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CHAPTER 20

Future Directions in Metacommunity Ecology

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The rich and diverse contributions gathered in this book champion the utility of the metacommunity as an important concept for understanding the nature of biological diversity, and do so using a variety of theoretical and empirical perspectives. We view the current state of work on metacommunities as being just the beginning of a much broader effort to understand how biological diversity is structured over multiple spatial scales. Numerous issues yet remain to be addressed, and obvious gaps in the perspectives covered in prior chapters are numerous and potentially important. Further, there are many links between metacommunity ecology and other disciplines, such as behavioral ecology, evolutionary ecology, and landscape ecology that need to be explored more fully. Work at these interfaces, we believe, is crucial to a deeper understanding of metacommunity patterns and processes. Here we provide an overview of where we believe future work on metacommunity ecology might go.

Before delving into directions of future growth in metacommunity ecology, it is useful to survey very briefly key insights that have emerged from the theoretical and empirical material presented in the chapters in this book. In chapter 1, we sketched four schematic models for metacommunities, which we labeled as the patch dynamics, species sorting, mass effects, and neutral perspectives (see also Leibold et al. 2004). The empirical contributions in this book reveal that elements of all of these perspectives can be discerned in the workings of natural systems. For instance, Mark McPeck's damselfly system (see chapter 15) may match the assumptions of the neutral theory. Species sorting is evident whenever one examines landscapes with heterogeneous habitats, and often mass effects as well (e.g., the zooplankton system examined by Cottenie and De Meester in chapter 8, and the beetle assemblage in fragmented eucalypt forest studies by Davies et al. in chapter 7). Patch dynamics in its purest sense (colonizations balancing extinctions) is strongly evident in the community modules centered on the Glanville fritillary (see chapter 4 by Van Nouhuys and Hanski). The importance of dispersal in maintaining population abundances and species richness is central to many studies, for instance in the experimental analysis of habitat fragmentation in moss microlandscapes described by Gonzalez (chapter 6). Nearly all these examples also demonstrate the crucial importance of interspecific interactions in determining local community composition, filtering the available pool provided by dispersal processes at the regional scale. Metacommunity ecology thus involves an

expansion and enrichment of traditional community ecology, not a replacement for it.

The reviews of theory by Hoopes et al. (chapter 2), Holt and Hoopes (chapter 3) and Mouquet et al. (chapter 10) crystallize basic spatial processes that influence the outcome of traditional community interactions—including the impact of spatial asynchrony in dynamics and heterogeneity in local conditions, patterns of dispersal, and nonlinearities in interactions—in effect permitting an expanded niche theory to be formulated. The relative weighting of species similarity and differences required for robust species coexistence may be played out at large spatial scales, larger than the typical scales of field experiments.

Moreover, the theoretical chapters collectively provide a set of powerful techniques that could be applied in future studies to these and other empirical metacommunity studies; they also provide pointers to critical data that need to be gathered. Holt and Hoopes (chapter 3) sketch some ideas on how extensions of classical island biogeographic theory may be applied to assembly dynamics in metacommunities; this suggests that understanding colonization and extinction rates as a function of measures of local community structure is a key empirical desideratum. Law and Leibold (chapter 11) likewise show that when the timescales of local dynamics (births and deaths) and regional dynamics (colonizations and extinctions) are reasonably distinct, one can embed assembly dynamics and metapopulation processes in a formal framework. They illustrate their general approach with an example of a nontransitive competitive interaction (which cannot stably persist in any single local community, but robustly persists with recurrent extinctions and colonizations in a metacommunity setting), but the general approach should be much more widely applicable. Chapters 12 and 13 by Chesson et al. and Melbourne et al., respectively, provide an invaluable function by pulling together a set of abstract conceptual tools for analyzing how dynamical rules change as one changes scale in ecological systems, and then applying these tools to several concrete interactions. This approach retains the details of local dynamics, and highlights the role of both local and emergent regional nonlinearities in species' dynamics for understanding their dynamics. The approach also avoids one common limitation of metacommunity theory that it typically abstracts the world into two or three scales (e.g., a patch scale, and a patch ensemble scale). The latter kind of theory will nonetheless continue to play a central role in metacommunity studies because it permits one to isolate in relatively simple fashion some key aspects of species persistence and assemblage dynamics.

Several of the empirical contributions (e.g., the pitcher plant study of Miller and Kneitel in chapter 5, and the rock pool metacommunity studied by Kolasa and Romanuk in chapter 9) in like manner reveal that the spatial dynamics of ecological communities are multiscale in nature. An important direction for future theoretical studies is thus to focus explicitly on multiscale dynamics. To complement the perspective provided by Peter Chesson and his coworkers, in the next

two sections we sketch some ideas that can lead to multiscale metacommunity theory. We then discuss issues at the interface of metacommunity ecology and landscape ecology. Both the study of beetle community dynamics described by Davies et al. (chapter 7) and the microlandscapes of Gonzalez (chapter 6) reveal that the detailed spatial structure of landscapes can have crucial effects on metacommunity processes. As noted by Loreau et al. (chapter 18), a consideration of abiotic constraints and feedbacks to population and community processes may be essential in unraveling such landscape effects, because dispersal and other flows lead to energy and material transfers that can drive local processes (see examples in Polis et al. 2004).

There are important temporal dimensions to metacommunities. Metacommunity processes surely will influence the relationship between diversity and stability that has been the focus of much attention (not to mention heat) in the ecological literature. Furthermore, over long timescales, the relationship between regional and local species richness, the strength of dispersal coupling local communities, and the range of interspecific variation present in key traits that determine both interspecific interactions and ecosystem roles all must reflect evolutionary processes. McPeck and Gomulkiewicz (chapter 15) argue that speciation can readily generate species that are near-neutral in their dynamics, so that ecological drift becomes a process of real importance for understanding patterns of species richness at broad biogeographical scales. Grappling with the historical processes that generate the species pool in the first place is of great importance in determining the patterns of the relationship between local and regional abundance (see Shurin and Srivastava, chapter 17). Chapter 19 by Leibold et al. examines the proposition that metacommunities may function as “complex adaptive systems”; the “fit” of organisms to the environment can in principle be examined at any hierarchical scale, and metacommunity processes can help mold the overall distribution of traits in the community in a way that matches species traits to local environments, with or without ongoing microevolution.

