

Food Webs in Space: An Island Biogeographic Perspective

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Introduction

All ecologists are familiar with graphical portrayals of food webs such as that shown in Figure 29.1a—tinkertoy constructions of nodes (e.g., species) connected by lines (feeding relations). This depiction of food webs (or, more formally, its matrix equivalent) has without question helped articulate many important questions in community ecology (e.g., Pimm (1982), Pimm et al. (1991), and Cohen et al (1990)). Yet, as with any powerful conceptual schemata in science, this characterization of community organization both liberates—organizing one's thoughts in fruitful directions—and enslaves—subtly constraining the questions one tends to ask. In particular, most descriptions of, and models about, food web structure make no explicit reference to space. But all ecological interactions, including trophic relations, are necessarily played out in a spatial arena. For some purposes this observation may well be irrelevant. However, it is becoming increasingly clear that the resolution of many classical problems in community ecology, from the coexistence of competitors (e.g., Hanski (1983)), to the stabilization of predator-prey interactions (e.g. Hassell et al. (1991), to the interpretation of species richness patterns (Cornell and Lawton, 1992), requires a consideration of spatial dynamics. Food web ecology, too, should profit from an explicit incorporation of spatial perspectives.

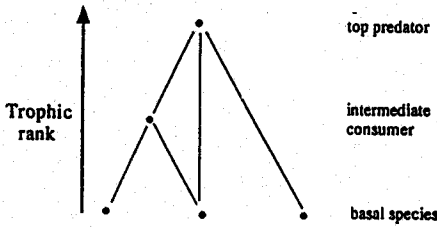
The problem of understanding spatial aspects of food web dynamics (e.g., community assembly) (Post and Pimm, 1983) has

begun to receive some attention (e.g., Kitching and Pimm (1985), Drake (1990), Luh and Pimm (1993), Schoener (1989), and Pahl-Wostl (1993)), but in my opinion the linking of spatial ecology with food web ecology warrants much more attention than it has received to date. My hope is that the ideas presented here will help foster such linkages. Following some general remarks, I present several simple models for the island biogeography of food chains—first steps toward a spatially explicit theory of food webs.

Local communities comprise organisms experiencing the world at vastly different spatial scales (Holt, 1993). Figure 29.1b schematically indicates hypothetical spatial scales for the nonspatial web of Figure 29.1a. The dotted line bounds a focal community under study (a spatially bounded sample of a larger landscape). Three plant species are restricted to distinct microhabitats; the herbivore is wider-ranging, but confined within the local community; a mobile predator straddles this and surrounding communities. An enveloping landscape can profoundly influence local food web structure and dynamics, for instance by permitting the persistence of a top predator not sustainable with just the local prey. If the focal community boundary coincides with the foraging area of an individual or social group of the largest-bodied predator at a location, the spatial unit is the ecotrophic module (ETM) proposed by Cousins (1990).

Even if in certain systems sharp boundaries seem to circumscribe the relevant spatial scales in a natural manner, as in a lake or an ETM defined by a sedentary top predator,

A Nonspatial Food Web



B Food Web in Space (schematic)

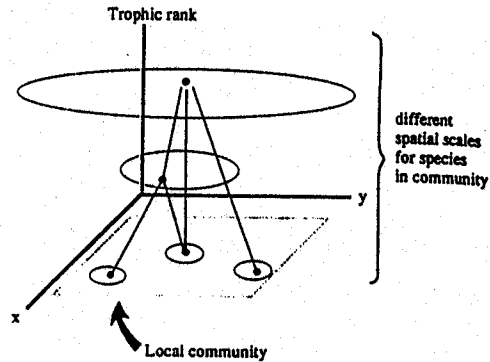


Figure 29.1. A simple food web in its standard representation as nodes connected by links; (B) the same food web shown in a nonstandard way, splayed in space. The horizontal box is the area an investigator has defined as a local community under study. The spatial domain pertinent to the population dynamics of each species are indicated by ovals. Three plant species occupy distinct microhabitats; the herbivore species has a larger spatial domain, but is relatively confined within the local community; predator dynamics are significantly influenced by events outside the community.

one cannot assume spatial dynamics are irrelevant to food web structure. At all but the most trivial spatial scales, some community members (e.g., microbes) experience the world at yet finer scales; for such species, internal spatial heterogeneities may critically influence food web organization and dynamics (e.g., allowing coexistence of small-bodied competitors). Moreover, all local communities are historical entities drawn from regional species pools (Davis, 1986; Cornell and Lawton, 1992) by the spatial process of colonization.

