be colonized by prey originating from patches with both the basal prey and the intermediate predator. Likewise, c''_{01} denotes colonization of empty patches by basal prey emigrating from patches with both the intermediate and top predators (as well as the basal prey), and c''_{12} describes colonization of prey patches by intermediate predators dispersing from patches with the full food chain. If these parameters are positive, colonization dynamics at lower trophic levels involves habitat heterogeneity, comparable in spirit to model (1) (although such heterogeneity is not a fixed landscape feature, but instead emerges as a dynamical feature of the trophic interactions).

The most important assumption made in the above model is that the food chain builds up via sequential colonization (see, e.g., Glasser, 1982), and that if a prey population goes extinct in a patch, so does any predator directly or indirectly supported by that prey. Within the confines of these key premises, a wide range of assumptions about local dynamics can be embodied in the model.

It is useful to examine the properties of this model by building it up from its base. The basal species, on its own, satisfies the standard metapopulation model

$$\frac{dp_1}{dt} = c_{01}p_1(h - p_1) - e_{10}p_1.$$

At equilibrium, $p'_1 = h - e_{10}/c_{01}$. The basal prey species persists provided

$$h > \frac{e_{10}}{c_{01}}. \quad (7)$$

This inequality also ensures that the basal species increases when rare.

A. Two Trophic Levels

When the intermediate predator is also present, the model takes the form

$$\begin{aligned} \frac{dp_1}{dt} &= (c_{01}p_1 + c'_{01}p_2)(h - p_1 - p_2) \\ &\quad - c_{12}p_2p_1 + e_{21}p_2 - e_{10}p_1 \\ \frac{dp_2}{dt} &= c_{12}p_2p_1 - (e_{20} + e_{21})p_2. \end{aligned} \quad (8)$$

The model resembles a standard predator–prey model, but with the crucial difference that the predator patches also contain prey and can therefore contribute to the rate of generation of new prey patches, either by prey colonization of empty patches, or by predator extinctions unaccompanied by prey extinctions. For simplicity, we will assume that the predator goes extinct locally only if the prey also goes extinct (i.e., $e_{21} = 0$), so here I consider only the former effect.

There are two kinds of effects a specialist predator may have on its prey in this model: it may alter the prey extinction rate, or it may change the rate of prey colonization of empty patches. In general, these effects could be either positive or negative:

1. Biogeographic “Donor Control”

Some predators may have negligible effects on local prey dynamics and so are unlikely to alter prey colonization or extinction rates, i.e., $e_{10} = e_{20}$ and $c_{01} = c'_{01}$. This is “donor control” (DeAngelis, 1992) in a spatial context: prey dynamics may constrain the distribution of the predator, without reciprocal effects by the predator on its prey.

2. Increased Prey Extinction

The scenario that has received by far the most attention in the literature on local predator–prey interactions is the one in which predators reduce prey abundances so greatly that both populations face enhanced extinction risks (i.e., $e_{10} < e_{20}$) (e.g., Gilpin, 1975; Taylor, 1991; Hassell *et al.*, 1992). Even in the absence of any effect of the predator on prey abundance in “typical” years, the predator may heighten the risk of prey extinction during episodes of disturbance, reduced prey resources, or extreme climatic events. Even in predator–prey models with stable equilibria bounded well away from zero, following large perturbations there can be transient phases at low densities, greatly increasing the likelihood of local extinction for both species (R. D. Holt, unpublished results).

3. Decreased Prey Extinction

In a wide range of circumstances, predators can reduce the magnitude of fluctuations in prey abundances (May, 1973b; Rosenzweig, 1973) or even in-

crease average prey abundances (Abrams, 1992). For instance, if prey respond behaviorally to predators by reduced exploitation of their own resources, over-exploitation may be less likely in the presence of a predator. Sih *et al.* (1985) reported a surprising number of cases in which removal of a predator led to a decrease in the abundance of the focal prey. Many of these cases seem to involve indirect interactions in multispecies assemblages (e.g., competitive interactions among prey, held in check by generalist predators), but it is not clear that all do. In cases where a predator enhances the mean abundance or reduces the temporal variability of its prey, it is conceivable that $e_{10} > e_{20}$.