Our focus in this volume has been on basic ecological principles and theory. But we fully recognize that in our rapidly changing world, the ideas we put forth could pertain to many significant problems of great human concern. We conclude this chapter with a few comments on potential important applications of these ideas.

The Importance of Spatial Strategies in Metacommunities

Community ecologists often describe broad patterns in communities in terms of frequency distributions of among-species variation—of relative abundances, body size, metabolic rates, and degree of trophic connectance, to name a few. Another important pattern is the distribution among species in the degree to which their local dynamics are spatially open, or closed, (e.g., as measured by the frac-

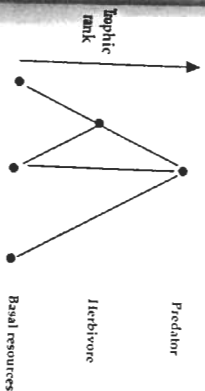
tion of individuals of each species leaving their natal site, or distances moved). As noted in Holyoak et al. in chapter 1, local communities mix species with a wide variety of spatial strategies, and in effect these species experience the world at different spatial scales (Holt 1993; Ritchie and Olff 1999). Understanding the consequences for community organization of weaving together diverse spatial strategies presents a large challenge to researchers.

There is a growing recognition that even in classic “open” communities such as coral reef fishes, larvae in some species are retained at their natal reef; the community is a blend of species with open patterns of recruitment, and others with relatively little recruitment (Mora and Sale 2002). Conversely, even classic “closed” communities such as oceanic islands are visited by migratory birds. Detailed studies of local communities within a continental setting (e.g., the Eastern Wood bird study by Beven (1976)) typically reveal some species that are persistently present and recruited locally, others that are irregular community members (exhibiting local extinction and recolonization), and some that spill over via mass effects from other distinct habitats. Yet other species occur regularly in the community, but have individual home ranges considerably greater than most other community members. If such a community were suddenly blocked from coupling via dispersal with the larger world, we would expect this heterogeneity in spatial strategies to lead to considerable among-species variation in times to local extinction (Holt 1993).

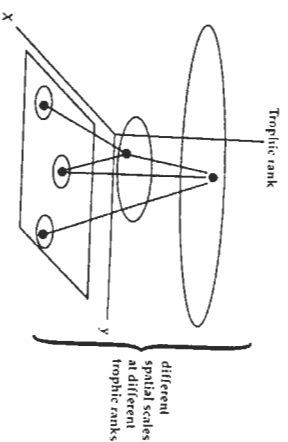
Differences in dispersal syndromes are often coupled to differences in body size, life history variables, and resource exploitation traits. The interrelationship among key traits is obviously important in mechanisms for coexistence that depend on metacommunity dynamics (e.g., competition-colonization trade-offs; Kneitel and Miller 2004). Relationships among traits may be particularly crucial when considering the food web dimensions of metacommunities, because species engaged in trophic interactions often have radically different spatial strategies and experience the world at different spatial scales. Kolasa and Romanuk (chapter 9) present tantalizing evidence that invertebrate species in a rock pool system have a hierarchy of scales, with entire groups of species having similar abundances and perhaps responding to similar scales of variation in the environment.

Several chapters in this volume begin to relate trophic structure to metacommunity dynamics (Holt and Hoopes, chapter 3; Cottenie and De Meester, chapter 8; Van Nieuwenhuys and Hanski, chapter 4; Miller and Kneitel, chapter 5, Leibold et al. chapter 19). However, much remains to be done. Figure 20.1 depicts a theoretical scheme for how the spatial scaling of population dynamics might depend on trophic level in a community. Figure 20.1A depicts the usual kind of nonspatial food web. In figure 20.1B, species’ spatial scale increases with trophic rank. For instance, a vertebrate herbivore with large home ranges may impact several plant species whose dynamics play out on much smaller spatial arenas; in turn, this herbivore might be sustained by a carnivore with a yet larger home range re-

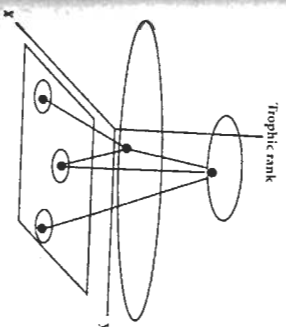
A. Nonspatial food web



B. Food web in space - mobile top predator



C. Food web in space - mobile herbivore



D. Food web in space - mobile basal resources

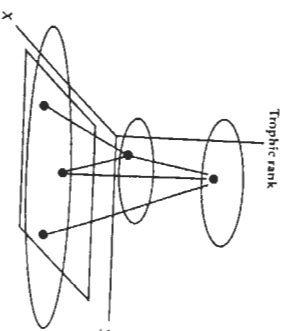


Figure 20.1 A theoretical view of how the spatial scaling of population dynamics might depend on trophic level in a community. Panel A depicts a typical nonspatial food web with species depicted by circles at nodes and lines indicating feeding relationships such that species at higher trophic levels feed on those at lower trophic levels. The same food web is shown in B–D with various spatial scaling relationships for species at particular trophic levels. In B, species’ spatial scale increases with trophic rank, such that top predators have the largest area requirements within a generation. In C, species at intermediate trophic levels have the largest area requirements. In D, basal species are species that are very mobile within generations, such as marine plankton that are carried around by ocean currents. Modified from Holt (1996).

quirement. If trophic rank correlates with body size, and body size defines home range requirements (Schoener 1989), this is the general pattern one expects. Some vertebrate top predators have enormous home ranges (Terborgh et al. 1999). In general, among mammals, for a given body size carnivores have larger home ranges than do omnivores, which in turn have a larger home range than do herbivores (Kelt and Van Vuren 2001). In Arctic tundra ecosystems, mobile avian predators such as jäegers (*Stercorarius* sp.) can aggregate locally due to influx of

individuals drawn from large areas; this behavioral response permits them to act as key regulators of vole and lemming population dynamics (Oksanen et al. 1999). The spatial scale of the rodents' dynamics in turn substantially exceeds that of the clonal and edaphically restricted plant species they eat. There is also often heterogeneity in spatial scaling within trophic levels; for instance, larger-bodied species of herbivores may experience spatial variation in food availability in a coarser fashion than do small-bodied species (Ritchie and Olff 1999). Roland and Taylor (1997) describe how within a well-defined functional group of species with similar body size (insect parasitoids), different species respond to changes in forest structure at different spatial scales.