There has been considerable debate among food webologists about the relative merits of qualitative food webs (Figure 29.1a), vs. webs with quantitative weights (e.g., energy flow, interaction strength) attached to links, and about the importance of donor control vs. top-down effects. Similar issues arise in spatial community ecology. Qualitative spatial models track species presence/absence in defined spatial units; quantitative spatial models monitor local abundances as well. In nonfeedback spatial models, spatial effects are external forcing factors imposed on local communities; in feedback spatial models, communities exchange reciprocal effects through space either symmetrically (e.g., many metapopulation models) or asymmetri-

cally (e.g., source-sink models) (Pulliam, 1988; Holt, 1985, 1993).

By their very nature, quantitative spatial models require a detailed specification of local dynamics; fluxes of individuals matter only as gauged against local births and deaths. Such flows can profoundly influence predator-prey interactions (Holt, 1985; Taylor, 1990) and, more broadly, the character of entire local communities (Polis, this volume; Polis and Holt, ms.). As one of many possible examples, Figure 29.2 uses a modified predator-prey isocline model (see, e.g., Rosenzweig (1973) to illustrate that a steady input of predators can generate alternative community states (viz., with, or without, a given prey species). Inflows of alternative prey can subsidize predators, to similar effect (Holt and Lawton 1994, Polis and Holt unpublished manuscript). Spatial flows can also stabilize intrinsically unstable trophic interactions by setting up regional ensembles of sources and sinks (e.g., McLaughlin and Roughgarden (1993), Holt (1984, 1985), Holt and Hassell (1993), and Nisbet et al. (1993)). Rates of immigration that seem trivial in abundant populations may be critical in maintaining low-abundance populations, moderating population fluctuations, and fostering population persistence (Holt, 1993). Elucidating such

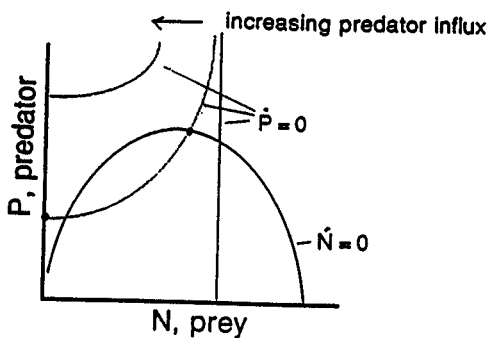


Figure 29.2. A graphical model illustrating the effect of predator immigration on predator-prey dynamics. The solid vertical line is the predator zero-growth isocline; the solid humped line is the prey zero-growth isocline (see, e.g., Rosenzweig (1973)). A steady input of predators bends the predator isocline to the left and permits the predator to persist were there no prey at the level given by the intersection of the predator isocline with the predator axis. Increasing immigration pushes the predator isocline up and to the left. With moderate immigration and a humped prey isocline, there can exist two locally stable equilibria (denoted by solid dots), respectively with and without the resident prey. At sufficiently high predator immigration the prey is excluded by predation.

quantitative effects usually requires detailed analyses of particular models. Qualitative models, by contrast, aim at gleaning insights into community structure not tightly dependent upon specific model forms.

Towards an Island Biogeography of Food Webs

The quintessential example in ecology of a qualitative, nonfeedback spatial model is the theory of island biogeography (MacArthur and Wilson, 1967), which focuses on species presence/absence on islands and how the opposing forces of colonization and extinction influence island community structure. Colonizing species are drawn from source pools with a fixed composition, implying nonfeedback spatial dynamics. On oceanic islands and many isolated continental habitat patches, immigration may mainly seed a community; once a species colonizes, its further immigration will often be quantitatively insignificant relative to in situ dynamics (with

less isolation, immigration leads to the rescue effect (Brown and Kodric-Brown, 1977)). The spatial factors considered in island theory are principally island area, and distances to and spatial configurations of sources and stepping stones (MacArthur and Wilson, 1967; Williamson, 1981; Taylor, 1987).

The theory of island biogeography has largely concentrated on species at the same trophic level, assumed either not to interact, or, if they do interact, to compete. Some empirical studies have examined island biogeographic patterns of species at different trophic levels (e.g., Heatwole and Levins (1972), Lomolino (1984), Schoener (1989), Patterson (1984), Pimm and Kitching (1987), Mikkelsen (1993), and Kruess and Tschardtke (1994), Spencer (1995), but there has been little development of formal theory. The two models presented below constitute an island biogeographic theory for food chains. The first is a static distributional model, whereas the second is a Markov model of colonization-extinction dynamics. Schoener (personal communication) has recently independently developed an island biogeographic model for food chains, similar to the latter (Schoener et al., in press). At the close of the paper, I touch on possible extensions and limitations in the basic approach.

