Spatial Dynamics of Foodwebs

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coexistence, competition, dispersal, predation, spatial heterogeneity, spatial structure

Abstract
Foodwebs are important units of biodiversity, and yet, our knowledge of their spatial dynamics is sketchy at best. Here I attempt to synthesize existing knowledge into a framework that can both identify crucial gaps in the theory as well as facilitate empirical investigations. The synthesis is based on two major axes, foodweb complexity and type of movement, and considers two types of spatial effects, foodweb persistence via a reduction in local extinction and foodweb diversity via an increase in species coexistence. It highlights both invariant properties that are robust to increasing foodweb complexity and emergent properties that result from the interplay between foodweb dynamics and type of movement. It underscores the need for a comparative theoretical framework that can yield testable predictions.
1. INTRODUCTION

Foodwebs, collections of species that are linked by trophic interactions, are an important unit of biodiversity. They are also inherently spatial entities, made so by species using dispersal as a means of both procuring key resources and avoiding natural enemies. Foodwebs are also complex entities because indirect interactions between species often have nonintuitive outcomes. Thus, our grasp of their spatial dynamics is necessarily poorer than our grasp of spatial dynamics in pairwise species interactions. Although recent years have seen significant progress in understanding foodwebs in a spatial context, most of this knowledge remains sketchy and fragmented.

Here I attempt to synthesize current knowledge on spatial foodweb dynamics into a framework that serves both to identify key gaps in the theory as well as to stimulate empirical investigations. To this end, I introduce two major axes, foodweb complexity and type of movement, along which existing knowledge could be organized. I consider two types of spatial effects: mechanisms that increase foodweb diversity by allowing coexistence of species that cannot otherwise do so within foodwebs, and mechanisms that increase foodweb persistence by preventing, or reducing the risk of, species extinctions during periods of low abundances. I discuss both the invariant properties that carry over from nontrophic (e.g., competition) and pairwise trophic (e.g., predator-prey, host-parasite) interactions, and the emergent properties that result from the interplay between spatial processes and local foodweb dynamics. I end with suggestions for future directions, both theoretical and empirical.

2. BACKGROUND

2.1. Axes for Studying Spatial Foodweb Dynamics

Foodweb complexity and type of movement provide two major axes for synthesizing current knowledge on spatial foodweb dynamics. I consider foodweb modules [subsets of interacting species within larger foodwebs (Holt 1997a)] because these are the units whose spatial dynamics have thus far been studied. On the complexity axis I consider two distinct categories of foodweb modules (Figure 1) with well-characterized spatial dynamics. On the spatial axis I consider two fundamentally different types of movement.

2.1.1. Foodweb complexity. The complexity axis is based on two properties. The first is local niche partitioning, the ability of species to coexist within a community by partitioning resources and/or natural enemies in the absence of any differences between species in when or where they exploit resources or respond to natural enemies (i.e., no spatial or temporal niche partitioning; Chesson 2000). When two or more species are limited by a single niche axis (e.g., a single limiting resource or a natural enemy), local niche partitioning is not possible. In contrast, when two or more species are limited by multiple niche axes (e.g., multiple resources and/or natural enemies), local niche partitioning is possible.

The second property that characterizes the complexity axis is the potential for local extinction. Foodweb modules with fluctuating species abundances are more susceptible to local extinctions because species experience demographic stochasticity and/or Allee effects during periods of low abundances. Fluctuations in abundances typically occur when foodweb modules contain strong consumer-resource links, i.e., when resource species have high growth rates and consumer species have high attack rates (McCann et al. 1998). Such fluctuations can be transient (e.g., decreasing fluctuations that precede the attainment of steady state), persistent (e.g., bounded fluctuations such as limit cycles and chaos), or divergent (e.g., increasing fluctuations that eventually cause
Figure 1
Foodweb modules of increasing complexity. (a) Exploitative competition involves two consumer species engaging in an indirect, mutually negative interaction through their use of a common limiting resource. (b) Apparent competition involves two prey species engaging in an indirect, mutually negative interaction through a common natural enemy. (c1) Intraguild predation involves two consumer species that interact indirectly via exploitative competition and directly via predation or parasitism. It is a special case of omnivory (c2) where a consumer species exploits resources that occupy different trophic levels. (d) Predation involves two consumer species that interact indirectly via exploitative and apparent competition.
population crashes). Persistent or divergent fluctuations typically result from saturating functional responses in consumers or from time delays in density-dependent feedback processes (Murdoch et al. 2003). The greater the number of strong consumer-resource links within a foodweb module, the greater the potential for population fluctuations that predispose species to extinction at low abundances.

Exploitative and apparent competition represent foodweb modules (Figure 1) in which local niche partitioning is not possible. With exploitative competition, the $R^*$ rule operates in the absence of dispersal, and the consumer species that can depress resource abundance to the lowest level excludes all others (Tilman 1982). With apparent competition, the $P^*$ rule operates in the absence of dispersal, and the prey species that can support the highest predator abundance excludes all others (Holt et al. 1994). Species-specific differences in the nonlinearity of functional responses can allow coexistence in the absence of spatial processes (Armstrong & McGehee 1980), but this mechanism operates only weakly at best when consumer species are limited by a single niche axis (Abrams 2006) and is in fact augmented by spatial processes (Wilson & Abrams 2006).

Exploitative and apparent competition modules each contain two consumer-resource links (Figure 1). If both links are sufficiently strong they can cause fluctuations in species abundances. Alternatively, a strong consumer-resource link counteracted by a weak one can cause a damping of fluctuations (McCann et al. 1998).