4. Decreased Prey Colonization

If local prey densities are greatly reduced by predation, the flux of dispersers available for colonizing empty patches is likely to be reduced and, hence, we could expect that $c_{01} > c'_{01}$.

5. Increased Prey Colonization

If predators increase local prey density, as noted above, then predators may also indirectly facilitate prey colonization. Alternatively, if prey differentially disperse in response to perceived increases in the local risk of predation, rates of prey emigration may be higher from patches with predators than from patches without predators. In such cases, one might expect that $c'_{01} < c_{01}$.

In general, I suspect that scenarios 1, 2, and 4 are more likely than either 3 or 5. In comparisons among systems, however, it is important to keep in mind the potential for "counterintuitive" effects of predators on prey extinction or colonization rates.

As noted above, when the prey occurs alone it equilibrates at $p'_1 = h - e_{10}/c_{01}$. The predator can increase when rare provided that $c_{12}p_1 - e_{20} > 0$, or

$$h > \frac{e_{10}}{c_{01}} + \frac{e_{20}}{c_{12}}. \quad (9)$$

This simple result has several implications. First, as May (1994) notes, the requirement for persistence of a specialist predator in a metapopulation is more stringent than the requirement for the persistence of its prey (compare conditions (9) and (7)). Specialist predators are not likely to persist in rare habitats, unless they have very high colonization rates or very low extinction rates. Predators which increase the extinction rate of their prey are particularly unlikely to persist in rare habitats.

As a limiting case, consider a donor-controlled system (i.e., $e_{20} = e_{10}$) in which the predator colonization rate is a times that of its prey. In this case, the predator can increase when rare provided $a > (1 - I)/I$, where I denotes the equilibrial incidence of the prey when alone. A predator specializing on a prey with low incidence (i.e., $I \ll 1$) must have a much higher colonization rate than that of its prey. Hence, in a heterogeneous landscape, specialist predator-prey

interactions should occur disproportionately in the more widespread habitat types. Those specialist interactions which do occur in rare habitats should involve predators which either have unusually high colonization rates, or little effect on prey extinction rates, or involve prey which themselves are habitat generalists.

The above conclusions were drawn from the condition for the predator to increase when rare, a condition which provides a criterion for robust persistence in the face of large perturbations in the fraction of patches occupied by either species. The above model also defines a joint equilibrium for the predator and prey with both present at positive occupancies, as follows (recall we are assuming that $e_{21} = 0$):

$$\begin{aligned} p_1^* &= e_{20}/c_{12}, \\ p_2^* &= \frac{1}{2}[A \pm \sqrt{A^2 + 4B}], \end{aligned} \tag{10}$$

where

$$\begin{aligned} A &\equiv h - p_1^* \left(1 + \frac{c_{01}}{c'_{01}} + \frac{c_{12}}{c'_{01}} \right), \\ B &\equiv c_{01} \frac{p_1^*}{c'_{01}} \left(h - p_1^* - \frac{e_{10}}{c_{01}} \right). \end{aligned}$$

If both $A < 0$ and $B < 0$, then $p_2^* < 0$, and hence a joint equilibrium with both species present in positive numbers does not exist. If $B > 0$, then the positive branch in the above solution leads to a unique positive equilibrium. The condition that $B > 0$ is equivalent to the condition for invasion by the predator, when the prey is at a predator-free equilibrium. The condition for $B > 0$ can be expressed as $p_1^* < p'_1$. Thus, when the predator invades, the system settles into a unique equilibrium in which the prey is reduced to a lower occupancy than when alone.

If $B < 0$, the predator cannot increase when rare. However, a joint equilibrium may nonetheless exist if $A > 0$, (the larger branch in the above solution). When this occurs, the system exhibits alternative, locally stable states, one with, and one without, the specialist predator. Moreover, the equilibrium with the predator present has the prey at a higher occupancy than when the prey is present alone.

However, this outcome is impossible if $c'_{01} < c_{01}$, and $e_{20} > e_{10}$. For alternative equilibria to exist in this predator-prey system, the predator must either enhance the prey colonization rate, or reduce the prey extinction rate, or both. As noted above, there are reasonable circumstances leading to such counterintuitive effects of predation on prey dynamics. When such effects are present, it is feasible for the metacommunity to exist in alternative stable states.

