CHAPTER 3

Food Web Dynamics in a Metacommunity Context

Modules and Beyond

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Introduction

Most natural metacommunities are also food webs, with producers and consumers at different trophic levels. What is the relationship between metacommunity processes and food webs?

The "ur-theory" of metacommunities is surely the theory of island biogeography developed by MacArthur and Wilson (1967), in which dispersal is asymmetrical between a continental source and island recipient communities. This famous monograph and the rich literature it spawned almost entirely focused on the "horizontal" structure of communities, such as the number of species within a taxon as a function of island size, and largely ignored food web interactions (Whittaker 1992; but see Lomolino 1984 and Spencer and Warren 1996). Likewise, a vast literature documented the importance of "vertical" forces in communities, ranging from reciprocal controls of predator diversity and prey diversity, to indirect impacts of predators on plant production (e.g., Holt and Lawton 1994; Pace et al. 1999; Estes et al. 2001; Persson et al. 2001; Chase et al. 2002). Food webs are a basic organizing theme in studies of many core ecological issues (Pimm 1982; Lawton 1989; Warren 1994; Cohen et al. 2003), yet until relatively recently ecologists paid scant attention to how spatial processes might influence food web structure and dynamics (Schoener 1989; Holt 1993; Polis, Holt, et al., 1996; Polis, Power, et al. 2004).

An important challenge in community ecology, and the theme of this chapter, is to weave together traditional food web ecology and metacommunity dynamics. A growing body of evidence points to the importance of space in food web ecology. Consider for instance food chain length (Post 2002; Holt and Post, MS). There are suggestive hints from surveys of connectance webs that food chains are longer in larger ecosystems (e.g., Rey and McCoy 1979; figure 5 in Schoener 1989; figure 7.2 in Holt 1993). Stable isotope analyses show that trophic rank of the top predator in lakes of the northeastern United States is strongly correlated with lake volume, with little residual effect of productivity (Post et al. 2000). A further line of evidence for metacommunity effects on food web structure comes from

species-area relationships, which can reflect the impact of regional processes on species richness (Holt 1993; Rosenzweig 1995; Rosenzweig and Ziv 1999). For instance, on patches of clover and vetch in agricultural landscapes in central Europe, parasitoid species richness increases much more rapidly with area than does the richness of their hosts (Kruess and Tscharntke 2000), leading to lower rates of parasitism on smaller patches (Kruess and Tscharntke 1994). In European calcareous grasslands, habitat fragmentation affects species of higher trophic rank and trophic specialists particularly strongly (Steffan-Dewenter and Tscharntke 2002). Habitat fragmentation differentially impacts species at different trophic ranks (Didham et al. 1998; Holyoak 2000; Davies et al. 2001). Vertebrate carnivores seem particularly vulnerable to extinction in small fragments (e.g., Crooks and Soule 1999), which can have devastating consequences for the remainder of the community (Terborgh et al. 2001). Spencer et al. (1999) examined the trophic structure of arthropod assemblages in temporary ponds in Israel, and observed that the fraction of species that are predators increases strongly with pond area. Oceanic island biotas are often particularly poor in predator species (Rosenzweig 1995; Schoener et al. 1996) and so have short food chains (Schoener 1989).

These examples provide tantalizing evidence that ecosystem size and distance from source pools have profound effects on food web structure. For reasons discussed below, these effects could partly reflect metacommunity dynamics. (Further discussion of metacommunities and ecosystem properties can be found in Loreau et al., chapter 18.) Chapter 1 (see also Leibold et al. 2004) outlines four different perspectives on metacommunities: patch dynamics, species sorting, mass effects, and neutrality. All of these perspectives could pertain to food webs.

Strictly neutral models have not been developed for food webs, and in any case, in the development of neutral food web theory some constraints must be surely be placed on the system (e.g., one cannot have predators in a persistent food web without also including their prey). If species have roughly equivalent resource requirements, and are experiencing similar sets of predators, then sometimes they are lumped in food web analyses (e.g., functional groups). These may be candidate pieces of the full web where neutral models could apply.

Species sorting involves classic and familiar issues in community ecology (rules of dominance, invasibility, and exclusion due to the combined impact of abiotic factors and local interactions; e.g., Chase and Leibold 2003). Food web models often predict a plethora of alternative stable equilibria, with the one being realized depending on initial conditions. If there is dispersal, and occasional local disturbances that reinitiate local community assembly, then one of these states tends to dominate regionally (Shurin et al. 2004). Alternative food web states are most likely to be observed if alternative communities can sort out along environmental gradients (Shurin et al. 2004).

The mass effect has recently received a great deal of attention from food web ecologists under the rubric of "spatial subsidies" (Polis, Anderson, et al. 1997;

Polis, Power, et al. 2004). Mass effects have many potentially important impacts on local food webs, ranging from stabilization of otherwise unstable interactions (e.g., Huxel and McCann 1998), to generating reversals of local competitive dominance (Holt 2004).

Finally, patch dynamics occur if species in local communities often go extinct, but can persist overall because of colonization from a regional ensemble of local communities. If food webs experience frequent strong disturbances, or if local trophic interactions are quite unstable, such extinctions are likely. Below, we will consider in more details some models for simple metacommunities fitting the assumptions of patch dynamic theory.

Food web ecology is an enormous subdiscipline of ecology, and there are many legitimate approaches to studying food webs (Pimm 1982; Cohen, Beaver, et al. 1993; Cohen, Jonnson, et al. 2003; Polis and Winemiller 1996; Polis et al. 2004). One approach is to focus on entire, fully articulated webs, addressing issues such as connectance, patterns of interaction strength, the relationship between diversity and stability, and rigid circuit patterns. There are many challenges to developing adequate empirical characterizations of any but the simplest food webs (e.g., Cohen et al. 1993; Polis 1994). This is due in large measure to the large number of species in most webs, and the complex, reticulate, and variable network of interactions among these species. For these same reasons, theoretical models for the dynamics of entire webs are often built on highly simplified and unrealistic assumptions about interspecific relationships. A continuing challenge in both empirical and theoretical studies of food webs is to develop approaches to surmount this "curse of dimensionality" (Cohen et al. 1993).