Intraguild predation (IGP) [more generally, omnivory (Pimm 1982)] and predation (Figure 1) represent foodweb modules in which local niche partitioning is possible. Local niche partitioning can occur via interspecific trade-offs such that the superior resource competitor is more susceptible to predation or parasitism (Arim & Marquet 2004, Holt & Polis 1997, Leibold 1996). These modules contain more consumer-resource links (three in IGP/omnivory, four in predation; Figure 1) than exploitative and apparent competition. They therefore have a greater potential to exhibit fluctuations in species' abundances, particularly if strong consumer-resource links are more numerous than weak consumer-resource links.

Because local niche partitioning cannot occur in the exploitative and apparent competition modules, spatial dynamics are essential for species coexistence (in the absence of temporal processes or other ameliorating factors). Because local niche partitioning can occur in IGP/omnivory and predation modules, spatial dynamics are not essential for coexistence. However, two factors suggest a key role for spatial dynamics in these modules as well. First, coexistence via a competition-predation trade-off is possible only at intermediate levels of resource productivity or predator mortality: If productivity (or mortality) is too high or too low, one species gains an overall advantage and excludes the other (Amarasekare 2007b, Holt & Polis 1997, Leibold 1996, Noonberg & Abrams 2005). Thus, long-term coexistence in variable environments requires additional mechanisms besides the trade-off (Amarasekare 2007b). Second, the greater number of consumer-resource links increases the potential for transient or persistent fluctuations (Holt & Polis 1997, Noonberg & Abrams 2005) and hence the risk of local extinction during periods of low abundances. In the absence of spatial dynamics, such extinctions could substantially reduce species diversity within foodwebs (Amarasekare 2008, Noonberg & Abrams 2005).

### 2.1.2. Type of movement

There are two main types of movement that occur in foodwebs: movement associated with behavioral processes (e.g., foraging) that operates on faster timescales than local foodweb dynamics (e.g., births, deaths, species interactions) and movement associated with demographic processes (e.g., emigration, immigration, colonization) that operates on comparable or slower timescales than local foodweb dynamics (Table 1). Movement associated with behavioral processes leads to spatial coupling of foodwebs (McCann et al. 2005, Moore et al. 2004), while movement associated with demographic processes leads to metacommunity dynamics (Holyoak
Table 1  The two main types of spatial dynamics

<table>
<thead>
<tr>
<th>Property</th>
<th>Spatial coupling</th>
<th>Metacommunity dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type of movement</td>
<td>Behavioral (e.g., foraging)</td>
<td>Demographic (e.g., dispersal)</td>
</tr>
<tr>
<td>Timescale of movement</td>
<td>Faster than local dynamics</td>
<td>Slower than or comparable to local dynamics</td>
</tr>
<tr>
<td>Spatial scale of movement</td>
<td>Larger for consumers than resources</td>
<td>Similar in consumers and resources</td>
</tr>
<tr>
<td>Species</td>
<td>Consumers at upper trophic levels</td>
<td>Species at all trophic levels</td>
</tr>
<tr>
<td>Foodweb type</td>
<td>Fluctuating local dynamics</td>
<td>All types of local dynamics</td>
</tr>
<tr>
<td>Main effect(s)</td>
<td>↑ Foodweb persistence by ↓ local extinction</td>
<td>↑ Foodweb persistence by ↓ local extinction</td>
</tr>
<tr>
<td></td>
<td>↑ Foodweb diversity by ↑ species coexistence</td>
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et al. 2005, Leibold et al. 2004). Below I discuss the distinguishing features of these two types of movement.

Spatial coupling occurs via the foraging movement of consumers that are more mobile than their resources (McCann et al. 2005, Moore et al. 2004). Consumer movement occurs on a faster timescale than local foodweb dynamics and makes the dynamics of species at lower trophic levels spatially interdependent. Consumers’ impact on foodweb dynamics occurs largely through switching behavior and omnivory (McCann et al. 2005), and the nature of such impacts depend on the spatial scales of consumer foraging versus resource distributions (McCann et al. 2005, Moore et al. 2004). Spatial coupling has its strongest impact on foodweb modules with fluctuating local dynamics. Switching behavior and omnivory can dampen fluctuations and enhance foodweb persistence (McCann et al. 2005).

Metacommunity dynamics occur via the demographic movement (dispersal) of one or more species between foodweb modules in different localities (Holyoak et al. 2005, Leibold et al. 2004). Dispersal can be on the same timescale as local foodweb dynamics (in the case of emigration-immigration dynamics) or on a slower timescale than local foodweb dynamics (in the case of extinction-colonization dynamics). Unlike spatial coupling, dispersal of species at all trophic levels can influence foodweb dynamics. Dispersal that occurs on the same timescale as local foodweb dynamics can alter the outcome of species interactions (e.g., by preventing competitive exclusion or resource overexploitation by consumers). Dispersal that occurs on longer timescales has no impact on the outcome of local species interactions, but can allow species to recolonize habitats from which they are driven extinct (Amarasekare 2003, Amarasekare et al. 2004). Metacommunity dynamics can have strong effects on foodweb modules both with and without fluctuating local dynamics.