An increase in trophic rank need not always imply an enlarged spatial scale of population dynamics, and figure 20.1B therefore does not portray all communities. For instance, Thies et al. (2003) analyzed a tritrophic interaction among oilseed rape, the oilseed rape beetle, and its parasitoids in an agricultural landscape. The percent noncrop area in surrounding landscapes was correlated (negatively) with both herbivory and parasitism; the correlation coefficient was strongest for both trophic levels for landscapes surrounding the focal points at a spatial scale of about a 1.5 km diameter. Thus, both trophic levels responded to similar spatial scales of landscape structure. In some communities, species at intermediate or lower trophic levels operate over larger spatial scales than do top predators. For instance, the dynamics of the Serengeti plains of East Africa are driven by the migration of wildebeest and other ungulates, which are attacked by relatively sedentary predators such as lions (Sinclair and Arcese 1994). For this system, figure 20.1C might be a better descriptor of how spatial scale changes with trophic rank. In coupled benthic-pelagic aquatic systems, many filter-feeding trophic occupiers are herbivores or omnivores dependent on a plankton flux of phytoplankton, whose dynamics are determined by water movements at much larger spatial scales. If benthic predators also have in situ recruitment, these communities might be more accurately described by figure 20.1D.

Although figure 20.1 is cast in terms of how trophic rank might lead to variation in the spatial scaling of dispersal and population dynamics within a community, important heterogeneities in dispersal can also arise for other reasons. For instance, many species take a ride on other species to disperse (phoresis; e.g., Pederson and Peterson 2002). These species necessarily have interlocked dispersal rates; a bird-dispersed plant can move no further than the bird it uses, and typically much less. Species experience different mortality risks from disturbances (e.g., due to different microhabitat or resource requirements), which should lead to differences in how dispersal evolves in response to a given disturbance regime. Metacommunity models to date have only just begun to include such trophic structure heterogeneities in spatial scaling relationships. The challenge is to find general scaling relationships; to recognize the dynamical patterns that they generate (fueling further study); and to identify ways of representing these in quan-

titative models, so as to gauge the consequences of such heterogeneities in scale for metacommunity dynamics. Leibold et al. (chapter 19) provide one view of what some of these implications might be for the evolutionary dimension of metacommunities.

The Interface of Metacommunity and Behavioral Ecology

Species with high mobility can provide key linkages among local communities. Sometimes such mobility is driven by external environmental forces (e.g., winds, ocean currents). However, mobile species can also often adaptively modify their movement among habitats. This observation suggests that quantifying spatial linkages among communities will require a merging of the perspectives and theories of community ecology and behavioral ecology. Reseratis et al. (chapter 16) explore some important behavioral dimensions of metacommunity processes (e.g., habitat selection). Here we consider an additional range of issues that warrant more attention.

There are a wide range of empirical examples of mobile species that are likely to couple local communities and that could select habitats nonrandomly. For example, lakes appear islandlike, yet at times wide-ranging mergansers (*Mergus* sp.) and other fish-eating birds have substantial effects on fish. In turn, the effects of birds on fish may indirectly influence the remainder of the lake food web. In marine systems frigatebirds (*Fregata* sp.) can range over 200 km in a single day in their search for resource patches (Weimerskirch et al. 2003).

There is likely to be an interaction between the spatial strategy of a species and many aspects of its foraging ecology. A predator that regularly disperses among communities due to localized disturbances might be faced with a shifting array of available prey species, and so could show selection for trophic generalization and labile diet selection. This implies that the magnitude of spatial coupling between different communities can change rapidly, due to behavioral decisions made by such predators. Alternatively, the ability to move may permit a predator to refine specialized tactics required to attack a particular prey species found in a scattered array of patches, so that dispersal could instead foster trophic specialization. An important task for future work is to examine the evolution of trophic specialization, generalization, and diet plasticity in a metacommunity framework.

Incorporating behavioral responses to spatial variability opens up a rich array of potential effects on population and community dynamics, and many of these may lead to more complex effects in metacommunities. For instance, Sih and Wooster (1994) examined a simple model in which prey could emigrate (or not) in response to predators, and showed that in open systems, increasing local predator abundance could at times lead to an *increase* in local prey abundance. This occurred because reduced prey movements more than compensated for increased mortality. Habitat selection behavior can at times weaken the potential impact of

metacommunity effects (see Keesetaris et al., chapter 16). For instance, Holt (1984; see also Oksanen et al. 1995) considered a simple scenario, in which a predator could limit the abundance of two prey species, each in a distinct habitat. When the predator exhibits ideal-free habitat selection rules (i.e., predators move without cost between habitats and do not interfere with each other), and if the system settles into a demographic equilibrium, the equilibrium abundance of prey in each habitat is expected to be the same as if predators could not move at all. Although species sorting could still occur (e.g., each habitat could contain the prey superior at withstanding predation), the model predicts no mass effect altering local prey species composition or abundance. However, if the predator does not follow ideal-free habitat selection rules, mass effects arise, and prey in lower productivity habitats can be vulnerable to exclusion.

A wide variety of other models have looked at the effects of optimal foraging on metapopulation dynamics (e.g., Sabelis et al. 1991, Krivan 1997, 1998), but there is little work to date on metacommunities. A hint of the rich variety of effects one might expect comes from the work of Schmidt et al. (2000), who examined how coexistence between competitors was influenced by habitat selection when habitats included sinks as well as sources, and dispersal could freely evolve. Temporal variation in local conditions promoted the evolutionary maintenance of dispersal. Schmidt et al. found that if there was a trade-off between competitive ability in the source and mortality in the sink, coexistence could occur that would not be seen in a temporally constant landscape, or if there were fixed movement rules. In this case, because there were reciprocal flows among habitats, a mass effect for both species in the sink indirectly permitted coexistence of both species back in the source, and hence globally. Conversely, if in a stable environment competitive coexistence is permitted by habitat partitioning, temporal variation can select for competitors that behaviorally exploit both habitats, which increases overlap and hence makes coexistence more difficult.