In this chapter, we use a complementary approach to whole web analyses to address the interplay of food web and metacommunity dynamics. A conceptual way station between the relative simplicity of single-species population dynamics and the almost overwhelming richness of full food webs is the analysis of "community modules" (Holt 1997b; Persson 1999). The basic insight is that food webs contain recurrent structures that involve a small number of species (e.g., three to six) engaged in a defined pattern of interactions. At times, empirical systems may closely match the structure of a given module. Systems with strong interactors and well-defined functional groups often fit simple modules; this seems particularly true in the simplified communities of agroecosystems and other anthropogenic landscapes (e.g., Evans and England 1997; Muller and Brodeur 2002). Moreover, modules are basic building blocks of more complex communities. Analyses of modules can provide a handle for grappling with processes believed to be general drivers of community dynamics.

Van Nouhuys and Hanski (2002; chapter 4) provide a nice overview of real-world metacommunity dynamics for a number of modules, centered on the Glanville fritillary metapopulation in the Åland Islands off the south coast of Finland. After a brief discussion of some general issues, we consider several familiar community modules, embedded in a metacommunity context—pairwise trophic interactions, food chains, and shared predation. In the final section we sketch some thoughts on how to go beyond modules in relating food web ecology to metacommunity dynamics, and we present a novel, simple model extending island biogeography theory to multiple trophic levels. Further discussion of food web issues, particularly in the context of landscape ecology, can be found in chapter 20 by Holt et al.

Conceptual Overview

In an influential review, Kareiva highlighted how population dynamics may be fundamentally influenced by the fact that individuals disperse as well as interact (1990). The magnitude of the influence of dispersal on interactions depends on the spatial scale of environmental variation, relative to dispersal rates. If dispersal rates are very high, the metacommunity is just a well-mixed soup of interactions, creating one large spatially-distributed community. Conversely, if dispersal rates are vanishingly small, the only species expected to be present are those that can persist based on local environmental conditions and interspecific interactions; in this case, for all practical purposes communities are closed and could potentially be described by existing food web theory. Although Kareiva was concerned with single species and pairs of interacting species, his general point pertains to modules and indeed to entire food webs. The importance of metacommunity dynamics relative to local interactions in explaining food web structure should reflect the interplay of dispersal rates and the scale of patchiness and spatial heterogeneity (e.g., Hoopes et al., chapter 2). Moreover, the importance of dispersal must be gauged against the strength of local interactions (Holt 2004; see also below).

One of the key ways that dispersal and species interactions can come together is in the process of community assembly. Dispersal constraints define the species pool available for colonization into a local community (Belyea and Lancaster 1999), whereas local food web interactions can determine which colonists actually become established. For instance, Shurin (2001) experimentally demonstrated that predators attacking a zooplankton community facilitated invasion by competitor and prey species from a regional species pool, and that predator impact depended on community openness: predators reduced local species richness in closed communities, but enhanced richness in open communities. The likelihood of exclusion can itself have an implicit spatial dimension; for example, exclusion may be more likely in a small than in a large patch, because the latter may be more likely to have refuges from predation or competition.

Historical contingencies (e.g., priority effects) can arise because of the interplay of dispersal constraints and local web interactions. With strong negative interactions, low rates of extinction and low rates of dispersal, it is relatively easy to generate alternative community compositions in food web models (Luh and

Pimm 1993; Law and Morton 1996). Such alternative states get blurred at higher invasion rates (Lockwood et al. 1997), and are less likely to persist regionally if there are frequent local extinctions and global dispersal (Shurin et al. 2004). However, alternative states could be important contributors to metacommunity diversity at landscape or regional scales if disturbances are infrequent and dispersal is localized.

Community Modules and Metacommunities

Pairwise Trophic Interactions

Predator-prey interactions are the core building blocks out of which food webs are built, so their general features can influence the properties of the entire system. In chapter 2, Hoopes et al. consider in some detail the mechanisms by which spatial dynamics and spatial structure can lead to the regional persistence of predator-prey interactions, and so here we simply note key insights that pertain more broadly to multispecies food web interactions.

In pairwise predator-prey interactions, a necessary condition for a stable equilibrium is that at least one species experience direct density dependence. Similarly, in multispecies systems, direct, negative density dependence (measured by the trace—the sum of nonzero elements along the diagonal of the community matrix) is a necessary condition for a stable equilibrium (May 1973). Movement among habitats can create an "induced" form of local density dependence (Holt 1993); if a population of size N receives I immigrants into a population, the per capita effect on growth is I/N, a term which declines with increasing N. This negative density dependence can stabilize otherwise unstable local interactions. This effect helps explain the stabilizing impact of source-sink dynamics and spatial refuges in both pairwise and multispecies predator-prey interactions (Holt 1984, 1985, 1993; Nisbet et al. 1993; Huxel and McCann 1998; Briggs and Hoopes 2004).

Many food webs contain specialist predators and parasitoids. Specialist enemies impact their prey more when those prey are more common (an idea that stems back at least to Janzen 1970; for formal treatments see Armstrong 1989 and Grover 1997). This leads to density-dependent mortality, which frees space and resources for other species, thus promoting local diversity. If metapopulation dynamics promote persistence of a specialist predator-prey interaction (Hanski 1999; Bonsall et al. 2002), this indirectly facilitates the persistence of other species sharing that prey's resources. More broadly, if keystone species dominate local community structure, their dynamics also loom large in the metacommunity. For instance, a keystone predator may experience metapopulation dynamics because of recurrent extinctions unrelated to its impact on its food base (Britton et al. 2001; Shurin and Allen 2001). This sets up a parallel dynamic in the prey community, since local predator extinctions unleash competitive interactions among prey species and these lead to further local extinctions. Variation in the abundance and distribution of a keystone species due to dispersal should thus have reverberating effects on the rest of the community.