2.2. Mathematical Approaches to Studying Spatial Foodweb Dynamics

Spatial coupling is investigated using models that explicitly consider foodweb dynamics within localities (McCann et al. 2005, Moore et al. 2004). Metacommunity dynamics are investigated via several approaches. Extinction-colonization dynamics are typically studied in metacommunities consisting of an infinite number of patches (Levins 1969, 1970); species’ occupancy patterns are the state variable of interest. Emigration-immigration dynamics, in which species’ abundances are the state variable of interest, are studied via two approaches. One (implicit spatial structure and global dispersal) considers metacommunities with a small number of patches, the dynamics of which are explicitly modeled (Abrams & Wilson 2004, Amarasekare & Nisbet 2001, Amarasekare et al. 2004); exact spatial locations of patches are not typically considered, and dispersal is global
(i.e., organisms can traverse the entire spatial extent of the metacommunity). The other (explicit spatial structure and local or global dispersal) considers metacommunities with a large but finite number of patches, the dynamics of which are either explicitly modeled or reduced to a set of rules (Bonsall & Hassell 2000, Briggs & Hoopes 2004, King & Hastings 2003); exact spatial locations of patches are considered (typically organized in a lattice), and dispersal is local (only to a fixed number of neighboring patches) or global.

### 2.3. Insights from Spatial Dynamics of Competitive and Pairwise Consumer-Resource Interactions

I now discuss the key properties that emerge from investigations of spatial dynamics in competitive and pairwise consumer-resource interactions. These insights are based on studies of metacommunity dynamics. Spatial coupling does not apply to competitive interactions without resource dynamics (e.g., Lotka-Volterra competition models) and has not been studied in pairwise consumer-resource interactions.

#### 2.3.1. Spatial dynamics of competition

With competition, the main effect of spatial dynamics is to allow the coexistence of species that cannot do so in the absence of dispersal. This occurs via two mechanisms, both mediated by random dispersal. The first mechanism occurs in a spatially homogeneous competitive environment, i.e., species’ competitive rankings are invariant in space such that the same species is the superior competitor everywhere (Amarasekare 2003, Amarasekare et al. 2004). In such an environment, an inferior competitor cannot maintain a positive growth rate when rare in the absence of dispersal. Thus, all populations are sinks for the inferior competitor and sources for the superior competitor. As a result, the inferior competitor is excluded from the entire metacommunity. However, local coexistence of inferior and superior competitors is possible if the latter is more mobile (Kishimoto 1990, Takeuchi 1989). Higher emigration of the superior competitor from a given locality reduces the strength of interspecific competition and allows the inferior competitor to invade when rare even when it is immobile. Because coexistence requires high emigration of the superior competitor without requiring any dispersal of the inferior competitor, I term this mechanism emigration-mediated coexistence.

The second mechanism occurs in a spatially heterogeneous competitive environment, i.e., species’ competitive rankings vary in space such that each species has localities in the landscape where it is the superior competitor (Amarasekare 2003, Amarasekare et al. 2004). Such an environment leads to a source-sink structure with each species having localities within which it can exclude its competitors in the absence of dispersal (sources) and localities within which it cannot (sinks). Dispersal from source to sink populations can enable local coexistence of competitors provided species’ dispersal rates are sufficiently low so as to preserve spatial variation in competitive rankings, and the dispersal rate of the overall inferior competitor across the landscape is lower than that of the overall superior competitor (Amarasekare & Nisbet 2001, Amarasekare et al. 2004, Kishimoto 1990, Mouquet & Loreau 2002, Takeuchi 1989). Because coexistence requires the dispersal of both superior and inferior competitors from source to sink habitats, I term this mechanism source-sink coexistence. In both emigration-mediated and source-sink coexistence, negative density dependence induced by random immigration (Holt 1993) stabilizes coexistence provided dispersal levels are sufficiently low (Amarasekare & Nisbet 2001, Amarasekare et al. 2004, Mouquet & Loreau 2002). Both mechanisms require that the overall inferior competitor be less mobile than the overall superior competitor. However, in emigration-mediated coexistence this requirement has to be met at the local community scale, while in source-sink coexistence it has to be met at the metacommunity scale.
Very little is known about the effects of nonrandom dispersal on spatial competitive coexistence. The one study I am aware of (Armsworth & Roughgarden 2005) compared the effects of random versus fitness-dependent dispersal (i.e., movement from areas of lower fitness to areas of higher fitness) on species coexistence. Given spatial variation in competitive rankings, low rates of random dispersal increase both local and regional diversity, while high rates decrease both local and regional diversity. In contrast, fitness-dependent dispersal decreases local diversity and increases regional diversity. Fitness-dependent dispersal also results in more distinctive local communities and hence greater between-community ($\beta$) diversity (Armsworth & Roughgarden 2005).

2.3.2. Spatial dynamics of pairwise consumer-resource interactions. The main effect of spatial dynamics is to increase the persistence of consumer-resource interactions with fluctuating species abundances. This can occur via three mechanisms (Briggs & Hoopes 2004, Murdoch et al. 2003). The first mechanism arises when spatial heterogeneity (e.g., spatial variation in species’ traits) leads to asynchronous consumer-resource dynamics in different localities of the landscape. Limited amounts of random dispersal between localities cause the per capita immigration rate into a locality to decrease with increasing local density (Briggs & Hoopes 2004; Holt 1993; Murdoch et al. 1992, 2003; Nisbet et al. 1992). The resulting negative density dependence in per capita growth rate stabilizes the local community, i.e., a consumer-resource interaction that exhibits neutral or limits cycle oscillations is converted into one that exhibits a stable-point equilibrium (or a consumer-resource interaction that exhibits complex dynamics, such as chaos, is converted into one that exhibits simpler dynamics, such as a stable-limit cycle). Reduced fluctuations at the local community scale lead to reduced fluctuations at the metacommunity scale, thus enhancing consumer-resource persistence at both scales. This mechanism typically emerges in models of explicit consumer-resource dynamics within patches and emigration and immigration between patches. It requires that dispersal be sufficiently low so as to preserve asynchronous population trajectories in different localities (Briggs & Hoopes 2004, Murdoch et al. 2003).