More generally, Bolker et al. (2003) reviewed theoretical studies of community-level effects of behavior and suggested that as a rule of thumb, relative to no behavior, perfect optimization of behavior tended to be more stabilizing for community dynamics, and that suboptimal but adaptive forms of behavior were still stabilizing, but less so. It is not clear whether that generalization would carry across to metacommunities, since there are already both examples that fit and others that do not.

A potential metacommunity effect of habitat selection is seen in work on mobile predators. Mobile predators can selectively move among habitats, permitting the dynamics of different local communities to be indirectly coupled via predator behavior. For instance, outside the breeding season, avian predators can concentrate on areas with high prey density and thereby reduce spatial variability in prey abundance (Norrdahl and Korpinaki 1996, 2000). Kondoh (2003) has argued that adaptive predator foragers (e.g., choosing between prey occurring in differ-

ent patches) could lead to a positive relationship between food web complexity and community persistence because of environmental fluctuations. This formalizes an idea stemming back to MacArthur (1955), and is related to the notion that predator switching broadly stabilizes predator-prey interactions (Post et al. 2000).

Although appealing, there are also clear counter-examples to the notion that adaptive behaviors are a generic stabilizing influence; in some situations, adaptive behaviors by predators moving among habitats can destabilize population dynamics (Abrams 1992; Schmitz et al. 1997; Abrams and Kawecki 1997). The precise nature of the impact of adaptive behaviors on population dynamics depends closely on behavioral details (e.g., do predators instantaneously achieve adaptive optima, or is there a time lag? Abrams and Matsuda, forthcoming; Holt and Kinzler, forthcoming). There are some situations where adaptive foraging can be strongly destabilizing. For instance, localized disturbances can generate spatial ripples in plant-herbivore-predator interactions, the magnitude and spatial extent of which depend on the detailed nature of local foraging and patch use behaviors (Holt and Barfield, unpublished results). If a disturbance greatly reduces prey availability in a given patch, sensible mobile consumers will emigrate into other patches, leading to spikes in consumption there. Mobile consumers can thus magnify the spatial extent of otherwise localized disturbances. So, as with dispersal itself, adaptive foraging by mobile consumers is not likely to be a universal stabilizer of metacommunity dynamics.

Landscape Perspectives on Metacommunities

Many issues in landscape ecology are pertinent to metacommunity issues. Metacommunities are hardly ever comprised of cookie-cutter replicate patches, but instead contain considerable variation in local conditions such as productivity and disturbance regimes. Such heterogeneity has profound implications for metacommunity dynamics. One of the simplest but crucial effects is that if different species are differentially superior in different local conditions, the regional species pool can be maintained (and hence local communities enriched) because of the existence of environmental gradients. This is a critical feature of species sorting models (Leibold 1998; introduced in Holyoak et al., chapter 1). In this section we consider two important sets of phenomena that arise from landscape structure: spillover effects and edge phenomena, and spatial patterning and disturbance.

Spillover Effects and Edge Phenomena

An important topic to which we can barely do justice is that metacommunity dynamics may be strongly influenced by the detailed structure of landscapes. In heterogeneous landscapes, this can lead to the juxtaposition of habitats with sharp differences in productivity and species abundances. Spatial fluxes in resources or

organisms can then be large and asymmetric, leading to effects such as source-sink dynamics and spatial subsidies (the mass effect perspective). A recent book (Polis et al. 2004) is replete with examples of the importance of such fluxes or subsidies for the dynamics of populations, pairs of interacting populations, and entire community structure. Allochthonous inputs of resources (e.g., prey) can have profound consequences for the stability and persistence of local food webs (e.g., Huxel and McCann 1998, Holt 2002). A trickle of allochthonous prey can stabilize locally unstable interactions; conversely, if mobile predators are sustained by productive prey, those mobile predators can severely overexploit prey elsewhere in the landscape. In a wide-ranging review, Polis et al. (1997) highlighted the profound implications for food webs of movement of resources and organisms across habitat boundaries (for recent examples see Fausch et al. 2002; Henschel et al. 2001; Nakano and Murakami 2001; Power 2001). Such flows typically have strong spatial and landscape signals. For instance, rodent damage in Australian macadamia stands is greater in edges next to forests, than in edges next to grasslands (White et al. 1997). In agricultural landscapes, there is a strong effect of distance from the nest site of avian predators on their impacts on prey assemblages, whereas in forests, which have greater habitat structural complexity, the effects may be weaker and more evanescent (Forsman et al. 2001). Stahl et al. (2002) reported that landscape features (e.g., distance to forest) were excellent predictors of lynx predation on sheep in the French Jura.

In a metacommunity context, the concept of subsidies is a simplification of reality, in that the notion of a subsidy implicitly assumes a donor-controlled supply of allochthonous materials, rather than a true dynamic coupling across habitats (or patches, e.g., Donahue et al. 2003). Loreau et al., chapter 18, introduce the idea of metaecosystems as a fuller view of the spatial dynamics of ecosystem coupling. This topic offers a rich set of possibilities, from theoretical to empirical, for coupling systems more fully and for synthesizing a broad swath of ecology.

Interactions between consumers, their required resources, and their predators play out on complex spatial landscapes. This has a variety of consequences. The individual state or condition of a consumer (influencing both demographic parameters and interaction strengths) integrates landscape features as filtered through an organism's movement rules. For instance, Bommarco (1998) found that the fecundity and internal energy reserves of a generalist carabid beetle in heterogeneous agricultural landscapes were sensitive to the perimeter-to-area ratios of arable fields. Consumer movement among foraging patches can be driven by a number of factors, including localized resource depletion, temporal variation in resource supply rates, shifts in vegetation structure (including those due to impacts of food web interactions), and spatial variation in the risk of predation. Movement permits individuals to exploit spatial variation by moving

among habitat patches, thus buffering the effects of temporal variation. But such movements can also lead to enhanced predation risks, and other costs. The magnitude and spatial expression of such risks should depend on the body size of the consumer, and the degree of diet specificity of the predator. Body size influences the size and spatial distribution of suitable foraging patches, and also the nature of predation risk. Generalist predators may exert a relatively fixed background mortality varying across space, whereas specialist predators are likely to temporally shifting landscape of mortality risk. Mobile consumers are likely to engage in "foraging games," which at times can exhibit highly complex dynamics.