B. Three Trophic Levels

Let us then return to the full food chain model, Eq. (6). Rather than attempt a full analysis of this model here, I will simply touch on some interesting limiting

cases. Consider a system which is donor-controlled at each level and where predators in a patch face extinction only when its prey goes extinct, but predators do not affect prey extinction rates (i.e., $c_{01} = c'_{01} \equiv c$, $e_{30} = e_{20} \equiv e$, and $e_{31} = e_{21} = 0$). Without the top predator, the intermediate predator has an equilibrium occupancy of

$$p_2^* = h - \frac{e}{c} - \frac{e}{c_{11}}.$$

The top predator invades if $p_2^* > e/c_{23}$, or

$$h > \frac{e}{c} + \frac{e}{c_{12}} + \frac{e}{c_{23}} \quad (11)$$

Alternatively, if the intermediate predator shuts down prey emigration (i.e., $c'_{01} = 0$), and $e_{21} = e_{31} = e_{32} = 0$, the top predator increases when rare provided

$$h > \frac{e_{10}}{c_{01}} + \frac{e_{20}}{c_{12}} + \left(\frac{c_{12} + c_{01}}{c_{01}} \right) \left(\frac{e_{30}}{c_{23}} \right). \quad (12)$$

For both special cases, the condition for invasion by the top predator is more stringent than the condition for invasion by the intermediate predator (compare conditions (11) or (12) to (4)). A habitat that is too rare to sustain the intermediate predator will not contain the top predator, either. However, more common habitats may be able to sustain a specialist intermediate predator, but not a similarly specialized top predator. Thus, if there are constraints on species' colonization abilities, long food chains composed of trophic specialists are not likely to characterize rare habitats (see also Schoener, 1989).

The basic conclusion that emerges from this model is that metapopulation dynamics can constrain the length of specialist food chains, particularly in heterogeneous landscapes where the basal species is specialized to a rare habitat. Trophic specialization on such species automatically forces habitat specialization on species of higher trophic rank, which thereby experience all the spatial constraints on the distribution of the lower-ranked species, compounded by additional limitations of their own (Holt, 1993).

The full model can admit alternative stable landscape states. For instance, a top predator may be able to stabilize an intrinsically unstable interaction between an intermediate predator and its own prey (May, 1973b; Rosenzweig, 1973), thus extinction rates may be low for patches with the full chain. If the landscape initially has all species in all patches, then it may persist in this state because of low extinction rates. However, if the system starts with just the intermediate predator and its own prey, the intermediate predator may go extinct because of highly unstable local dynamics. In this case, obviously the top predator cannot invade, because its own prey is absent. Thus, the landscape may either have just the prey alone or the entire food chain.

IV. APPARENT COMPETITION IN METACOMMUNITIES

Food chains are useful starting points for examining the implications of metapopulation dynamics for community structure, but most natural food webs are much more complex, because there are typically multiple species on each trophic level and complex linkage patterns across levels (e.g., Polis, 1991). I will next examine the potential for strong indirect interactions arising in metapopulations, constraining species membership in local communities. In standard food web models, species richness at intermediate trophic levels is often limited by a combination of two mechanisms: exploitative competition (via effects of species at these levels on abundances of lower trophic levels) and apparent competition (via effects on the abundance of higher trophic levels) (Pimm, 1982).

Consider a landscape of patches of two habitat types, each containing a single habitat specialist. A generalist predator which can exploit both prey species in the two habitats is present. If predators can colonize patches of both habitat types from patches of either type, the dynamics of the two prey species are indirectly linked. If predators increase prey extinction rates or depress prey colonization rates, it may be possible for one prey species to exclude indirectly the other species, in effect by providing a reservoir maintaining a resident predator population (Holt and Lawton, 1994)