The second mechanism arises when consumer and resource individuals interact in spatially continuous environments that are also homogeneous. Such interactions are studied via spatially explicit, individual-based models that link individual behavior with population dynamics (de Roos et al. 1998, McCauley et al. 1996). When the resource species has limited dispersal but the consumer disperses globally, resource density becomes highly variable in space. The combination of spatial variation in resource density and a nonlinear (Type II) functional response in the consumer reduces overall consumer efficiency and stabilizes the consumer-resource interaction (Briggs & Hoopes 2004, Murdoch et al. 2003). The outcome is a stable spatial distribution with areas of high and low resource density and uniform consumer density (de Roos et al. 1998, McCauley et al. 1996). This mechanism differs from the first in three ways: (a) it arises in a spatially homogeneous environment, (b) it involves limited dispersal in the resource but not the consumer, and (c) stability arises from the interplay between spatial variation in resource density and a nonlinear consumer functional response rather than through the negative feedback effect of random immigration.

The third mechanism also arises in spatially explicit, individual-based models of consumer-resource interactions in spatially homogeneous environments. It differs from the first two mechanisms in that there is no stabilization of the consumer-resource interaction at the local scale. Limited consumer dispersal enables the maintenance of locally distinct consumer-resource dynamics in different parts of the landscape. Species’ abundances within such localities exhibit persistent fluctuations, but the total abundance across the metacommunity exhibits greatly damped fluctuations (de Roos et al. 1991, McCauley et al. 1993). This is a purely statistical effect (termed statistical
Table 2  Current knowledge on spatial foodweb dynamics\(^a\)

<table>
<thead>
<tr>
<th>Foodweb module</th>
<th>Spatial coupling (foraging)</th>
<th>Extinction-colonization dynamics</th>
<th>Metacommunity dynamics (dispersal)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Implicit(^b)</td>
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<td></td>
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<td>Local(^c)</td>
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<tr>
<td>Exploitative competition</td>
<td>-</td>
<td>-</td>
<td>X(^{(1)})</td>
</tr>
<tr>
<td>Apparent competition</td>
<td>-</td>
<td>X(^{(1)})</td>
<td>-</td>
</tr>
<tr>
<td>IGP/omnivory</td>
<td>X(^{(1)})</td>
<td>X(^{(1)})</td>
<td>-</td>
</tr>
<tr>
<td>Predation</td>
<td>X(^{(1)})</td>
<td>X(^{(1)})</td>
<td>-</td>
</tr>
</tbody>
</table>

\(^a\) The number of studies that have investigated a particular topic is given in superscripted parentheses.

\(^b\) Type of spatial structure.

\(^c\) Scale of dispersal.

stabilization; de Roos et al. 1991) that arises owing to the summation of asynchronous population trajectories across different localities. It does, however, have an important effect on consumer-resource persistence. Fluctuations may cause local extinction of consumers and resources in some parts of the landscape, but asynchronous dynamics and limited dispersal prevent global extinction of the metacommunity (Briggs & Hoopes 2004, Murdoch et al. 2003).

3. SPATIAL DYNAMICS OF FOODWEB MODULES

Table 2 summarizes existing theory on the spatial foodweb dynamics, and Table 3 summarizes the main findings. Here I discuss the major insights that emerge from synthesizing current knowledge along the foodweb complexity and movement axes. I pay particular attention to invariant properties, mechanisms operating in competitive and pairwise consumer-resource interactions that also appear in foodweb modules, and novel properties, mechanisms that emerge from the interplay between foodweb dynamics and spatial processes.

3.1. Foodweb Modules with No Local Niche Partitioning and Weak Tendency for Fluctuating Dynamics

Spatial coupling via foraging movement has not been investigated in these community modules. The spatial effects discussed below are due to metacommunity dynamics. I first present general insights from emigration-immigration dynamics that are robust to spatial structure (implicit versus explicit) and the scale of dispersal (local versus global). I then discuss the more specific outcomes. The greater emphasis on emigration-immigration dynamics is because of the paucity of studies investigating extinction-colonization dynamics in these foodweb modules.

Although exploitative competition involves species that necessarily occupy the same habitats because they share a common resource, apparent competition can involve prey species that occupy the same habitats or are specialized to different habitat types. In the former case, dispersal of the apparent competitors themselves can influence coexistence, while in the latter case it is the predator’s dispersal that influences coexistence. I consider both cases.

3.1.1. Exploitative and apparent competitors co-occurring in the same habitats. Dispersal allows local consumer coexistence via the two mechanisms observed in competitive interactions. The first, emigration-mediated coexistence, operates in the exploitative competition module when resource traits (e.g., resource productivity) vary spatially but consumers’ traits do not, i.e., the
<table>
<thead>
<tr>
<th>Type of movement</th>
<th>Foodweb complexity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No local niche partitioning (LNP), weak tendency for fluctuating dynamics</td>
</tr>
<tr>
<td></td>
<td>Exploitative competition</td>
</tr>
<tr>
<td>Spatial coupling (persistence)</td>
<td>Omnivory → ↑ persistence&lt;sup&gt;a,c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Metacommunity dynamics (persistence)</td>
<td>Low dispersal + asynchrony → ↑ persistence</td>
</tr>
<tr>
<td></td>
<td>High dispersal → ↓ asynchrony → ↓ persistence</td>
</tr>
<tr>
<td>Spatial coupling (diversity)</td>
<td>Persistence → ↑ diversity</td>
</tr>
</tbody>
</table>
| Metacommunity dynamics (diversity) | Dispersal of inferior competitor (apparent competitor) | Dispersal of superior competitor (apparent competitor) | Coexistence mechanism | Dispersal of predator-resistant inferior competitor<sup>c</sup>:
| Zero/low | High | Emigration-mediated | Low → LNP + source-sink |
| Lower | Higher | Source-sink | High → LNP + emigration-mediated + source-sink |

<sup>a</sup>Increased persistence when the consumer's local foraging scale is larger than the resource habitat scale.