Local communities coupled by dispersal necessarily have edges. Fagan et al. (1999) classify edge effects on species interactions into four categories: edges as dispersal filters, edge impacts on mortality, edges as arenas for strong spatial subsidy effects (e.g., consumers that nest in one habitat, but forage in adjacent habitats, e.g., Cook et al. 2004), and edges as generators of novel interactions. As an example of the latter, edges of patches of tropical forest are often "hot spots" of plant production, which sustain insect herbivores, which in turn attract insectivorous predators, which in turn forage some distance into the forest patches themselves (Lovejoy et al. 1989, in Fagan et al. 1999). Thus the patches themselves have additional attributes that may have further implications for metacommunity dynamics. Patches that have their own inherent dynamics (e.g., due to recurrent localized disturbances causing extinctions and initiating succession) are likely to exhibit metacommunity dynamics quite different from patches that are fixed in time and space.

In fragmented landscapes, there can be complex responses of trophic interactions to fragmentation (see also Gonzalez, chapter 6). In forest fragments in the Midwestern United States, nest predation increases with degree of fragmentation and proximity to habitat edge (Robinson et al. 1995). By contrast, ground-nesting birds in chaparral fragments in southern California enjoyed lower predation (mainly from snakes) in smaller fragments (Patten and Bolger 2003). Some of the best examples of trophic cascades in terrestrial systems come from fragmented habitats (e.g., Terborgh et al. 2001).

A key distinction at the interface of landscape ecology and food web theory is between species that are habitat specialists, and those that are habitat generalists, which straddle habitats (Waltho and Kolasa 1994; Cook et al. 2002). Spillover effects from a habitat matrix into embedded patches are likely common in anthropogenically-fragmented landscapes (e.g., Davies et al. 2001, Davies et al., chapter 7). Among species that decline in fragments (not able to utilize the matrix), predators at the top of food chains typically decline more than do their prey (e.g., Davies et al. 2000). Such landscape effects have also been suggested to play an important role in driving population cycles in arctic ecosystems. Oksanen et al. (1999) argue that spillover from productive to unproductive habitat patches

strongly influences the likelihood of population cycles in lemmings and voles in arctic Fennoscandia. Spillover effects are important in many settings, but are particularly striking when sharply different ecosystems are juxtaposed. For instance, Polis and his colleagues (e.g., Polis and Hurd 1996) found that inputs of marine materials onto the verge of small, unproductive desert islands in the Gulf of California had strong impacts on land communities; such effects were negligible in the interior of large islands. Marine reserves are an applied example of where spillover of fish (and other organisms) from protected areas can potentially enhance the annual catch in adjacent fisheries (Roberts et al. 2001).

Spillover effects challenge us to define the relevant spatial scale for considering meta-ecosystem dynamics. Power and Rainey (2000) coined the term *resource shed* (analogous to *watershed*) to define the spatial scale pertinent to resource availability at given points in space. In like manner, even sedentary consumers can cast spatially delimited resource shadows, altering flows of resources among habitats, and these effects may dissipate with distance. Some of the area effects on food chain length noted in Holt and Hoopes (chapter 3) might actually reflect the differential impact of landscape flows on patches or islands of different sizes (Holt and Post, MS).

Spatial Patterning and Disturbance

Much of the metacommunity theory we have considered has ignored the detailed structure of spatial pattern. The pattern of connectivity in landscapes can have profound consequences for trophic interactions, and thus food web structure (With et al. 2002). This may be particularly important when contrasting systems like streams with prairies and the open ocean. Wilson et al. (1995) carried out studies of an individual-based model for Lotka-Volterra predator-prey interactions, contrasting habitats that differed in dimensionality. For example, one-dimensional habitats might include rivers or coastlines, two-dimensional habitats, an open prairie, and three-dimensional habitat, open bodies of water. Wilson et al. (1995) found strong differences in dynamics as a function of habitat dimensionality. One-dimensional habitats were generally less stable and more prone to extinctions, and phase-locked oscillations in abundance occurred at larger scales than in two- or three-dimensional habitats (Wilson et al. 1995). Although their work dealt with two interacting species, habitat dimensionality is likely to have important implications at the level of entire food webs.

The explicit spatial arrangement of habitats within a landscape can have important consequences for metacommunity dynamics. This volume shows a number of important kinds of dynamics that are possible in spatially explicit models, but not in spatially implicit models (see Hoopes et al., chapter 2, and Holt and Hoopes, chapter 3, for examples). However a great deal remains to be done to explore the consequences of spatially referenced landscape structures. If some spe-

cies refuse to cross areas with unsuitable habitat, the flow of dispersers across a landscape becomes sensitively dependent on the presence and spatial arrangement of corridors linking patches. Theoretical models of movement suggest the existence of thresholds in degrees of connectivity, below which dispersal is greatly hampered (With and King 1999; With et al. 1997). Empirical studies have shown that corridors can have substantial effects on dispersal rates, with consequences for population persistence and stability (see e.g., Gonzalez, chapter 6; Tewksbury, Levey, et al. 2002). Dispersal rates are often quite sensitive to landscape structure. For instance, Diffendorfer et al. (1999) showed that the rate of distance of movement by rodents in an old field community was sensitive to the degree of habitat fragmentation; in a more highly fragmented landscape, fewer individuals moved, but those that did move went much further in space, than in a comparable but less fragmented landscape. One great challenge in developing spatially explicit, realistic metacommunity models is that estimating dispersal rates is inherently difficult; this difficulty is greatly magnified if dispersal rates are sensitive to the details of landscape composition and structure, and if one must estimate dispersal across an entire community of interacting species.