Competitive Modules

Other chapters in this book deal with competitive interactions (e.g., Mouquet et al., chapter 10), so here we only touch on this important topic. In any food web, if consumers overlap in their diet, exploitative competition may occur. Spatial dynamics may help explain the coexistence of consumers competing for shared resources. For instance, Ruxton and Rohani (1996), building on an earlier coupled lattice model of Hassell et al. (1994), showed that coexistence between two parasitoids competing for a single host species can occur in a metacommunity, given a trade-off between local attack rates and ability to move among local populations. Such coexistence was robust to varying assumptions about spatial and temporal heterogeneity. Shurin and Allen (2001) explore a metacommunity model in which a predator permits competing prey species to coexist locally, when the competitors cannot coexist in the absence of the predator (for related models see Caswell 1978 and Britton et al. 2001). The model splices together metapopulation models for competing prey (e.g., Levins and Culver 1971) and metapopulation models for predator-prey interactions (e.g., Holt 1997a; May 1994). Shurin and Allen (2001) found that predators generally promoted regional coexistence, but could have positive or negative effects on mean local diversity. They suggest that with multiple generalist predators, each with different impacts on their prey, one could observe a positive correlation between the local diversity of predators and prey. Below we will develop a quite different model that leads to a similar conclusion.

Spatial Determinants of Food Chain Length: Metacommunity Perspectives

The food chain module describes a tritrophic interaction of a basal resource (e.g., a plant), sustaining a consumer (e.g., a herbivore), which in turn supports another consumer (e.g., a predator). Interpreted literally, an unbranched food chain arises from interlocked trophic specializations, leading to stacked specialists (Holt 1993). Theoretical studies of food chains are central to the hypothesis of exploitation ecosystems (e.g., Oksanen, Fretwell, et al. 1981; Oksanen, Oksanen, et al. 1992; Oksanen, Schneider, et al. 1999), a hypothesis that emphasizes the interplay of top-down and bottom-up forces in community organization (Leibold 1996; Sinclair et al. 2000). Here we address several questions about this module. What factors determine food chain length, both in the absence and presence of dispersal? How do tritrophic interactions respond to spatial flows among different habitats?

Traditional explanations of the factors limiting food chain length emphasize ecological energetics and the stability of local interactions (Pimm 1982; Post

2002). Schoener (1989) extended the energetic hypothesis to a "productive space" hypothesis, which is that food chain length is governed by the total energy available to a given trophic level (productivity per unit area or volume, times area or volume). However, productivity alone does not at present seem to be a good predictor of food chain length, whereas habitat area or volume can influence chain length (Post 2002; though see Rosenzweig 1995 and Vander Zanden et al. 1999). This area effect could arise from metacommunity dynamics (Holt and Post, MS).

Given tight trophic specialization, spatial effects influencing the persistence of basal resource species are automatically transmitted to higher-ranked species (Holt 1993; Holt et al. 1999; Van Nouhuys and Hanski 2002). Colonization-extinction dynamics in a metacommunity can constrain food chain length. We illustrate this with a simple "donor-controlled" model. By donor control, we mean that a resource population has extinction and colonization dynamics that are independent of top-down effects of consumer populations. However, we assume that consumers can only colonize a patch if their required resource is already present, and if the resource goes extinct, so too does the consumer, so there are strong bottom-up effects.

For a species of trophic rank j in this donor-controlled food chain, a standard metapopulation model (Holt 1996, 1997a, 1997b) is

$$\frac{dp_j}{dt} = c_j p_j (h_j - p_j) - e_j p_j, \tag{3.1}$$

where p_j is the fraction of patches occupied by species j, h_j is the fraction of the landscape suitable for species i, c_i is the per patch colonization rate, and e_i is the rate of extinction. The basal species in the chain persists only if $h_1 > e_1/c_1$, and if it persists its equilibrial occupancy is $p_1^* = h_1 - e_1/c_1$.

What about the species of rank 2? Because it requires the prior presence of species 1, suitable habitat for species 2 is the current fraction of the landscape containing species 1. If species 1 is at equilibrium, we can set $h_2 = p_1^*$ in equation (3.1); the equilibrial occupancy of species 2 is $p_2^* = h_2 - e_2/c_2 = h_1 - e_1/c_1 - e_2/c_2$, hence species 2 persists only if $h_1 > e_1/c_1 + e_2/c_2$. (Note that p_i^* is also the equilibrial fraction of patches that have a food chain of length i.) Similarly, habitat patches suitable for the top predator contain both the intermediate consumer and the basal species, so the top predator persists only if $h_1 > e_1/c_1 + e_2/c_2 + e_3/c_3$. By induction, for a donor-controlled food chain of length n the criterion for persistence of the top-ranked species is

$$h_1 > \sum_{j=1}^{n} e_j/c_j. \tag{3.2}$$

As one ascends the food chain, by inspection of expression 3.2 it is clear that there are increasingly stringent criteria for persistence of the top-ranked species (whose presence determines chain length). Sparse habitats, which have small values for h_1, are particularly unlikely to sustain food chains comprised of specialists (Holt 1997a, 1997b, 2002; Melian and Bascompte 2002). Moreover, the basal species is unlikely to sustain a long food chain if it has a low maximal occupancy (e.g., because of its own high extinction or low colonization rates).

If a species at any given trophic rank goes extinct on a patch, so do all higher-ranked species that depend on it, so extinction rates must stay the same or increase with trophic rank. A striking example comes from fragmented boreal forest, where specialist food chains of a bracket fungus, a tineid moth herbivore, and a specialist tachinid fly parasitoid become increasingly truncated with increasing time since fragmentation (Komonen et al. 2000). The presence and abundance of fungal fruiting bodies is highly variable through time (Hanski 1989), which makes it harder for this resource to sustain a chain of specialist consumers. Another example is provided in chapter 4 by Van Nouhuys and Hanski, who argue that metacommunity effects are the dominant factor explaining the restricted distribution of a specialist parasitoid with limited dispersal abilities in the Åland Islands; this system matches an assumption of the model, which is that the specialist parasitoid experiences donor control (Van Nouhuys and Tay 2001).