A quite different approach to coupling food webs and island biogeography was recently developed by Cohen and Newman (1992), who spliced the cascade model with an empirical species-area relation and concluded that spatial effects might be unimportant for certain aspects of food web structure. Cohen and Newman reasoned as follows: A central parameter in the cascade model is S , the species richness of the community. Expected food chain length increases, but rather weakly, with S . The species-area relation describes how the number of species occupying an island or habitat patch increases with island or patch area, A . Often (MacArthur and Wilson, 1967; Conner and McCoy, 1979) this relation fits a power law $S = cA^z$, or

$$\log(S) = \log(c) + z \log(A), \quad (1)$$

with characteristic values for z between 0.15 and 0.45. (Note that $\delta \log(S)/\delta \log(A) = z$; this fact is useful below.) Because expected food

chain length increases weakly with S , and S in turn increases only logarithmically with A , Cohen and Newman (1992) concluded that there should be a very weak relation between community area and food chain length.

This may well prove a valid generalization. However, I suspect that spatial effects could sometimes loom large, at least for parts of food webs. A natural link between island biogeography and food web ecology comes from noting that food webs embody information about sequential dependencies among species, dependencies which should influence colonization and extinction dynamics. Here we explore the implications of such dependencies for an unbranched food chain of stacked specialists, say, a plant species supporting a specialist herbivore and, indirectly, a specialist predator, all co-occurring in a source pool. Our concern is with the distributional ecology of this food chain on an archipelago of islands varying in area, distance, etc., but all potentially colonizable from the source (but not inter alia). There are two complementary but logically distinct reasons to expect food chain length to vary with island size or distance (Holt, 1993).

First, trophic rank may predict population attributes that directly influence colonization or extinction. For instance, under many reasonable assumptions stacked specialists should exhibit a classical pyramid of numbers, such that population size declines with trophic rank. Species of high rank may be differentially vulnerable to extinction on small islands, where absolute population sizes are small.

Second, with sequential dependencies there can be a magnification of area or distance effects because high-ranked species indirectly experience spatial constraints on the distribution of lower-ranked species, in addition to any direct effects on themselves. Extinction of a low-ranked species can take with it higher-ranked species directly or indirectly dependent upon it; successful colonization by higher-ranked species requires prior colonization by lower-ranked species (Glasser, 1982).

A Static Incidence Function Model

As a first pass at understanding the spatial implications of sequential dependency, con-

sider the concept of an incidence function, denoted $p(i)$, which describes how the fraction of islands occupied by species i varies with an island characteristic such as area (Diamond, 1975). Label a given species by its trophic rank (viz., 1 for a basal producer, 2 for a specialist herbivore, 3 for a specialist parasitoid, 4 for a specialist hyperparasitoid, etc.). For isolated islands, it is clear that in general $p(i) < p(i-1)$; every island with species i must have species $i-1$, but species $i-1$ may be present without species i .

To go beyond this simple nesting in species distributions, define the conditional incidence function, $p(i|i-1)$, as the probability species i is present, given that its required food, species $i-1$, is present (Holt, 1993). The incidence function for species i compounds the incidence function for the basal species with conditional incidence functions for intermediate species 2, ..., $i-1$, as follows:

$$p(i) = p(i|i-1)p(i-1) = p(1) \prod_{j=2}^i p(j|j-1) \quad (2)$$

This identity permits one to examine how expected food chain length $E_n(L)$ varies with island area A , given n species in the source food chain. The expected fraction of islands with just i species is $p(i)[1 - p(i+1|i)]$, so (Holt, 1993)

$$E_n(L) = \sum_{i=1}^n ip(i) [1 - p(i+1|i)] \quad (3)$$

$$= \sum_{i=1}^n p(i)$$

Assume the conditional incidence function for each $i > 1$ increases with A , as does the basal species' incidence, $p(1)$. Examining the form of $\delta p(i)/\delta A$ immediately shows that total incidence $p(i)$ also increases with area. Because expected food chain length is a sum of incidence functions across levels, expected food chain length should also increase with island area. Similarly, were conditional incidence functions to decrease with increasing distance from the source, expected food chain length should decrease with distance.