<sup>b</sup>Increased persistence when the consumer's local foraging scale is smaller than the resource habitat scale.

<sup>c</sup>Keystone disperser effect.

consumer species' \( R^* \) values do not vary in space (Abrams & Wilson 2004, Namba & Hashimoto 2004). Emigration-mediated coexistence occurs in the apparent competition module when the predator's traits (e.g., attack rate, mortality) vary spatially but the prey species' traits do not, i.e., the prey species' \( P^* \) values do not vary in space (Namba 2007, Namba et al. 1999). In exploitative competition, if the superior competitor (i.e., the species with the lower \( R^* \)) is mobile but the inferior competitor is immobile, random dispersal leads to a net movement of the superior competitor from habitats of higher resource productivity to habitats of lower resource productivity. This reduces the strength of competition in the more productive habitat and allows the inferior competitor to invade when rare. Now the inferior competitor can maintain a self-sustaining population and coexist with the superior competitor in the more productive habitat (Namba 2007). If the inferior competitor also disperses but is less mobile, it can maintain a sink population in the less productive habitat (Abrams & Wilson 2004, Namba & Hashimoto 2004). Thus, dispersal ensures both local and regional coexistence. The same outcome occurs in apparent competition. When the superior apparent competitor (i.e., the species with the higher \( P^* \)) is mobile and the inferior apparent competitor is immobile, random dispersal leads to the net movement of the superior apparent competitor from the habitat with higher predator mortality to the habitat with lower predator mortality. This reduces the strength of apparent competition in the habitat with higher predator mortality and allows the inferior apparent competitor to invade when rare. If the inferior apparent competitor is mobile but less so than the superior apparent competitor, it can maintain a sink population in the habitat with lower predator mortality (Namba 2007, Namba et al. 1999).
The second mechanism, source-sink coexistence, operates when there is spatial variation in consumer (exploitative competition) or prey (apparent competition) species’ traits, i.e., species’ R* and P* values vary in space such that each species has localities in the landscape where it is the superior competitor (or apparent competitor). Dispersal can allow both local and regional coexistence provided both species’ dispersal rates are sufficiently low and the overall inferior competitor’s dispersal rate is lower than the overall superior competitor’s dispersal rate (Namba 2007, Namba & Hashimoto 2004, Namba et al. 1999). Both emigration-mediated and source-sink mechanisms allow stable consumer coexistence via negative density dependence induced by random immigration (Amarasekare et al. 2004, Briggs & Hoopes 2004, Holt 1993).

Consideration of explicit spatial structure and local dispersal provides additional insights into the spatial coexistence of apparent competitors. These insights emerge from coupled map lattice models with explicit within-patch dynamics and nearest-neighbor dispersal (Bonsall & Hassell 2000). When the apparent competitive interaction between two insect hosts that share a common parasitoid exhibits divergent oscillations, limited mobility of the inferior host (i.e., a lower dispersal rate than that of the superior host and parasitoid) results in the superior host and the parasitoid having a high degree of spatial overlap and the inferior host and the parasitoid having minimal overlap (Bonsall & Hassell 2000). Spatial patterning due to differential dispersal thus creates refuges for the inferior host, allowing it to coexist with the superior host. Interestingly, with explicit spatial structure and local dispersal, coexistence can also occur if the inferior host is more mobile than the superior host or the parasitoid; a higher dispersal rate allows the inferior host to escape parasitism locally and to move to parasitoid-free areas (Bonsall & Hassell 2000). Thus, when dispersal is localized to the neighboring habitats, both the fugitive and the sedentary strategies allow an inferior apparent competitor to coexist with a superior apparent competitor.

The spatial patterns that enable the coexistence of apparent competitors under localized dispersal (Bonsall & Hassell 2000) may not necessarily be robust to spatial environmental heterogeneity or habitat loss (King & Hastings 2003). Consideration of explicit spatial structure and global dispersal [via coupled map models with explicit within-patch dynamics and metacommunity-wide dispersal (King & Hastings 2003)] shows that coexistence does not require spatial patterning. Rather, it occurs via the formation of clusters, collections of patches that exhibit identical dynamics. Within a given cluster, the inferior apparent competitor could be driven to low densities but is rescued from extinction via immigration between clusters that exhibit asynchronous dynamics. Interestingly, here too coexistence is possible when the inferior apparent competitor has a higher dispersal rate, but this is due less to the fugitive life style than to having a higher between-cluster immigration rate and hence a stronger rescue effect (King & Hastings 2003). As with pairwise consumer-resource interactions, a dispersal rate that is sufficiently low so as to preserve asynchronous dynamics in different clusters is necessary for coexistence.

3.1.2. Exploitative and apparent competitors specialized to different habitat types. Prey species that share a predator do not experience apparent competition when they occupy different habitat types and the predator is immobile. However, predator dispersal between habitat types can create apparent competition and cause the inferior apparent competitor’s exclusion from the entire metacommunity. This result emerges in analyses of both emigration-immigration dynamics (Holt 1984) and extinction-colonization dynamics (Holt 1997b).

3.1.3. Summary of key results. Effects of spatial dynamics on exploitative and apparent competition modules are broadly similar to those observed in competitive and pairwise consumer-resource interactions. Spatial coexistence occurs via the same mechanisms (emigration-mediated
and source-sink). When local dynamics fluctuate, asynchronous dynamics and limited dispersal increase both local and metacommunity persistence.