Alternative Stable States in Food Chain Length at the Landscape Scale

More generally, predators will influence prey colonization and/or extinction rates. For instance, if predation reduces average prey population size, or generates strongly unstable dynamics with fluctuations to low levels, predators can elevate prey extinction rates. Relaxing the assumption of donor control (allowing top-down effects to occur) leads to models with a more complex algebraic structure, but does not change the fundamental conclusion that food chain length can be constrained due to coupled metapopulation dynamics (Holt 1997a, 1997b). This is particularly true if extinction rates always increase with a lengthening of the food chain in a patch. However, interesting novel effects can arise in tritrophic metacommunities with top-down effects that *enhance* local stability, such as alternative, stable landscape states with different food chain lengths. Holt (1997a) generalizes the model (equation 3.1) to include such effects, and Holt (2002) presents examples of alternative states. Rather than describe this model in all its algebraically complex glory, we here attempt to give the reader a flavor for why alternative states can arise if top-down effects are sufficiently strong.

A tritrophic predator-prey model described by May (1973) reveals that local dynamics can be stabilized by a top predator, which can lead to alternative stable states for food chain length on a landscape. Unstable dynamics in a two species system can lead to low densities of the basal prey species, leading to its possible extinction, followed by extinction of the intermediate predator. Such extinctions in a metacommunity context can imply low occupancies for the intermediate predator—too low for the top predator to increase when rare. However, if the top predator is sufficiently common, it may reduce extinction rates in the patches it occupies, and colonization from these occupied patches can permit the stable persistence of the entire food chain in the metacommunity.

An alternative scenario for tritrophic interactions in a metacommunity was explored by Jansen (1995). In contrast to the above model, Jansen assumed that for consumers (either the herbivore or top predator), dispersal occurred solely due to local extinction of their required resource. Such dispersal can be strongly destabilizing. The reason is that dispersal permits a delay in the response by the consumer population to declining resource levels, allowing consumers to push resources even lower across the landscape and thus increasing the time required for resource recovery. The model also permits alternative states, with both stable three-species equilibria and limit cycles emerging in a given environment, but from different initial conditions.

Shared Predation and Apparent Competition

Top predators can stabilize the dynamics of other species, and so facilitate prey persistence. Conversely, top predators can attack prey at sufficient rates to exclude some prey species from communities. In particular, generalist predators can lead to the extinction of prey species due to the maintenance of the predator by alternative prey. This indirect interaction, called apparent competition, has been studied extensively theoretically (e.g., Holt 1977, 1984) and has received a considerable amount of empirical attention as well (Chaneton and Bonsall 2000). Indirect exclusion of prey due to shared predation can occur in a metacommunity, even among prey species that are never found together. An experimental demonstration of this effect is provided by Bonsall and Hassell (1997, 1998). In their system, each of two moth hosts (*Plodia interpunctella* and *Ephestia kuehniella*) for a parasitoid (*Venturia canescens*) was maintained in a separate laboratory arena, so in effect each species occupied a distinct habitat, with no interspecific competition. Each host species could persist for long time periods when coexisting with the parasitoid alone. However, when both host species were present, and the parasitoid (but not either host) was permitted to move freely between the habitats, one host species was rapidly excluded due to the spillover of parasitoids moving between habitats. This exclusion arose because parasitoids were produced in sufficient numbers by the host with higher intrinsic rate of increase (*P. interpunctella*) to drive the exclusion of the other host.

A simple two-patch metacommunity model (Holt 1997a; for similar models see Swihart et al. 2001; Melian and Bascompte 2002) illustrates that for a predator that feeds on two prey species, predator mobility is a critical determinant of prey coexistence. For simplicity, assume the two prey species use distinct resources in different patches, and so do not directly compete (as in the experiment just described). The potential for indirect competitive exclusion in metacommunities is illustrated by the following model. We show the equations just for prey species 1 and predators occupying patches with that prey (a similar pair of equations describes prey 2 with subscripts 1 and 2 reversed and the predator occupying patches with prey 2):

$$\frac{dp_1}{dt} = c_1 p_1(h_1 - p_1 - q_1) - e_1 p_1 - p_1(c_{11}q_1 + c_{12}q_2), \tag{3.3}$$

$$\frac{dq_1}{dt} = p_1(c_{11}q_1 + c_{12}q_2) - e_{1q}q_1. \tag{3.4}$$

In equation 3.3, h_i is the fraction of the landscape with habitat suitable for prey species i. The fraction of the landscape occupied by prey species i alone is p_i. The fraction of the landscape occupied simultaneously by prey i and the predator is q_i. We assume that predators can only colonize patches in which one or the other prey species already resides. The parameter c_i scales colonization by prey i of patches of type i; e_i is the extinction rate of prey i, in the absence of the predator; c_{ij} is the rate of colonization by predators into patch type i, drawn from patch type j. Finally, e_{iq} is the rate at which predators drive prey (and thus themselves) extinct within patches. The model assumes that predators have a very strong effect on local prey abundance, making those prey in patches with predators essentially irrelevant to prey colonization into empty patches; successful prey colonization depends on dispersers emitted by predator-free patches.

A key feature of this model is that alternative prey species occupy mutually exclusive habitats, and so do not directly interact. The predator, however, can colonize across as well as within the two habitats, and so provides a conduit of indirect negative interaction between prey species. This can lead to apparent competitive exclusion in the metacommunity. If prey i is present alone, it persists if $h_i > e_i/c_i$. The predator can persist on prey i alone if $c_i(h_i - e_{iq}/c_{ii}) - e_i > 0$. We assume this is true. Coexistence requires that each prey species be able to increase when rare, given that the other prey species and predator are at equilibrium, implying the following joint condition for coexistence:

$$\frac{c_1(h_1 - e_{1q}/c_{11}) - e_1}{c_1 + c_{11}} < \frac{c_2 h_2 - e_2}{c_{21}}, \tag{3.5}$$

and

$$\frac{c_2(h_2 - e_{2q}/c_{22}) - e_2}{c_2 + c_{22}} < \frac{c_1 h_1 - e_1}{c_{12}}. \tag{3.6}$$

Expressions 3.5 and 3.6 imply that if the predator has little cross-habitat colonization, prey coexistence is assured; if for each prey species, cross-habitat colonization by the predator is less than within-habitat colonization, there is a range of parameters permitting coexistence; and, there is a range of habitat availabilities that implies the indirect exclusion of the prey species requiring that habitat, which would suffice for that prey to persist together with the predator, were they alone. If the inequalities in equations 3.5 and 3.6 are reversed, one expects prey species exclusion. The model suggests that prey species may be vulnerable to exclusion from a metacommunity for many reasons: vulnerable species may be specialized to rare habitat types, have lower intrinsic rates of colonization, have higher intrinsic rates of extinction (independent of predation), or be more vulnerable to extinction when confronted by the predator.