To explore the potential for apparent competition in a landscape context consider the following model, which splices the forms of model (1) (metapopulation dynamics in a heterogeneous landscape) and model (7) (predator-prey metapopulation dynamics):

$$\begin{aligned}
 \frac{dp_1}{dt} &= c_1 p_1 (h_1 - p_1 - q_1) - e_1 p_1 - p_1 (c_{11} q_1 + c_{12} q_2) \\
 \frac{dp_2}{dt} &= c_2 p_2 (h_2 - p_2 - q_2) - e_2 p_2 - p_2 (c_{21} q_1 + c_{22} q_2) \\
 \frac{dq_1}{dt} &= p_1 (c_{11} q_1 + c_{12} q_2) - e_{1q} q_1 \\
 \frac{dq_2}{dt} &= p_2 (c_{21} q_1 + c_{22} q_2) - e_{2q} q_2.
 \end{aligned}
 \tag{13}$$

Here, the p_i are the fraction of patches of type i occupied by prey i , and the q_i are the fraction of such patches occupied by both this prey and the generalist predator. In the absence of the predator, each prey obeys a standard metapopulation model, in which c_i and e_i are respectively the colonization and extinction parameters of the prey species specialized to habitat i (which occupies a fraction h_i of the landscape). The quantities c_{ij} scale the rate of colonization of prey patches of type i by generalist predators dispersing from type j patches (as in model 1). The predator and prey go extinct in each habitat at a habitat-specific rate e_{iq} .

As in the food chain model (6), we assume here sequential colonization, so that predators do not colonize a patch until it is occupied by a suitable prey population. However, model (13) deals with only a subset of the predator-prey interactions feasible in model (6). In particular, prey colonization occurs only from patches in which the predator is absent. (Permitting colonization from patches with predators would make an already parameter-rich model even more complicated, so I defer until future work consideration of such more general models.) Predators over-exploit their prey, coupling predator to prey extinctions.

When prey i is at equilibrium and alone, it occupies a fraction $p_i = h_i - e_i/c_i$ of the landscape. The predator, when rare and invading a landscape with prey i only present a equilibrium, grows at an instantaneous rate $\lambda_i = c_{ii}p_i - e_{iq}$. If both prey are present at equilibrium, then expression (2) defines the initial growth rate of the predator population, as a function of its growth rate λ_i in each habitat, considered separately. All the above conclusions about the consequences of habitat generalization on persistence and equilibrial incidence carry over to a trophic generalist that encounters different prey in different habitats, including prey species unable to sustain the predator population by themselves, and so forth. However, the present system is dynamically much more complex than was possible in model (1), because the prey have their own colonization-extinction dynamics, constraining the predator's dynamics, and the predator can in turn drive prey extinctions.

Consider a system in which prey 1 and the predator are present at their respective equilibrial occupancies:

$$p_1^* = \frac{e_{1q}}{c_{11}}, \quad q_1^* = \frac{c_1(h_1 - e_{1q}/c_{11}) - e_1}{c_1 + c_{11}}.$$

Prey species 2 can increase when rare provided

$$\frac{1}{p_2} \frac{dp_2}{dt} = c_2 h_2 - e_2 - c_{21} q_1^* > 0.$$

The analogous equilibrial occupancies and criterion for invasion by species 1 are given by transposing the indices 1 and 2 in the above expressions. The prey species may coexist at the landscape level if both invasion criteria are satisfied simultaneously.

The resident prey indirectly reduces the rate of invasion by a second prey species, because it sustains a predator metapopulation which can invade patches once they contain the invading prey. This indirect inhibitory effect, called apparent competition (Holt, 1977), arises even though the two prey species never co-occur within any given habitat patch. Such apparent competition raises the possibility of exclusion due to shared predation in a metacommunity.