How does the species-area relation vary

with trophic rank? To address this it is helpful to use explicit expressions for $p(i|(i-1))$. One flexible form is

$$p(j|j-1) = \frac{A^x_j}{A^x_j + q}, \quad (4)$$

(modified from Gilpin and Diamond (1981)), which says that conditional incidence increases with island area; x_j governs the response of species of trophic rank j to area. If there are m chains of stacked specialists in the source pool, all species of rank j have the above form for their conditional incidence function, and the basal species has an unconditional incidence function similar in form to Equation (4), the expected number of species of rank i on an island of size A is

$$S_i = mp(i) = m \prod_{j=1}^i \left(\frac{A^x_j}{A^x_j + q} \right)$$

Taking logs, and assuming q large leads to

$$\log(S_i) = [\log(m) - i \log(q)] + \left[\sum_{j=1}^i x_j \right] \log(A). \quad (5)$$

Comparing expressions (5) and (1), the slope of the log species-log area curve for species of trophic rank i is

$$z_i = \sum_{j=1}^i x_j$$

Hence $z_1 < z_2 < z_3 < \dots$. This simple model predicts that the slope of the species-area relation on a log-log plot should increase with trophic rank, in effect due to a compounding of area effects up the food chain. Similarly, the species-distance relation should be more pronounced at higher ranks.

A Dynamic Colonization-Extinction Model

The above model ignores dynamics. We now turn to a model explicitly tracking species' colonizations and extinctions.

For a single species in isolation, the standard patch occupancy model for the fraction P of an island ensemble (all of the same area,

distance to the source pool, etc.) occupied by the species is as follows (Hanski, 1992):

$$\frac{dP}{dt} = c(1-P) - eP. \quad (6)$$

The first term is the rate of colonization of empty islands, the second term is the extinction rate of occupied islands. Equilibrium occupancy is $P^* = c/(c+e)$. If colonization or extinction rates are functions of island area or distance, one can construct incidence curves from this (or, conversely, use incidence data to infer colonization and extinction rates (Hanski, 1992)).

Figure 29.3 portrays colonizations and extinctions in a three-link food chain model. For illustrative purposes, the basal plant is assumed present everywhere, so that food chain dynamics is confined to the herbivore (denoted *prey* below) and predator. An island has three possible states: state 1, basal species is alone; state 2, basal species + herbivore are present; state 3, the full food chain (basal species + herbivore + predator) is present. Colonization occurs sequentially, with no direct transition $1 \rightarrow 3$. By contrast, extinction of the top species need not imply extinction of the intermediate species, hence $3 \rightarrow 1$ and $3 \rightarrow 2$ are both feasible.

Let P_i be the fraction of islands in state i , the subscript ij denote transitions from state i to state j , and c and e be colonization and extinction rates. A Markov model generalizing the above single-species model to a food chain is:

$$\begin{aligned} \frac{dP_1}{dt} &= e_{21}P_2 + e_{31}P_3 - c_{12}P_1 \\ \frac{dP_2}{dt} &= c_{12}P_1 - e_{21}P_2 - c_{23}P_2 + e_{32}P_3 \\ \frac{dP_3}{dt} &= c_{23}P_2 - e_{32}P_3 - e_{31}P_3 \end{aligned} \quad (7)$$

The P_i s sum to unity, so there are only two independent equations. Rewriting (7) to bring out its correspondence with (6), we have:

$$\begin{aligned} \frac{dP_2}{dt} &= c_{12}(1 - P_2 - P_3) - e_{21}P_2 - c_{23}P_2 \\ &\quad + e_{32}P_3 \end{aligned} \quad (8)$$

$$\frac{dP_3}{dt} = c_{23}P_2 - e_{32}P_3 - e_{31}P_3.$$

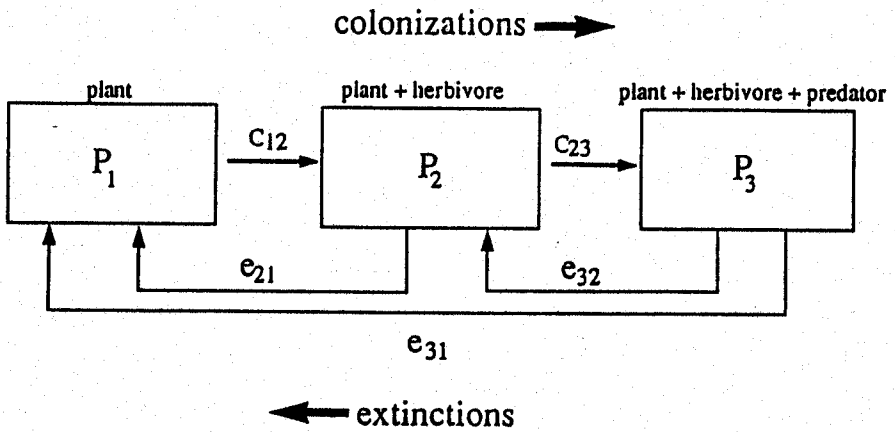


Figure 29.3. Diagrammatic representation of colonization-extinction dynamics for a three-level food chain, where the basal level is always present. P_i denotes the fraction of islands (with defined characteristics, e.g., area and distance from source) in state i , defined by the number of trophic levels present. The parameters c_{ij} and e_{ij} respectively indicate rates of colonization or extinction, transforming state i into state j . As noted in the text, the colonization dynamics could be either those of island biogeography (source to island) or in a metapopulation (among patches).