Heterogeneous landscapes with large-scale disturbances may exhibit interesting patterns reflecting spatial dynamics of food chains and sequential invasions. Many arthropod systems have patterns that are consistent with these processes (e.g., Rey and McCoy 1979). For example, a popular hypothesis to explain why some species become such rampant pests when introduced into novel environments is that they have escaped their natural enemies (Elton 1951; Keane and Crawley 2002). Wolfe (2002) demonstrated that *Silene latifolia* suffered much higher rates of herbivory, particularly by specialists, in Europe (its native range) than in the site of introduction (North America). She suggested that this “escape” hypothesis was more likely to result from leaving behind specialist enemies, than generalists, because the former is unlikely to be encountered in the novel environment. Although the focus of the invasion literature has been on transcontinental scales, comparable phenomena may be observed (if more subtly) at local scales if there are constraints on the rate of colonization of consumers (relative to their prey) following a disturbance (Glasser 1982). These constraints are particularly pronounced when consumers are specialists. In the first place, colonization by such consumers often must await colonization by their required prey. Moreover, even if a required prey species has colonized, its numbers are likely to initially be too low to permit successful establishment of a specialist natural enemy. These two processes together lead to the expectation that during succession, natural enemies (at least those with specialized diets) may be more sluggish in colonization than are their prey. A limitation of this pattern is that succession does not always proceed lockstep up food chains, because of the role of generalist consumers. For example, Hodgkinson et al. (2002) observed that often the initial stage

of primary succession consists of heterotrophs, whose numbers can be sustained by the allochthonous input of both dead organic matter and living invertebrates, in sufficient numbers to sustain populations of detritivores and predators. Steiner and Leibold (in press) found that assembly models of food web structure involving specialist and generalist consumers could result in strong cyclical assembly trajectories; food chains that build up become vulnerable to invasions by species that compete with low trophic level members of the food chain, that also escape their enemies by immigrating. These successful colonists can then in turn support the assembly of their own food chains, which can be reciprocally invaded by the original low trophic level competitors. Shifts in species composition at one level drive changes in species composition at the adjacent level, which feeds back to alter the species composition of the original level.

Spatial aspects of food chain dynamics can critically influence community responses to disturbance. In 1980, a volcanic eruption at Mount Saint Helens, Washington, extirpated plant and animal communities over a large region, which then underwent succession, a central feature of which was spread of a perennial herb, *Lupinus lapidus*, from remnant patches near the edge. This species plays a key role in ecosystem restoration, because it ameliorates physical conditions and enriches the nitrogen content of the soil. After an initial spurt, reinvasion into available habitat greatly slowed, thereby reducing the rate of succession over a broad landscape. Fagan and Bishop (2000) used experimental manipulations (buttressed by reaction-diffusion models) to show that herbivory by insects was substantially stronger at the invasive edge, than in core regions further from the edge. The magnitude of herbivory was sufficient to greatly hamper the invasive spread of the lupine into empty habitat. Fagan and Bishop argued that the contrast between the core and peripheral zones was likely the result of spatial variation in the impact on insect herbivores of both generalist predators such as spiders (which, though present at the edge, were scarcer there) and specialist parasitoids (which were absent at the edge). In effect, succession occurs up the food chain and because of a lag in response of the top trophic level, herbivory can constrain the spatial spread of crucial producer populations. Indeed, if invasion of the top level is sufficiently slow, there can be a "collapse" of an original range of the basal plant species.

As the chapters in this volume have shown, these various elements—including behavior, heterogeneity of spatial scale among different groups of species, complex attributes of patches and landscapes, and the explicit spatial features of landscapes—all have potentially fascinating implications for refining the views of metacommunity dynamics we have presented in this volume. It is clear that all these factors and the interactions among them have consequences that could potentially modify our views about metacommunity processes. An important challenge for future theoretical and empirical work is to integrate these issues into a deeper theory of metacommunity ecology.

Stability, Complexity, and Metacommunity Dynamics

Metacommunity dynamics have profound implications for our understanding of local interactions. Immigration can lead to the reversal of local competitive dominance and alter both the stability and species richness of predator-prey interactions (Holt 2002; Holt et al. 2003; reviews: Hoopes et al., chapter 2; Mouquet et al., chapter 10).

A central and controversial issue in ecology is the relationship between stability (variously defined) and food web complexity (e.g., May 1973, Polis 1994). Metacommunity dynamics can influence this relationship. First, if there are recurrent weak flows among communities (e.g., adjacent distinct habitats in a landscape). In some circumstances trophic dynamics are directly stabilized (Holt 1984, Closs et al. 1999) so that metacommunity dynamics enrich local communities by reducing local extinction rates (as with allochthonous flows; Polis et al. 1996; Huxel and McCann 1998). Alternatively, if the metacommunity mainly defines a species pool for occasional local colonization episodes, and if local diversity reduces local stability (as in Lotka-Volterra models without strong direct density dependence; May 1973), the realized local stability of communities may be less stable when they occur in metacommunities with richer species pools. Thus the effects of metacommunity species richness on the stability of local communities may depend on the connectivity of the metacommunity patches.

It is unlikely that anything very general can be said about the relationship between rates of external input in complex multispecies webs, and equilibrium population sizes for resident community members. Most ecologists are familiar with the notion of a press perturbation as a kind of experimental manipulation. Less familiar is the recognition that a press perturbation is formally identical to a change in a constant rate of input from external sources. In other words, a press perturbation provides an assessment of the net impact of a small change in external coupling (e.g., the magnitude of a spatial subsidy, such as the immigration rate of a focal species) on all species in the community, including both direct and indirect effects among resident community members. The nature of the problem of predicting equilibrium population sizes can be seen by considering a simple example. Assume that the dynamics of all species in the community are defined by $dN_i/dt = N_i f_i(N) + I_i$, where N_i is the abundance of species i , $\{N\}$ denotes the vector of abundances, and I_i is the input from external sources of species i . The effect of a small increase in input of species i on the equilibrium abundance of species j can be found by evaluating the inverse of the Jacobian matrix (Yodzis 1988; Nakajima 1992; Higgashi and Nakajima 1995), comprised of terms found by evaluating $\partial f_j/\partial N_i$ near equilibrium. In principle, this protocol provides an assessment of how a change in spatial coupling alters local abundances. In practice, Yodzis (1988) showed that a given sign structure of interactions could be compatible with a wide range of quantitatively different impacts, depending on the detailed

magnitude of the interaction matrix elements. But in some circumstances (e.g., relatively simple modules) this approach can be used to gauge the relative impact of allochthonous inputs on different community members. Higashi and Nakajima (1995) provide a methodology for partitioning out interaction chains in terms of direct effects along paths and loops, which may be usefully applied to this problem. In metacommunities, however, the situation is much more complex: populations are regulated at different scales so the functions describing growth involve heterogeneous spatial scales. It is unclear what the consequences of this might be for this matrix approach to quantifying spatial effects.