This model shows how apparent competitive exclusion in a metacommunity can arise because of predator dispersal. Were such exclusion to occur, one is likely to miss the mechanism in observational field studies, since at equilibrium the predator will be absent from any patch without prey!

Community Modules in Spatially Explicit Landscapes

These metacommunity models for modules of interacting species assume global dispersal; patch arrangement is ignored. In spatially explicit metacommunity models with localized dispersal, spatial patterns may arise that are important in determining persistence (see also Hoopes et al., chapter 2). Spatiotemporal dynamics can produce dynamics that are consistently out of phase in different parts of the landscape; dispersal between populations at peaks and those at low abundances can help rescue local populations from extinction.

Consider the two modules we have discussed above: food chains and apparent competition due to shared predation. Wilson et al. (1998) examined a stochastic tritrophic model in a cellular lattice with nearest-neighbor dispersal and strongly unstable local interactions, and showed that lattice size (a measure of metacommunity "size") had a strong effect on the persistence of the food chain. Small lattices did not permit the simultaneous existence of local populations in sufficiently different phases to generate the stability rescue effect of dispersal, which could have prevented local (and regional) extinction. To persist, a three-species system required lattices an order of magnitude larger in area than did a two-species host-parasitoid system. These area effects on food chain length were particularly pronounced with large differences among species in dispersal rates. In effect, expected food chain length should increase with lattice size, because larger lattices permit regional mechanisms of persistence to operate more effectively. It is likely that this effect contributes to the observed influence of ecosystem size on food chain length in some natural systems (Post 2002; Holt and Post, MS).

The model for apparent competition explored above (equations 3.3 and 3.4) assumes global dispersal for all species. With spatially explicit interactions and local dispersal, in a metacommunity one can observe coexistence under shared predation that would otherwise not occur. This is illustrated by a model studied by Bonsall and Hassell (2000), who examined apparent competition between two hosts species sharing a parasitoid in a lattice. Within cells, parasitism is described by a Nicholson-Bailey model. Dispersal is among nearest-neighbor cells. Within a single closed patch the dynamics are unstable, and host coexistence does not occur. In a homogeneous, well-mixed system, the theoretical expectation is that the host species with the higher value of the intrinsic growth rate, scaled against the attack rate, should tend to displace the alternative host species (Holt and Lawton 1993).

In the model of Bonsall and Hassell (2000) there are no within-patch mechanisms permitting coexistence, but dispersal is limited. The parasitoid inflicts parasitism evenhandedly on the two hosts, and one host has a higher intrinsic growth rate. The model predicts apparent competitive exclusion in a wide range of circumstances (as expected from the results of Holt and Lawton 1993). But it also shows that coexistence can occur in a metacommunity, and for two distinct reasons. The inferior host species could persist if it is a fugitive species, with a higher dispersal rate than the superior species (an analogue for apparent competitive interactions of the familiar colonization-competition trade-off; see Hoopes et al., chapter 2). More surprisingly, the inferior species may also persist if it has a much *slower* rate of dispersal! The interesting finding that sluggish inferior prey can persist reflects phenomena that arise only in a spatially structured metacommunity with limited dispersal. If the superior host and parasitoid are both dispersing, but dispersal is localized, parasitoid numbers tend to be highest in patches temporarily containing the superior host. In effect, the sedentary behavior of the inferior host means it will be left behind by waves of parasitoids tracking the superior host over space, so the inferior host enjoys transient refuges (often found in the troughs of the spiral waves these models can generate on the lattice). In chapter 2, Hoopes et al. describe parallel spatial mechanisms of escape in systems of directly competing species.

Beyond Modules

The module approach, although useful (and indeed we would argue essential) as a tool for analyzing the structure and dynamics of complex communities, is not sufficient for understanding all aspects of food web structure. As the number of species being considered explicitly grows, the number of possible module configurations grows much faster. As an example, Sinclair et al. (2000) in reviewing tritrophic dynamics with just three components note that there are twenty-seven possible configurations of interactions (including direct density dependence). One way to circumvent the issue of dimensionality is to lump species into broad functional groups. However, ignoring heterogeneity within nodes of lumped food webs must be done cautiously. Seemingly slight differences in the web of interactions can at times profoundly influence dynamics. For instance, Persson et al. (2001) experimentally enriched aquatic food webs in tanks, and found that the detailed structure of the system (e.g., the presence of inedible as well as edible producers) was essential for interpreting impacts of enrichment. Similarly, Abrams (1993) in studies of food web models observed that disparate responses of biomass to increased productivity arose between models with slight differences in the configuration of food web interactions (e.g., presence or absence of omnivory).

Despite these cautionary remarks, relatively simple effects may emerge when one considers shifts in diversity in food webs with well-defined trophic levels. Caswell and Cohen (1993) superimposed disturbance regimes on patch dynamic models of competing species, and found that species richness tended to be maximal at intermediate levels of disturbance. Wootton (1998) considered how disturbance influenced species diversity in a community with multiple species at several trophic levels. His model consisted of MacArthur's resource-consumer equations, with superimposed density-independent mortality and immigration from an external source. Depending on the details (e.g., which species immigrates) immigration could either enhance or eliminate the effect of disturbance on coexistence. The latter effect was particularly likely when top consumers were mobile. Wootton concludes that "the surprisingly different effects of immigration... suggest that its effects on more complex situations also merit further exploration" (1998). In the following section, we examine communities with well-defined trophic levels by using an approach that deliberately ignores the detailed pattern of trophic interactions among species to examine how ecosystem size influences species richness at different trophic levels.

Trophic Island Biogeography: A Step toward Generality

The stacked specialist models for food chains discussed above provide a first step toward a generalization of island biogeography and metapopulation theory to food webs. Yet these models are limited, because they assume tight trophic specialization, which is not necessarily the norm for predators. Developing comparable models for trophic generalists that keep track in detail of each possible community configuration and transitions amongst them leads to models of daunting complexity. An alternative approach we explore here is to radically simplify the problem by assuming a minimal set of assumptions about the likely relationships between trophic diversity on adjacent levels. Our aim is to develop a qualitative theory predicting how species richness at various trophic ranks scales with area (e.g., of islands, or habitat patches).