The model is linear, so one can fully characterize its equilibril and nonequibril behavior; for simplicity, here we emphasize equilibrium (see Holt and Polis, in preparation).

By varying the relative magnitudes of the e_{ij} one can span a wide range of within-island predator-prey dynamics:

- A. $e_{21} = e_{31}$: the rate of prey extinction is independent of the predator. This is biogeographic donor control; whenever the prey goes extinct, so does the specialist predator, but the predator does not alter prey extinction rates. (Schoener et al. (in press) assume such donor control.) Predators may at times moderately reduce prey abundances without thereby endangering prey population persistence, so biogeographic donor control is logically distinct from local donor control. However, if predators do dramatically reduce prey numbers, local extinction rates are likely to be modified, too.
- B. $e_{21} < e_{31}$: the predator increases the extinction rate of the prey. Predation is often destabilizing (e.g., Huffaker (1958) and Murdoch and Bence (1987)). Merely noting that predators eliminate their prey does

not suffice; what is needed is for predators to drive prey extinct more rapidly than would occur otherwise.

- C. $e_{21} > e_{31}$: the predator reduces the rate of prey extinction. In food chain models, a top predator may stabilize a system by preventing the prey from overexploiting its own resource base and thereby experiencing periods of dangerously low densities (May, 1973; Rosenzweig, 1973).
- D. e_{32} describes the rate at which the predator goes extinct on its own, without the prey also becoming extinct.

The equilibril occupancies are $P_2^* = c_{12}(e_{31} + e_{32})/Q$, and $P_3^* = c_{12}c_{23}/Q$, where $Q = c_{12}c_{23} + c_{12}e_{31} + c_{23}e_{31} + e_{21}e_{31} + c_{12}e_{32} + e_{21}e_{32}$. If colonization and extinction parameters vary with island area A and distance D to the source, so too will occupancies and incidences. We assume $de_{ij}/dA < 0$ and $dc_{ij}/dD < 0$.

This colonization-extinction model predicts equilibril incidences for the predator and prey, respectively, of $I_3 = P_3^*$, $I_2 = P_2^* + P_3^*$. The conditional incidence for the predator is $I_3/I_2 = c_{23}/(c_{23} + e_{32} + e_{31})$; this

would be the equilibrium fraction of patches occupied by the predator, were all patches occupied by prey. From (3), expected food chain length is $E_n(L) = 1 + I_2 + I_3$ (recall the basal plant is assumed ubiquitous).

Now, consider the effects of area and distance on incidence. Taking partial derivatives of the above expressions with respect to each of the colonization and extinction parameters reveals the following trends:

1. Predator incidence always increases with decreasing extinction rates (e.g., e_{ij} lower on larger island sizes) or increasing colonization rates (e.g., c_{ij} larger on closer islands), for either predator or prey.
2. Given biogeographic donor control ($e_{21} = e_{31}$) prey incidence is simply $c_{12}/(c_{12} + e_{21})$, as predicted without predation.
3. With stabilizing predation ($e_{21} > e_{31}$), prey incidence increases with decreasing extinction rates or colonization rates at either level. For both donor control and stabilizing predation, expected food chain length increases on larger or closer islands, as predicted by the static incidence model. Pimm (1982) has argued (using models of local trophic dynamics) that lower resilience of long food chains is a dynamical constraint limiting food chain length. In a sense, the very existence of a food chain itself implies a dynamic constraint on food chain length, one emerging necessarily from linked colonization and extinction events played out in a spatial arena.
4. If the predator is destabilizing (i.e., $e_{21} < e_{31}$), area or distance effects that enhance predator colonization (i.e., larger c_{23}) or reduces the likelihood of the predator going extinct alone (i.e., smaller e_{32}), depress prey incidence. A prey species may be less frequently encountered on larger islands because predators persist there long enough to be able to eliminate their food base. Likewise, prey may be more frequent

on more distant islands, where predator colonization is reduced.

With a large enough destabilizing effect of predation (the precise condition is $e_{31} > c_{12} + 2e_{21}$), expected food chain length may decrease on larger or closer islands (viz., with smaller e_{32} or larger c_{23}). This counterintuitive effect occurs because any factor increasing predator incidence also magnifies the importance of the extinction shunt back to the basal state. At equilibrium more islands may be in a basal state on larger or near islands, than on smaller or more distant islands.