In communities, in principle one could observe a wide variety of sequences of introductions by species to local communities. Both theoretical and empirical studies suggest that the order of colonization events may matter greatly in determining both the composition of the community, and its temporal dynamics in abundance. For instance, Sait et al. (2000) demonstrated that in a host-pathogen-parasitoid system, the dynamical behavior of the system depends on whether or not the pathogen or the parasitoid is first introduced. This is likely to influence both local extinction rates and the average potential output of propagules that could colonize other sites. Sait et al. suggested that one effect could be a long transient, which could be quite relevant to the dynamics of metacommunities with recurrent local extinctions (e.g., Hoopes et al., chapter 2, Law and Leibold, chapter 11).

There have been relatively few attempts to directly examine the implications of spatial dynamics in entire food webs. Keitt (1997) constructed a spatially explicit, individual-based model of species interactions on a lattice, with spatially localized interactions, and compared the persistence of communities with that expected in a comparable Lotka-Volterra mean-field model with global dispersal. He concluded that spatial localization of local interactions typically permitted the persistence of richer and more strongly connected webs. Adding spatial heterogeneity further promoted the persistence of rich, highly connected webs. The internal spatial structure of a metacommunity thus may have profound consequences for its trophic organization. Documented food webs have structures that have complexities that exceed those predicted by stable linear matrix models, similar to those described above. Much work has gone into identifying ecological factors that could explain the stability of these more complex food webs, including behavioral effects such as functional responses, prey switching, and the presence of refuges. However, it may also be that these food webs do not always represent a local community but rather represent a description of species that interact at various spatial scales; or it may be that dispersal from nearby communities stabilizes the dynamics of these complex food webs. In evaluating these ideas, it would be useful to have more experiments that examine food webs, closed off from their prior connections to a broader metacommunity. Useful insights arise from studies of anthropogenically fragmented habitats (e.g., Digham et al. 1998; Crooks

et al. 1999), but in such studies there is almost always a blending of disruption of an original pattern of spatial flows within the natural landscape, with an imposition of novel flows (e.g., by invasive species) from matrix habitats (e.g., Cook et al. 2002). Disentangling these effects is a difficult yet essential challenge.

The Temporal Dimension of Metacommunities

The metacommunity perspective inevitably focuses on space, and the consequences of coupling among communities, particularly in heterogeneous landscapes. Yet many important aspects of metacommunity dynamics reflect temporal variation in the environment, both directly and indirectly. This is a theme to which we cannot do justice in the remainder of this chapter, but it is worth noting a few key issues.

First, the patch dynamic perspective (Tiljolk et al., chapter 1) includes as a crucial driver rates of local extinctions experienced by different species. Extinctions may arise due to endogenous causes (e.g., due to predator-prey interactions) but also can be caused by disturbances and other causes of temporal spikes in mortality. The relative influence of species sorting versus patch dynamics may reflect the impact of temporal variation in the environment. A crucial desideratum for future work is to integrate metacommunity ecology with disturbance ecology, and, more broadly, nonequilibrium perspectives on community processes (e.g., DeAngelis and Waterhouse 1987).

Second, movement among communities should often vary through time—for many reasons and across many different temporal scales. Many species alternate in their life cycle between relatively sedentary stages and more mobile stages correlated with the annual cycle, which will lead to corresponding variation in spatial coupling among habitats. As a simple example, impacts of migratory birds on small habitat patches or islands located along the migratory route are likely to be seasonally pulsed. If mass effects into a focal habitat arise from emigration from productive habitats, the magnitude of such emigration should fluctuate with temporal variation in abundance of source populations. Mortality during dispersal vary strongly through time (e.g., because of variation in abiotic factors or intensity of predation experienced in transit among patches), so the strength of spatial coupling among patches should also vary. The impact of movement on population size, local coexistence, and stability depends on the strength of local interactions, which themselves can be highly variable (Benedetti-Cecchi 2000); hence, it is likely that the strength of metacommunity processes (e.g., the impact of mass effects, viewed as a press perturbation of a local community) is also quite variable.

Third, unique phenomena may arise when one couples temporal variation with spatial patchiness and heterogeneity. For instance, storage effects promoting coexistence can arise because spatial variation coupled with dispersal permits the retention of local, temporal pulses in production (Chesson et al., chapter 6). Con-

versely, Holt et al. (2003) have shown that mass effects can be greatly magnified in sink habitats if local growth rates are temporally variable and positively autocorrelated through time. Temporal variation in sinks can greatly increase the average abundance of sink populations, making it difficult for locally superior species to persist in the face of an onslaught of immigrants.

Finally, dispersal itself is an evolved attribute of species. There is an enormous literature on the evolutionary ecology of dispersal (e.g., Clobert et al. 2001), and we will not even attempt to summarize it here. Dispersal should be viewed as part and parcel of an organism's life history, determining where an organism will spend its life. Basically, dispersal is expected to be favored most often when there is temporal variation in the environment, with different patterns in different habitats (e.g., weak spatial autocorrelation). Holt (1997) for instance showed that continued utilization of a sink habitat could be an evolutionarily stable strategy, provided the source habitat experienced temporal variation in fitness. Thus, the magnitude of the mass effect imposed on a focal habitat may indirectly reflect the evolutionary consequences of temporal variation in source habitats. Organisms have many alternative evolutionary responses other than dispersal to temporal variation in the environment, including diapause, the development of perenniality and seed banks, and the maintenance of energy reserves during unfavorable seasons. There will often be trade-offs between dispersal and these alternative mechanisms for coping with temporal variation, so species that utilize these alternatives to dispersal in their life-history mechanisms may experience a reduced magnitude of spatial coupling among habitats. This observation suggests that a valuable direction for future research will be to link metacommunity dynamics to general issues of life-history evolution in temporally and spatially varying environments, as this may define which components of the community are most directly involved in metacommunity processes via dispersal.