Assume that multiple species can co-occur at each trophic level (either regionally, locally, or both), but that broad, qualitative constraints define coexistence. General ecological theory (e.g., Whittaker 1975) predicts that a more diverse resource base should support a more diverse consumer base, given that many consumers are relatively specialized in their diets; there is suggestive support for this hypothesis from the plant and arthropod communities of Cedar Creek, Minnesota (Siemann 1998). We develop a "minimalist" island biogeographic model for two trophic levels, where we deliberately ignore many details of trophic interactions. Let P denote the number of predator species present on an island of size A, and S denote the number of prey species. We assume that the number of species at each trophic level is determined by colonization from a source pool, and extinctions. Moreover, we assume that trophic interactions are donor-controlled, so that colonization-extinction dynamics of the prey level are not driven by changes in the predator community. However, the converse will not be true; an increase in the number of prey species present should affect colonization and extinction rates in the predator trophic level.

Following MacArthur and Wilson (1967), prey species dynamics are described by

$$dS/dt = C - E = (c - sS) - eS. \qquad (3.7)$$

Here, C is the total rate of colonization of new prey species into the community (colonization entails establishment of viable populations), and E is the total rate of extinction of resident, established prey species. To make the model algebraically transparent (as did MacArthur and Wilson), we make these rates depend in a simple linear manner on species richness. The parameter c is the rate at which new prey species successfully colonize empty islands, s describes the reduction in rate of colonization with increasing island richness, and e is the rate of extinction, per resident species. At equilibrium, we have $S^* = c/(s + e)$.

Let a power law, $S = qA^z$, describe among-island variation in prey species richness, where A is island area, z describes the strength of the species-area relationship, and q is a taxon-specific parameter. After taking natural logs and differentiating S^* with respect to natural log of area we can form the identity

$$\begin{aligned} z &= \partial \log S^*/\partial \log A \\ &= (1/c)\partial c/\partial \log A - (1/(s + e)(\partial s/\partial \log A + \partial e/\partial \log A). \end{aligned} \qquad (3.8)$$

In principle, any of the parameters c, s, and e describing community dynamics could vary with island area. For instance, a larger area provides a larger target (larger c), holds more species when saturated (smaller s), and has a lower extinction rate of resident species (lower e). The two terms in the right-hand parenthesis are thus negative, so $z > 0$.

In like manner, the dynamics of the predator community can be described by colonization and extinction:

$$dP/dt = C' - E' = (c' - s'P) - e'P. \qquad (3.9)$$

Here the symbols match those for the prey. Equilibrial richness of predators is $P^* = c'/(s' + e')$.

Again, we would like to know how predator species richness scales with island area. We assume that predator colonization and extinction rates are determined not directly by area, but rather by the number of prey species present. There may still be emergent area effects on predator richness arising indirectly via area effects on prey richness.

One expects predator colonization to increase with prey species richness S (i.e., $\partial c'/\partial \log S > 0$). If a predator is a specialist, to successfully colonize its required prey species must be present. It is reasonable to hypothesize that in general, a particular prey species is more likely to be present if the total number of prey species is larger. For generalist predators, colonization success may also increase with increasing prey species for several distinct reasons. First, if total food supply scales with prey species richness, colonization should be more likely if there are more prey species resident. Second, if different prey provide different limiting nutrients (the obligate-generalist case of Holt et al. 1999), it is more likely the predator can colonize into a richer prey community.

With more prey species, there is also a greater chance that predators can have sufficiently distinct diets that competition is moderated. Even if there is no competition among predators, a greater diversity of prey permits bet-hedging in the face of temporal variability. So, the number of predators that can be sustained in a saturated community should increase with prey richness ($\partial s'/\partial \log S < 0$), and the extinction rate of predators already present will be lower with more prey species present ($\partial e'/\partial \log S < 0$). Ritchie (1999) presents evidence for one system (prairie dog colonies sustained by herbaceous plant communities) where local extinction rates decline with increasing prey species richness.

Using these inequalities, and with an application of the chain rule to the expression for equilibrial predator richness, we have

$$z' = \partial \log P^*/\partial \log A = (\partial \log S^*/\partial \log A) \times [(1/c')\,\partial c'/\partial \log S^* - (1/(s' + e'))(\partial s'/\partial \log S^* + \partial e'/\partial \log S^*)] \quad (3.10)$$

or compactly,

$$z' = zQ, \quad (3.11)$$

where Q is the right-bracketed expression in (3.10). The quantity Q describes the strength of the species-area relationship in the predator community, relative to that in the prey community on which they depend. With our assumptions, an increase in prey species richness should increase predator colonization rates (higher c' and / or lower s'), and reduce predator extinctions (lower e'). Hence, Q is positive, so predator richness should always scale positively with island area. However, for predator species richness to scale *more strongly* with area than does the prey (predators have a higher z-value), we must also have Q greater than 1.

It is likely that the magnitude of Q will depend on whether or not the predators in question are specialists, or generalists. Several distinct processes could make Q lower for generalist predators than for specialists, making it more likely z would not always increase with increasing trophic rank. Consider first colonization dynamics.

Generalist consumers may be able to readily colonize, given only a small subset of the resident prey community. Moreover, initial colonization should not strongly depend on the richness of the resident prey community (lowering $\partial c'/\partial \log S$). A specialist consumer by contrast requires that a particular prey species be present, before it can colonize. By chance, many species-poor communities (e.g., on small areas) will lack its required prey, whereas species-rich communities will harbor that prey. This automatically increases the dependency of c' on prey species richness for specialists, compared to generalists. So considering just the first term above suggests that it is reasonable that Q should be lower for generalists.

If all consumers are specialists, their extinction rates can be no lower than the extinction rates of their required prey (and may be higher). If a generalist can subsist on various subsets of the prey it can utilize, there should be a reduction in the dependency of extinction rates on prey species richness for generalist predators, compared to specialists (hence, a decrease in the magnitude of $\partial e'/\partial \log S$). This should also reduce Q for generalists.