### 3.2. Foodweb Modules with Local Niche Partitioning and Strong Tendency for Fluctuating Dynamics

Metacommunity dynamics have been investigated in both the IGP and predation modules. Spatial coupling has been investigated in the omnivory module and in a modified predation module (consumer-resource webs in different localities are linked by predator foraging). Below I discuss the key outcomes of these investigations.

#### 3.2.1. Metacommunity dynamics

Metacommunity dynamics of the IGP and predation modules differ from those of exploitative and apparent competition. This is because of the potential interplay between local and spatial coexistence mechanisms. Local consumer coexistence can occur via an interspecific trade-off if the inferior resource competitor is less susceptible to a common predator [keystone predation (Leibold 1996, Noonberg & Abrams 2005)] or preys on or parasitizes the superior competitor [IGP (Arim & Marquet 2004, Holt & Polis 1997, Polis et al. 1989)]. Such a trade-off is typically considered to arise from life history differences (Holt & Polis 1997, Leibold 1996). It can also arise via limited movement of individuals within spatially structured local communities. For instance, two consumer species that differ in their reproductive rates but have similar levels of predator susceptibility (i.e., no life history trade-offs) can coexist if the consumer with the higher reproductive rate (superior competitor) attains a more clumped spatial distribution and is therefore subject to more predator attacks than is the consumer with a lower reproductive rate [inferior competitor (Kondoh 2003)]. Long-term coexistence requires intermediate rates of predator attack, with lower or higher attack rates causing the exclusion of the inferior and superior competitors, respectively.

The two types of metacommunity dynamics (extinction-colonization versus emigration-immigration) have quite different effects on foodweb persistence and diversity. I discuss these next.

#### 3.2.1.1. Extinction-colonization dynamics: local versus regional diversity

When a competition-predation trade-off allows local coexistence of consumers that share a predator, extinction-colonization dynamics can significantly enhance consumer coexistence at the metacommunity scale. Coexistence requires that predators have high colonization rates and only weak effects on consumer extinction (Shurin & Allen 2001). Local niche partitioning via a competition-predation trade-off can also cause local species diversity to increase linearly with regional diversity and provides a potential mechanism for the observation of such linear relationships in nature (Shurin & Allen 2001). The important implication is that a combination of local and spatial coexistence mechanisms can both increase diversity as well as mediate diversity relationships at different spatial scales. However, recent studies show that trade-off-mediated local niche partitioning does not guarantee coexistence when communities exhibit fluctuating local dynamics and/or experience spatial variation in resource or predator traits (Noonberg & Abrams 2005, Amarasekare 2008). Thus, it is unclear whether the same diversity relationships would emerge if trade-off-mediated local coexistence were reduced due to spatial heterogeneity and/or local extinctions during periods of low abundances.

#### 3.2.1.2. Emigration-immigration dynamics: dispersal asymmetries

Emigration-immigration dynamics can increase foodweb persistence in two ways (Amarasekare 2006, 2007a, 2008). First,
when local foodweb dynamics involve transient or persistent fluctuations, dispersal can enhance trade-off-mediated local coexistence by rescuing species from local extinction during periods of low abundances. Second, when trade-off-mediated coexistence restricts species to habitats with intermediate levels of resource productivity or predator mortality, dispersal can increase both local and regional persistence by allowing species to maintain sink populations in areas that they cannot otherwise inhabit.

Emigration-immigration dynamics have a strong effect on foodweb diversity. The interplay between local foodweb dynamics and global dispersal leads to emergent properties that cannot be predicted from the spatial dynamics of purely competitive or pairwise consumer-resource interactions. The most significant effect is an asymmetry between species in their dispersal effects and responses (Amarasekare 2006, 2007a, 2008). In both the IGP and the predation modules, dispersal of the inferior resource competitor that is less susceptible to predation has a large effect, but dispersal of the superior competitor that is more susceptible to predation has no effect on coexistence and species distributions. In the predation module, dispersal of the predator has no effect on coexistence and species distributions when the predator-resistant inferior competitor is immobile, and a large effect when the latter species is mobile (Amarasekare 2008).

This dispersal asymmetry arises from the different ways in which the two consumer species solve the conflicting problems of resource acquisition and predator avoidance. One species is better at resource acquisition and worse at predator resistance/tolerance, while the other species has the opposite trade-off. This difference leads to species-specific responses to spatial variation in resource productivity such that the predator-susceptible superior competitor’s abundance decreases with increasing productivity, while the predator-resistant inferior competitor’s abundance increases with increasing productivity. Random dispersal thus leads to a net movement of the superior competitor from areas of low productivity to areas of high productivity, and a net movement of the inferior competitor from areas of high productivity to areas of low productivity. The asymmetry arises because the inferior competitor’s net movement occurs in a direction that strongly affects the superior competitor (both directly, and indirectly via the predator), as well as prevents the superior competitor from having an impact on the inferior competitor (Amarasekare 2006, 2007a, 2008).