The likelihood of observing an inverse relation between food chain length and island area depends on the relative magnitudes of opposing area effects mediated through different parameters. For instance, expected food chain length always increases with c_{12} , and decreases with either e_{21} or e_{31} ; this may dominate the effects just noted via e_{32} and c_{23} . Moreover, we have assumed that each food chain is present with probability 1 in the source pool, which seems improbable if food chain length shows an inverse relationship with area (or at least requires mechanisms for persistence in the source not present in the assemblage of islands under study).

Finally, consider again the log species-log area relation expected among islands, given m food chains in the source pool, each with similar functional dependencies (by trophic rank) of colonization and extinction rates on area. For a given island, the expected number of species present at rank i is mi_i . The relationship between species richness and area is stronger for predators than for prey if $\delta \log(I_3)/\delta \log(A) > \delta \log(I_2)/\delta \log(A)$, which is equivalent to $\delta \log(I_3/I_2)/\delta \log(A) > 0$.

Now, the quantity I_3/I_2 is the conditional incidence function for the predator defined above. In analyzing model (2), we simply assumed that conditional incidence increases with A , which implies that \log (conditional incidence) increases with $\log(A)$. We can now evaluate this assumption using our colonization-extinction model. After substitution, we find predators to have stronger log species-log area relations if

$$\frac{1}{c_{23}} \frac{\delta c_{23}}{\delta \log(A)} > \frac{1}{c_{23} + e_{31} + e_{32}} \left(\frac{\delta c_{23}}{\delta \log(A)} + \frac{\delta e_{31}}{\delta \log(A)} + \delta \frac{e_{32}}{\delta \log(A)} \right) \quad (9)$$

This holds if predator extinction rates decline with area, or if predator colonizing rates increase with area; these are usually reasonable assumptions. We have assumed that basal species are ubiquitous, so their species-area relationship is flat. The argument leading to (9) does not guarantee that intermediate species have positive z , only that higher-ranked species have higher z . Observing positive z -values for intermediate species may imply that predators are not often strongly destabilizing (cases A or B rather than C above). If intermediate species increase in incidence with area, then predators should show a yet stronger positive species-area effect. Thus, I predict an increase in the strength of the species-area relationship (z) with increasing trophic rank. By like argument, distance effects should also be more evident for predators than for their prey.

Several caveats are in order.

First, I have here explicitly allowed colonization and extinction in only two trophic ranks. A preliminary analysis suggests similar results hold when basal species also have colonization-extinction dynamics (Holt, unpublished manuscript), though this warrants further scrutiny.

Second, the model does not determine the magnitude of the predicted effect. Weak effects of area and distance on colonization and extinction rates will generate weak effects of trophic rank on species-area or species-distance relationships. Finally, the predicted effect of trophic rank may not be observed if one deals directly with non-log-transformed data. Consider the above model with donor control ($e_{21} = e_{31} = e$) and no solo predator extinctions ($e_{32} = 0$). If extinction rates decline with island area with fixed colonization rates, it can be shown that the untransformed species-area relation is steeper for predators than for their prey only if $c_{12}c_{23} > e^2$. At low overall colonization rates, many islands will lack both predators and prey; the species-area relationship observed may be stronger for prey than for predators. Predators are likely to have a stronger species-area relation than their prey when overall colonization rates permit high occupancy for prey species. The dynamic model suggests that the relative slopes of the untransformed species-area relation for different trophic ranks may vary, depending upon the range of areas under consid-

eration. If areas are small enough that $c_{12}c_{23} < e^2$, prey will have a stronger species-area relation than predators; if the inequality is reversed, say because only larger areas are surveyed, predators will have the stronger species-area relation. A survey spanning a broad range of island sizes might find little systematic difference in raw species-area relationships of different trophic levels.

Future Directions

An island biogeographic model of even a simple, unbranched food chain has revealed a rich diversity of potential spatial effects. What, then, of the baroquely complex food webs faced by empirical ecologists? Empirical studies are beginning to address spatial aspects of food web organization (e.g., other papers in this volume; Kitching and Beaver (1990)). Schoener et al. (in press) and Kruess and Tschantke (1994) have recently observed striking area and distance effects in host-parasitoid communities, which seem especially likely to contain many trophic specialists. A preliminary survey of the literature (Holt et al., unpublished results) suggests that low-ranked species in food webs often do have weaker species-area relations than higher-ranked species. Theoretical studies such as those outlined here can help sharpen future empirical investigations into the spatial ecology of food webs. It thus may be useful to conclude by sketching directions worthy of further theoretical exploration.