Finally, if there were no local extinctions, the island predator community would equilibrate at $K(S) = c'/s'$, which we might consider to be the "saturation" richness of the community. An increase in the number of prey species may not greatly increase the number of generalist species, compared to specialists, because of the opportunity for overlap in diet, competitive interactions, and intraguild predation. In the above model, this could be described by decreasing the magnitude of $\partial s'/\partial \log S$, again lowering Q, and hence z'.

These observations suggest that generalist predators should have lower values of z than do specialists, and possibly even lower values than that of their prey (figure 3.1). Holt et al. (1999) reviewed empirical relationships between trophic rank and the species-area relationship, and observed instances of both $Q > 1$, and $Q < 1$. In systems dominated by trophic specialists (e.g., the parasitoids on habitat patches studied by Kruess and Tscharntke [2000]), one observes stronger species-area relationships at higher trophic ranks, so $z' > z$. However, in other systems (e.g., invertebrate consumers on islands in the Gulf of California; Holt et al. 1999; G. A. Polis, pers. comm.), predators (e.g., scorpions) are highly generalized and have lower z-values than do some lower-ranked trophic levels (e.g., plants). This suggests that in these systems $z' < z$; area has a stronger effect on species richness at low trophic levels. Steffen-Dewenter and Tscharntke (2000) showed that the predicted effect of trophic generalization on the magnitude of z is evident in butterflies differing in dietary breadth on habitat fragments; the regression coefficient of log(species) versus log(area) (the z-value) increases monotonically from butterflies, which are extreme generalists, to those which are oligophagous, to those which are tight specialists on a single host plant. Given that butterflies often show metapopulation dynamics (Hanski 1999), it would be interesting to know the relative contribution of colonization and extinction (as mediated through host species richness) to this pattern.

Several cautionary remarks are in order.

First, we assumed that predator dynamics depend solely on prey species richness. More generally, one might expect that predator extinctions and coloniza-

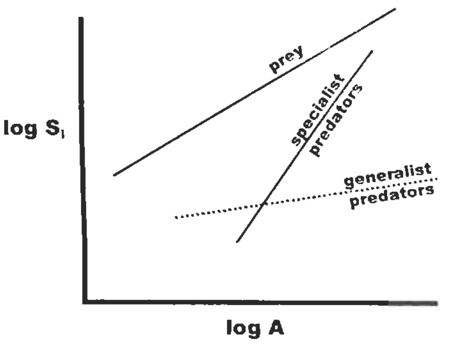

Figure 3.1 Species-area relationships as a function of trophic rank and trophic specialization. S_i is number of species of trophic rank i, and A is area.

tions could be directly influenced by island area, among islands with comparable prey species composition. For instance, large islands are larger targets for colonization, and can sustain larger population sizes. Incorporating direct area effects on predator colonization and extinction in the above formulation tends to increase the z-value of the predator assemblage (Holt et al. 1999, and unpublished results). If predators are much rarer than their prey (as is typically true of top endothermic predators), then these direct effects of area on predator-species richness may greatly outweigh the indirect effects of island area mediated through the prey trophic level.

Second, the above approach gives qualitative insight, but does not quantify the strength of the relationships. Some explicit food web models suggest rather weak dependencies with area (e.g., the cascade model; Cohen and Newman 1991). One practical complication in relating the model to field data is that food webs may not cleave neatly into distinct trophic levels (Polis 1994).

Third, we have ignored the potential for top-down impacts of predators on prey species richness (including apparent competition). As we saw in the sections on alternative stable states and apparent competition, top-down effects alter conditions for coexistence and could change extinction rates. For instance, Bengtsson and Ebert (1998) argue that parasites increase the extinction rates of *Daphnia* in rock pool metapopulations. Holt et al. (1999) suggest that top-down extinctions could weaken or even reverse the predicted relationship between trophic rank and z. A proper assessment of this suggestion will require the examination of more detailed models that make explicit assumptions about the web of interactions among predators and prey.

Finally, even if the suggested relationship exists, it may be obscured by other factors. For instance, although butterflies are typically somewhat restricted in larval host range (often monophagous or oligophagous in California, local butterfly species richness is not strongly correlated with host plant species richness, once

one factors out the influence of environmental covariates such as temperature (Hawkins and Porter 2003). One obvious difference between consumers on islands in the Gulf of California (Holt et al. 1999) and parasitoids on the habitat patches studied by Kruess and Tscharntke (2000) is that the island populations of consumers on these islands are not solely dependent on island populations of prey, but can also be supplemented by allochthonous resources from outside the system (Polis and Hurd 1996). In many systems movements of organisms and materials across habitat boundaries have profound consequences for within-habitat trophic dynamics and species composition (Polis et al. 1997; McCann et al. 1998; Power and Rainey 2000; Polis, Power, et al. 2004). Allochthonous inputs can lead to systematic deviations in species-area relationships away from that expected from island biogeographic theory, particularly on small islands or habitat patches, where such inputs may greatly exceed local productivity (Anderson and Wait 2001). In chapter 20 of this volume, Holt et al. provide further discussion of spatial fluxes and landscape scale influences on food webs and metacommunity dynamics.

Linking Food Web Theory to Empirical Studies of Metacommunities

Empirical studies that examine entire, fully-articulated food webs in a metacommunity context have not yet been conducted. Many studies (e.g., the scale transition analyses of Melbourne et al., chapter 13) focus largely on dynamics within single trophic levels. However, several of the empirical contributions in this volume do consider communities with species at different trophic levels. Overall, a comparison of these studies suggests that different patterns will be observed in different ecosystems, with the relative strengths of the four major modes of metacommunity dynamics (patch dynamics, mass effects, species sorting, and neutrality) varying greatly among systems.