The inferior competitor’s dispersal effects on coexistence can be understood as follows. When there is spatial variation in resource productivity such that only the superior (inferior) competitor can persist at low (high) productivity, and coexistence via a competition-predation trade-off occurs at intermediate productivity, the inferior competitor’s dispersal rate exhibits a threshold that induces a qualitative change in the type of spatial coexistence mechanisms operating (Amarasekare 2006, 2008). Below this threshold, coexistence in the low-productivity habitat occurs via source-sink dynamics in the inferior competitor, and coexistence in the high-productivity habitat occurs via source-sink dynamics of the superior competitor. In both cases, the intermediate-productivity habitat, where trade-off-mediated local coexistence occurs, functions as the source community. When the inferior competitor’s dispersal rate is above the critical threshold, coexistence in the high-productivity habitat occurs via the inferior competitor’s emigration, which requires no spatial dynamics of the superior competitor. Coexistence in the low-productivity habitat cannot occur via the superior competitor’s emigration, which still requires source-sink dynamics of the inferior competitor. Thus, while the same spatial mechanisms (emigration-mediated and source-sink coexistence) observed in purely competitive interactions and simpler foodweb modules also operate in these more complex modules, now they do so in combination with trade-off-mediated local niche partitioning. Most importantly, the inferior competitor’s dispersal determines which combination of local and spatial mechanisms operates (Amarasekare 2006, 2008).

Amarasekare
Not only does the inferior competitor's dispersal drive species coexistence, but it also determines species distributions. Because the inferior competitor is limited more by resources than by predation, it cannot invade the low-productivity habitat even with the superior competitor's net emigration from that habitat. Thus, the superior competitor's dispersal induces no qualitative change in the inferior competitor's abundance pattern. Because the superior competitor is limited less by resources than by predation, the inferior competitor's net movement from high- to low-productivity habitats allows the superior competitor to invade the high-productivity habitat and attain high abundances. The inferior competitor's net movement from high- to low-productivity areas also reduces predator abundance in the low-productivity habitat, thus creating an abundance gradient in the direction of increasing productivity for the predator. The resulting net predator movement from high- to low-productivity habitats inflicts high mortality on the superior competitor in the low-productivity habitat and decreases its abundance below that in the absence of dispersal. The net result is a qualitative change in the superior competitor's abundance pattern; abundances now increase with increasing productivity. This in turn induces a qualitative change in species' distributions across the landscape, from interspecific segregation in resource-poor and resource-rich habitats to interspecific aggregation in resource-rich habitats (Amarasekare 2006, 2007a, 2008).

The important implication of these results is that the interaction between competition and predation creates asymmetries between species that lead to unexpected effects of dispersal. While the top predator plays the key role in consumer coexistence in the absence of dispersal, it is the predator-resistant inferior competitor that plays the key role in the presence of dispersal.

3.2.2. Spatial coupling. Movement of consumers that are more mobile than their resources can couple foodweb modules in different localities (McCann et al. 2005). Coupling occurs via the foraging preferences of consumers such as switching to more abundant resource types. These behavioral responses occur on a faster timescale than local foodweb dynamics and allow rapid consumer responses to changing resource conditions. Resource species do not necessarily compete, but consumers must exert a preference for different resource types. Consumers can also be omnivorous, exploiting resource species that occupy different trophic levels. Spatial coupling has a strong effect on foodweb persistence when local foodweb dynamics involve fluctuations (McCann et al. 2005). There are two situations under which spatial coupling can enhance foodweb persistence.

When consumers are highly mobile and when the local spatial scale of consumer foraging (i.e., the area over which the consumer perceives the resource as being well mixed) is smaller than the spatial scale of resource habitat distribution, consumers must decide which habitats to forage in when they forage at the regional scale (i.e., across different resource habitats) (McCann et al. 2005). If consumer preference for resource types depends on resource abundance such that consumers switch from rare to abundant resources, consumer impact on rare resource species is reduced. This prevents resource overexploitation and dampens consumer-resource fluctuations. Such damping in turn reduces local extinction during periods of low abundances and enhances foodweb persistence. This effect requires that resource responses to consumers vary spatially so that foodwebs in different localities exhibit asynchronous fluctuations (McCann et al. 2005).

When the local spatial scale of consumer foraging is larger than the spatial scale of resource habitat distribution (i.e., the consumer perceives resources that occupy different habitats as being well mixed), switching is not possible and consumer-resource dynamics exhibit increasingly strong fluctuations (McCann et al. 2005). In this case, strong top-down effects by predators can favor omnivory. Omnivory in turn can dampen fluctuations by preventing the overexploitation of intermediate trophic levels. Thus, omnivory can enhance the persistence of spatially
coupled foodwebs when the foraging behavior of mobile consumers amplifies rather than dampens consumer-resource fluctuations (McCann et al. 2005).

### 3.2.3. Summary of key results

The crucial outcome of the spatial dynamics of the IGP/omnivory and the predation modules is the existence of keystone dispersers, species whose dispersal has disproportionately large effects on foodweb persistence and diversity. This result emerges under both spatial coupling and metacommunity dynamics. On the one hand, spatial coupling of foodwebs suggests that large-bodied consumers that are more mobile than their resources (e.g., large vertebrate predators that consume small invertebrate prey) may play a key role, through their foraging movements and behavior, in foodweb persistence across large spatial scales. On the other hand, metacommunity dynamics of foodwebs suggest that when consumers and resources have comparable mobilities (e.g., small invertebrate predators or parasites attacking prey or hosts of the same size or larger), intermediate consumers that are less efficient at exploiting resources but less susceptible to top predators may play a key role, through their dispersal, in foodweb distribution and diversity.

### 3.3. Foodweb Dynamics Under Nonrandom Dispersal

The spatial effects on foodweb persistence and diversity discussed thus far arise from random dispersal. Spatial coexistence mechanisms under random dispersal, emigration-mediated and source-sink, hinge on the net movement of organisms from areas of higher fitness to areas of lower fitness. This is a maladaptive decision from an individual organism’s point of view, particularly because the studies involved consider permanent spatial heterogeneity and hence a predictable environment where bet hedging does not confer an additional advantage (e.g., Abrams & Wilson 2004; Amarasekare 2006, 2007a, 2008; Namba 2007). This begs the question of what impact nonrandom dispersal has on foodweb persistence and diversity.