From Chains to Webs

Consider again the web of Figure 29.1 and assume that it is in a source pool. To amplify the static incidence model considered above we would have to concoct conditional incidence functions for each species, as a function of all possible combinations of prey species supporting that consumer. Similarly, the colonization-extinction model could be elaborated to allow transitions among a richer array of states.

One can a priori identify two extreme scenarios: (1) All prey species in a consumer's diet must be present before the consumer can successfully invade (e.g., because different essential resources are obtained from differ-

ent prey species). This is likely to aggravate the compounding of area or distance effects, leading to effects akin to those generated by the above food chain models. (2) All prey species are completely substitutable resources, and any one prey is sufficiently abundant to support the consumer. In this case, area or distance effects arising indirectly from interspecific dependencies might be difficult to discern. Thus, different biogeographic patterns might emerge from qualitatively distinct resource-consumer systems.

In general, most species are likely to be bracketed by these two extremes. It seems reasonable to expect the conditional incidence function (or colonization rate) to increase with an increasing representation of the set of prey supporting the consumer back in the source pool. Quantitatively characterizing how the conditional incidence function varies with prey community composition will require explicit consideration of how colonization and extinction rates vary with local community composition. This is difficult or impossible without considering more detailed models of within-island dynamics (e.g., to assess equilibrium abundances, which are correlated with extinction risk, or expected times to extinction in nonequilibrium situations). This is a tall order.

Qualitative, island biogeographic models might prove to be limited in their useful domain largely to simple subwebs, such as unlinked food chains. Nonetheless, these models do highlight a basic insight, namely, that the sequential dependency among species which is at the heart of any food web has important consequences for distributional ecology and, conversely, that spatial dynamics can influence the structure of local food webs.

From Islands to Continents

As in classical island biogeography, the above models assume a defined source pool, whose properties are determined outside the scope of one's inquiry. Ultimately, one needs to elucidate the mechanisms governing food webs in closed but spatially distributed system. One way to approach this in the framework of the above qualitative, presence/absence models is to modify the colonization term so as to be more appropriate for meta-

populations and metacommunities (Hanski, 1992; Holt, 1993).

Assume a large number of habitat patches are present and a fraction k of them are occupied by the basal species. A modified version of model (8) can describe dynamics in the fraction of patches found in each food chain state. Colonization by the intermediate species, for instance, can be represented in a modified version of (8) by $c_{12}'(k - P_2 - P_3)(P_2 + \varepsilon P_3)$, and colonization by the top species by $c_{23}'P_2 P_3$. Here, P_i is the fraction of patches in food chain state i , c_{ij}' are rates of colonization per occupied patch, and ε allows some colonization by prey dispersing from patches with the predator. Elsewhere (Holt, in preparation) I will report on the properties of this and related models (see also May 1994). For now, suffice it to say that long food chains are unlikely to persist if basal species occupy rare habitats (i.e., low k).

Here I have barely scratched the surface of spatial aspects of food webs. The fusion of spatial ecology with food web ecology promises to be an exciting, if at times daunting, adventure.

Acknowledgments

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References

- Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effects of emigration on extinction. *Ecology* 58:445-449.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community Food Webs: Data and Theory*. Springer-Verlag, New York.
- Cohen, J. E. and C. M. Newman. 1992. Community area and food-chain length: Theoretical predictions. *American Naturalist* 138:1542-1554.

- Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791-833.
- Cornell, H. V. and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology* 61:1-12.
- Cousins, S. H. 1990. Countable ecosystems deriving from a new food web entity. *Oikos* 57:270-275.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. In *Community Ecology*, eds. J. Diamond and T. J. Case, pp. 269-284. Harper & Row, New York.
- Diamond, J. A. 1975. Assembly of species communities. In *Ecology and Evolution of Communities*, eds. M. L. Cody and J. M. Diamond, pp. 342-444. Harvard University Press, Cambridge, MA.
- Drake, J. A. 1990. The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147:213-233.
- Gilpin, M. E. and J. M. Diamond. 1981. Immigration and extinction probabilities for individual species: Relation to incidence functions and species colonization curves. *Proceedings of the National Academy of Science, USA* 78:392-396.
- Glasser, J. 1982. On the causes of temporal change in communities: Modification of the biotic environment. *American Naturalist* 119:375-390.
- Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* 64:493-500.
- Hanski, I. 1992. Inferences from ecological incidence functions. *American Naturalist* 139:657-662.
- Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353:255-258.
- Heatwole, H. and R. Levins. 1972. Trophic structure stability and faunal change during recolonization. *Ecology* 53:531-534.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377-406.
- Holt, R. D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181-208.
- Holt, R. D. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds. R. Ricklefs and D. Schluter, pp. 77-88. University of Chicago Press, Chicago.
- Holt, R. D. and M. P. Hassell. 1993. Environmental heterogeneity and stability of host-parasitoid interactions. *Journal of Animal Ecology* 62:89-100.
- Holt, R. D. and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25:495-520.
- Holt, R. D., Lawton, J. H., Martinez, N., and G. A. Polis, unpublished manuscript. The effect of trophic rank on the species-area relationship: Theory and empirical patterns.
- Huffaker, C. B. 1958. Experimental studies on predation; dispersion factors and predator-prey oscillation. *Hilgardia* 27:343-383.
- Kitching, R. L. and R. A. Beaver. 1990. Patchiness and community structure. In *Living in a Patchy Environment*, eds. B. Shorrocks and I. R. Swingland, pp. 147-176. Oxford University Press, Oxford, U.K.
- Kitching, R. L. and S. L. Pimm. 1985. The length of food chains: Phytotelmata in Australia and elsewhere. *Proceedings of the Ecological Society of Australia* 14:123-140.
- Kruess, A. and T. Tschardt. 1994. Habitat fragmentation, species loss, and biological control. *Science* 264:1581-1584.
- Lomolino, M. V. 1984. Immigrant selection, predation and the distribution of *Microtus pennsylvanicus* and *Blarina brevicauda* on islands. *American Naturalist* 123:468-483.
- Luh, H.-K. and S. L. Pimm. 1993. The assembly of ecological communities: A minimalist approach. *Journal of Animal Ecology* 62:749-765.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, N.J.
- May, R. M. 1973. Time-delay versus stability in population models with two and three trophic levels. *Ecology* 54:315-325.
- May, R. M. 1994. The effects of spatial scale on ecological questions and answers. In *Large-scale Ecology and Conservation Biology* eds. P. J. Edwards, P. May, and N. R. Webb, pp. 1-17. Blackwell, Oxford.
- McLaughlin, J. and J. Roughgarden. 1993. Species interactions in space. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds. R. Ricklefs and D. Schluter, pp. 89-98. University of Chicago Press, Chicago.
- Mikkelsen, G. M. 1993. How do food webs fall apart? A study of change in trophic structure

- during relaxation on island fragments. *Oikos* 67:539-547.
- Murdoch, W. W. and J. Bence. 1987. General predators and unstable prey populations. In *Predation: Direct and Indirect Impacts on Aquatic Communities*, eds. W. C. Kerfoot and A. Sih, pp. 17-30. University Press of New England, Hanover, NH.
- Nisbet, R. M. et al. 1993. Two-patch metapopulation dynamics. In *Patch Dynamics*, eds. S. A. Levin, T. M. Powell, and J. H. Steele, pp. 125-135. Springer-Verlag, New York.
- Pahl-Wostl, C. 1993. Food webs and ecological networks across temporal and spatial scales. *Oikos* 66:415-432.
- Patterson, B. D. 1984. Mammalian extinction and biogeography in the Southern Rocky Mountains. In *Extinctions*, ed. M. Nitecki, pp. 247-293. University of Chicago Press, Chicago.
- Pimm, S. L., L. E. Cohen, and J. H. Lawton. 1991. Food web patterns and their consequences. *Nature* 350:669-674.
- Pimm, S. L. 1982. *Food Webs*. Chapman & Hall, London.
- Pimm, S. L. and R. L. Kitching. 1987. The determinants of food chain lengths. *Oikos* 50:302-307.
- Post, W. M. and S. L. Pimm. 1983. Community assembly and food web stability. *Mathematical Bioscience* 64:169-192.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Rosenzweig, M. L. 1973. Exploitation in three trophic levels. *American Naturalist* 107:275-294.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* 70:1559-1589.
- Schoener, T. W., Spiller, D. A. and L. W. Morrison, in press. Variation in the hymenopteran parasitoid fraction in Bahamian islands. *Acta Oecologica* 16:101-199.
- Spencer, M. 1995. The effect of habitat size on food web structure. Ph.D. dissertation. University of Sheffield, United Kingdom.
- Taylor, A. D. 1990. Metapopulations, dispersal, and predator-prey dynamics: An overview. *Ecology* 71:429-433.
- Taylor, R. J. 1987. The geometry of colonization. 1. Islands. *Oikos* 48:225-231.
- Williamson, M. H. 1981. *Island Populations*. Oxford University Press, Oxford, U.K.