Cottenie and De Meester (chapter 8) in their analysis of zooplankton communities among ponds showed that species sorting along environmental gradients had large impacts, relative to mass effects. One of the gradients had to do with the presence/absence of a top predator (fish), comparing high fish predation with no fish predation, and the other was a habitat variable (macrophyte presence), which could indirectly influence the strength of predation. The rock pools assemblages examined by Kolasa et al. (chapter 9) also broadly fit a species sorting paradigm. An important implicit message in these results is that they suggest interspecific interactions are strong. If a species with density N and continuous population growth is rare and being excluded at rate f, but is at the same time being input at rate I from the regional species pool, the equilibrial standing crop is $N^* = I/|f|$, where $|f|$ is the absolute magnitude of the rate of exclusion (Holt 1993, 2004). Species that are being weakly excluded can thus be present in substantial abundance. If there is temporal variation in the rate of exclusion (e.g., due to fluctuations in the abundance of locally superior competing species), this, if anything, tends to increase the average abundance of the excluded species, particularly if exclusion is weak (Holt et al. 2003). The fact that Cottenie and De Meester and Kolasa et al. observed strong species sorting and weak mass effects, despite considerable opportunity for dispersal, suggests that interspecific interactions leading to exclusion is quite strong in these zooplankton and rock pool communities. It would be interesting to tie these experiments more explicitly to theory, so as to assess this prediction directly.

The metacommunities associated with butterflies described by Van Nouhuys and Hanski (chapter 4) closely match the modules approach discussed above. This correspondence arises because butterflies are often specific consumers on one to a few plant species, and many of their natural enemies, in particular parasitoids, are likewise host-specific. The Glanville fritillary (*Melitaea cinxia*) in south Finland utilizes just two plant species as hosts; it is attacked by two specialist parasitoids, which in turn are attacked by two hyperparasitoids. The relative simplicity of this food web permits close analysis of mechanisms at work influencing food web structure and dynamics. The authors conclude that both local, within-community, and large-scale, among-community processes contribute to observed patterns. For instance, the interaction of the two specialist parasitoids when they co-occur can be explained by local processes, largely independent of metacommunity dynamics. By contrast, the parasitoid with more limited mobility can only persist in patch networks with the highest metapopulation capacity, consistent with the metacommunity models of food chain length discussed earlier.

The inquiline communities in pitcher plant leaves discussed by Miller and Kneitel (chapter 5) also reveal the interplay of local interactions, such as predation, and metacommunity processes such as dispersal. In particular, the relationship of species richness to dispersal rate at intermediate trophic levels was unimodal in the absence of top predators, but flat in their presence (see also Kneitel and Miller 2003). In this system, however, the top predators (e.g., mosquito larvae) did not maintain separate populations in each pitcher, but instead were pieces of a population operating at a coarser spatial scale. The moss microcosms examined by Gonzalez (chapter 6) found that habitat fragmentation led to extinctions, particularly of those species that had low abundances in the original, prefragmentation communities. In one experiment, there was also a significant effect of fragmentation on the proportion of predators in the final community. The trophic island biogeographic theory we have presented suggests that the impact of fragmentation upon the proportion of predator species present should be sensitive to the degree of trophic specialization or generalization present in the predator guild. The detailed trophic information required to assess this hypothesis is not yet available for this microarthropod community.

Finally, Resetarits et al. (chapter 16) review empirical studies of habitat selection and tellingly observe that local trophic interactions can also strongly influence dispersal rates among communities, particularly when individuals can choose local habitats (e.g., to avoid predation). This is more likely for some components of food webs (e.g., large vertebrates) than for others (e.g., seed plants). Dispersal is a topic of great importance in behavioral ecology as well as metacommunity ecology, and explicitly drawing out these linkages is a theme that warrants much more empirical work.

Conclusions

There is enormous opportunity for further empirical and theoretical work on all the themes we have touched on in this chapter. We have shown that surprising effects may emerge, even in familiar modules, when considered in a metacommunity context. The food chain model with sequential colonization and interlinked extinctions revealed that landscapes may exist in alternative states, reflecting how local interactions influence extinction risk. Shared predation may lead to exclusion of prey species that are never found together in the same local community because of habitat specialization, due to predator spillover. Conversely, metacommunity dynamics may permit alternative prey to coexist, when such coexistence is not expected in a single local community closed to dispersal. All these predictions are amenable to experimental test (e.g., in microcosm studies). Moreover, the specific models we discussed considered transitions between qualitative states (e.g., food chain length, presence/absence of a prey species in a habitat patch). Such patch dynamic approaches need to be complemented with analyses that pay close attention to numerical dynamics in each habitat, and how such dynamics are modulated by flows of individuals among habitats (mass effects). As noted above, such flows or mass effects can either stabilize or destabilize local interactions (Huxel and McCann 1998; Holt 2002), depending on the detailed functional nature of the interactions (see also Holt et al., chapter 20). If species sorting turns out to be the norm in describing food web dynamics in heterogeneous landscapes, this has important implications for our understanding of the strength of local interspecific interactions as a force governing the structure of ecological communities, relative to dispersal.

An important task for future work will be to work systematically through other familiar modules in community ecology (e.g., intraguild predation, two consumers on two biotic resources, interactions involving mutualisms, competitive systems with ecosystem feedbacks through detrital pools), and explore the consequences of colonization-extinction dynamics and mass effects for species coexistence. In all these modules, as with apparent competition, permitting dispersal between communities is likely to open up additional avenues both for coexistence and exclusion.

Finally, it is important to embed these analyses of modules in analyses of full, complex food webs. Are there generalities that transcend the manifold complexity of food webs, or does the "curse of dimensionality" loom so large that it is difficult to discern generality in the face of the many idiosyncrasies of web structure? For instance, can signatures of metacommunity dynamics be discerned in properties of whole webs, such as connection or the stability-diversity relationship? Analyses of compartments in food webs suggest that habitat boundaries typically provide suture lines between compartments (e.g., Krause et al. 2003); this observation is consistent with the importance of species sorting along gradients as a major dimension of metacommunity structure. The recent literature has suggestive hints that broad scaling relationships may exist among food webs, in effect allometric relationship relating branching properties in the web to the size of the web (Garlaschelli et al. 2003). Relating such scaling relationships to spatial flows and dynamics could help sharpen our understanding of how metacommunity dynamics bears on food web structure.

These are important and difficult challenges—but the nettle must be grasped for food web ecology and metacommunity ecology to at least achieve a full and coherent integration.

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