Evolution depends on variation. An evolutionary perspective on dispersal in a metacommunity context must consider the implications of intraspecific variation both in dispersal abilities and in niche characteristics. There often will be intraspecific variation in dispersal (e.g., residents versus floaters in bird populations), and dispersers may systematically differ from nondispersers in traits key to local interactions. Immigrants are likely to differ in state from residents (e.g., in body size or age), and the act of dispersal may itself entail energetic costs reflected in body stores, immunological responses, and so on. Such differences may have a wide range of consequences that have been almost entirely ignored in the literature of population and community ecology. For instance, the local population size of a consumer may be a very poor predictor of its attack rates on resources. As an example, Puscinus et al. (2000) showed that immigrant and resident voles inflict very different damage rates on tree seedlings.

If a metacommunity is spatially heterogeneous, a species that can persist in a variety of habitats can also develop local adaptations to those habitats, sometimes

very rapidly. This implies that immigrants will often be maladapted relative to residents. In the absence of local adaptation, for single species with direct density-dependence regulating numbers to a stable equilibrium, an increase in immigration will typically increase local population size (the mass effect at the level of single species population dynamics). However, if immigrants are genetically maladapted relative to residents, then an increase in immigration can either have no effect on total population size, or even depress it (Holt 1983). The most severe competitive effect of immigrants may not be exerted on other resident species, but instead on local adapted populations of their own conspecifics. All else being equal, it is likely that this intraspecific effect of dispersal will weaken the importance of mass effects at the community level, with respect to perturbing local competitive dominants. If immigrants are typically weaker and less well-matched to local conditions than are residents, they may be more vulnerable to predation, providing a source of spatial subsidies. Intraspecific variation in traits correlated with dispersal could thus matter greatly in determining the beneficial impact of a supply of allochthonous subsidies of prey for resident predator populations. Mass effects could simultaneously be weak relative to the competitive mechanisms of species sorting in determining local community composition, but key determinants of food web interactions and stability. We feel that a crucial area of future work in metacommunity ecology will be the integration of ecological models of local and regional processes, with microevolutionary theory on the evolution of species' traits such as dispersal and resource, and macroevolutionary theory on diversification (see also Leibold et al., chapter 19).

The Relevance of the Metacommunity Concept to Applied Ecology

This book has focused primarily on fundamental issues in basic ecology, such as understanding the factors maintaining the diversity of ecological communities. However, insights that emerge from the metacommunity perspective clearly have many messages for crucial issues in applied ecology. It would require another large volume to fully address this topic, so here we simply outline some key linkages between metacommunity ecology and applied ecology. The following observations are not meant to be exhaustive, but rather to indicate potential domains of application of metacommunity ideas and theories.

One of the dominant issues in global change is the destruction and fragmentation of natural habitats (Kruess and Tscharntke 1994). These changes can both shrink the regional species pool and reduce connectivity among remnant patches of the original habitat types. Given that in the original, unaltered habitats, metacommunity processes were important in determining the maintenance of local as well as regional species richness, and in determining the development of adaptive matches between organismal traits and the environment, anthropogenic perturbation of these dynamics can obviously entail a corrosion in biodiversity, and the

development of species assemblages that are not likely to be resilient to further change.

Another crucial aspect of global change is the homogenization of the world's biota via anthropogenic transport. Introduced nonnative invasive species can potentially impact metacommunity processes in a variety of ways. By reducing population sizes of natives, they may for instance make regional persistence more difficult, even if the invasive species do not directly cause local extinctions. If physical transport or phoretic processes are responsible for connecting habitat patches in a metacommunity, those invasive species that can potentially do the most damage are those that can be carried by those same processes. Coupling between anthropogenic matrix habitats and patches of natural habitats can have serious consequences because of the spillover of invasives into the natural fragments.

Many pest problems and solutions involve metacommunity dynamics. For instance, it is clear that impacts of biological control agents on target species are often quite sensitive to the structure of the landscape in which the control is being attempted (Thies and Tscharntke 1999). For instance, alternative prey present in one habitat may sustain a wide-ranging natural enemy population more effectively than would otherwise be possible, thereby contributing to control against a target pest.

Harvesting of natural populations is also strongly influenced by metacommunity processes. A very active area in fisheries biology, for instance, has been the development of the concept of marine and (more broadly) aquatic reserves (e.g., Roberts et al. 2001). These reserves matter precisely because there is expected to be a spatial coupling between protected reserves and unprotected harvested areas. This spatial coupling is experienced (albeit to different degrees) by all the species in the food web in which harvested species live, so a full understanding of the potential and risks of marine reserves requires a metacommunity perspective.

There is a growing appreciation of the need to apply insights from landscape ecology to the practices of natural resource management (Liu and Taylor 2002). We suggest that a deep understanding of metacommunity dynamics is also an essential ingredient in developing coherent strategies of natural resource management that pay due respect to the complex, multiscale, multispecies dynamics of the natural world.

Conclusions

Understanding how biological processes operate over multiple spatial and temporal scales is a central challenge in contemporary ecology. We suggest that in grappling with this challenge, the ideas we have put forth in this book will play a central role. Understanding the forces that influence the maintenance of biological diversity requires an appreciation of processes operating at multiple scales, from the level of individual interactions as mediated by behavior and life-history

traits, through the domain of landscape patterns and processes, to finally the realm of biogeography and macroevolutionary dynamics. An explicit consideration of metacommunity dynamics provides a bridge between the local processes that have dominated the ecological literature for so long, and the regional to continental scale processes that have long been relegated to biogeography and evolutionary biology. In turn, a mechanistic understanding of metacommunity dynamics will require a fusion of these large-scale pattern and process studies with analyses of individual behavior and life history variables, all in the context of explicit landscape structures. The metacommunity perspective, we suggest, provides a crucial link in the ongoing dialectic among ecologists about how best to relate patterns and processes at different levels in the hierarchy of life.

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