A limiting case of the above model suffices to illustrate the potential for exclusion by apparent competition. For simplicity, assume that there are no solo prey extinctions (i.e., $e_i = 0$), that the predator colonizes much more rapidly than

it goes extinct, and that the predator colonizes the two habitats indiscriminately (i.e., $c_{ij} \equiv c_q$). With these assumptions, the criterion for invasion by prey 2, given that prey 1 occurs at equilibrium with the predator, is approximately

$$\frac{c_2 h_2}{c_1 h_1} > \frac{c_q}{c_1 + c_q}.$$

Similarly, the criterion for invasion by prey 1 is

$$\frac{c_2 + c_q}{c_q} > \frac{c_2 h_2}{c_1 h_1}.$$

If $c_q \ll c_i$ ($i = 1, 2$), both inequalities will usually be satisfied, and hence the two prey species should be able to coexist in the landscape. By contrast, when $c_q \gg c_i$ ($i = 1, 2$), then one of the two inequalities will not hold. In this case, the prey species with higher $c_i h_i$ can increase when rare and the other prey species is common, whereas the alternative prey cannot reciprocally increase when rare.

The model shows that given a predator which is both a habitat generalist and a trophic generalist, alternative prey species specialized to different habitats may indirectly interact via predator colonization of prey patches—apparent competition (Holt, 1977, 1984; Holt and Lawton, 1994) at the landscape level. If such predators are effective colonizers and can induce local prey extinctions, one prey species restricted to the community in one habitat can indirectly exclude another prey species in a different local community.

The potential for prey exclusion via metacommunity dynamics raises an interesting methodological dilemma. Given such exclusion, a survey of seemingly suitable but empty habitat patches will not reveal the cause of absence—generalist predators, which can colonize only after the missing prey has invaded. The usual sort of descriptive surveys may completely miss the dynamical cause for species exclusion from a heterogenous landscape.

A criterion for dominance in apparent competition is given by the compound parameter $c_i h_i$. Prey species with a low value of this quantity are particularly vulnerable to exclusion by shared predation. Prey specialized to rare habitats (low h_i) are more likely to be excluded by predators sustained by prey inhabiting more widespread habitats. Likewise, prey species which are poor colonists (low c_i) are more prone to exclusion by apparent competition. A low c_i may reflect either poor individual dispersal abilities or low local prey population sizes.

I have previously (Holt, 1984) analyzed a one-predator, two-prey species model in which each prey was specialized to a different habitat. This model explicitly tracks abundances in each habitat (unlike (13)) and assumes density-independent predator dispersal (leading to a source-sink population structure). Such dispersal permits prey to experience apparent competition, despite habitat segregation. The prey species with lower intrinsic growth rate is vulnerable to exclusion by the alternative prey, and the likelihood of such exclusion increases with increasing predator dispersal.

These earlier results are consistent with the conclusions drawn above for shared predation in a metacommunity. Given low inherent extinction rates, the "intrinsic growth rate" of a prey metapopulation is its rate of colonization, which is $c_i h_i$. This compound parameter determines prey community composition, just as the usual intrinsic growth rate does in determining dominance in within-patch apparent competition (Holt, 1984; Holt and Lawton, 1993).

CONCLUSIONS

Classical metapopulation theory assumes that landscapes are comprised of a large number of patches available for colonization. Most models assume that the patches are physically homogeneous. Yet in natural landscapes, metapopulations are likely to span a wide range of local environmental conditions. In this chapter, I have used variants of the Levins metapopulation model to examine some potential consequences for community structure of habitat heterogeneity.

These theoretical results suggest that sparse habitats in a heterogeneous landscape are likely to sustain a biased array of species, including habitat specialists with unusually high colonization or low extinction rates and habitat generalists sustained via spillover from more abundant habitats.

Trophic specialization leads to a kind of magnification of these effects, so that each additional level must satisfy increasingly stringent criteria for persistence. One broad implication of this result is that metacommunity dynamics automatically tends to constrain food chain length.

Trophic generalization leads to an avenue for indirect interactions among alternative prey species. If alternative prey species are habitat specialists, but a predator is a habitat generalist, predator colonization can couple the dynamics of these prey species. This gives rise to apparent competition at the metacommunity level, which in some circumstances can lead to the exclusion of prey species that are poor colonists, or are specialized to rare habitat types.

The ideas presented here provide a first pass through the potential implications of habitat heterogeneity for metacommunity dynamics and structure. One promising direction for future work will be in developing spatially explicit models (Kareiva and Wennergren 1995; Nee *et al.*, this volume) with limited dispersal and various patterns of spatial heterogeneity. My expectation though, is that the general conclusions reached here will prove robust.

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