There are two types of investigations of nonrandom dispersal. The first type focuses on foodweb persistence when local dynamics fluctuate. The second type focuses on foodweb diversity when local dynamics do not fluctuate.

#### 3.3.1. Effects of nonrandom dispersal on foodweb persistence

In pairwise consumer-resource interactions with fluctuating local dynamics, high dispersal synchronizes dynamics and increases the extinction risk of the entire metacommunity (Briggs & Hoopes 2004). A novel property emerges when one considers the spatial dynamics of tritrophic interactions (Koelle & Vandermeer 2005). Now dispersal effects on asynchrony depend on the trophic status of the species dispersing. When dispersal is nonrandom (either because individuals are more likely to disperse to nearby patches or because they have a higher probability of surviving dispersal if they emigrate from a patch with high connectivity), dispersal of the intermediate consumer synchronizes dynamics of species at all trophic levels. However, dispersal of the basal resource species desynchronizes dynamics at all trophic levels. Dispersal of the top predator also synchronizes dynamics, but this effect depends on interpatch distances. When all three species disperse, an increase in the dispersal rate [via a reduction in the effective interpatch distance (Koelle & Vandermeer 2005)] reduces synchrony in the dynamics of the resource and the intermediate consumer but not in the dynamics of the top predator. These dispersal differences appear to persist in more complex foodwebs and larger metacommunities (Koelle & Vandermeer 2005), suggesting that the phenomenon may be general. The key point is that greater dispersal does not necessarily lead to greater synchrony because dispersal effects on synchrony depend on how a particular species’ dispersal affects other species in the community.
These findings raise the interesting question of whether species-specific differences in dispersal effects on asynchrony depend on the type of nonrandom dispersal, i.e., are such differences more likely when dispersal is distance-dependent? When tritrophic interactions are linked by fitness-dependent dispersal (Abrams 2007), the interplay between dispersal and fluctuating local dynamics leads to spatial cycles of predators and prey. Here again, dispersal effects on asynchrony depend on the trophic status of dispersing species. Rapid and fitness-sensitive predator movement makes synchrony more likely, while rapid and fitness-sensitive prey movement (combined with slow and fitness-insensitive predator movement) makes asynchrony more likely (Abrams 2007). The fact that this phenomenon emerges under two different types of nonrandom dispersal suggests that species-specific differences in dispersal effects on asynchrony may be a general property of foodwebs.

In contrast, investigations of density-dependent dispersal in communities with selective predation (two intermediate consumers sharing a common resource, one of whom is attacked by a top predator) and fluctuating local dynamics (Maser et al. 2007) yield results more consistent with the predictions from pairwise consumer-resource interactions. Low levels of localized dispersal stabilize local communities and hence the metacommunity, suggesting a negative feedback effect due to immigration. In contrast, high levels of localized dispersal increase local population fluctuations. However, because dynamics in different localities are asynchronous, population variability is reduced at the metacommunity scale (Maser et al. 2007).

3.3.2. Effects of nonrandom dispersal on foodweb diversity. We currently know very little about nonrandom dispersal effects on foodweb diversity. Here I discuss two studies that compare random and nonrandom dispersal in the IGP and the predation modules with nonfluctuating local dynamics (Amarasekare 2007a; P. Amarasekare, unpublished).

A comparative analysis of four dispersal strategies [random, density-dependent, habitat-dependent, fitness-dependent (Amarasekare 2007a)] in communities with IGP shows that interspecific aggregation (leading to greater local and regional diversity) is more likely when dispersal is random or less optimal (i.e., it occurs against the direction of increasing fitness), while interspecific segregation (leading to lower local diversity and greater regional diversity) is more likely as dispersal becomes more optimal (i.e., it occurs in the direction of increasing fitness). With random or less optimal nonrandom strategies, greater local and regional diversity is achieved at the cost of an overall reduction in species’ abundances. This is because species experience greater mortality (and/or lower reproduction) due to competition and predation when they move from areas of higher fitness to areas of lower fitness. With nonrandom strategies that are more optimal, lower local and greater regional diversity is achieved at the benefit of an increase in overall abundances. This is because species avoid greater mortality (and/or lower reproduction) when they move from areas of lower fitness to areas of higher fitness.

Interestingly, the keystone disperser effect observed under random dispersal (Amarasekare 2006, 2008) is preserved under nonrandom dispersal as well: The intraguild predator's dispersal strategy and dispersal behavior have a strong effect on the intraguild prey's spatial distribution, but the intraguild prey's dispersal strategy and dispersal behavior have no effect on the intraguild predator's spatial distribution. This effect also persists under nonrandom dispersal in the predation module (P. Amarasekare, unpublished), suggesting that it may be a general property of foodwebs with competition and predation.

3.4. Summary of Key Findings Under Nonrandom Dispersal

3.4.1. Asynchrony and foodweb persistence. Unlike with random dispersal, high rates of nonrandom dispersal do not always synchronize the dynamics of local communities. Whether dispersal
synchronizes or desynchronizes dynamics depends on the trophic status of the dispersing species. In general, dispersal of species at lower trophic levels has a desynchronizing effect (leading to greater foodweb persistence at both local and regional scales), while dispersal of species at higher trophic levels has a synchronizing effect (leading to reduced foodweb persistence at both local and regional scales).

3.4.2. Foodweb diversity and species distributions. When dispersal occurs in the direction of increasing fitness, local coexistence is reduced and regional coexistence is enhanced compared with random dispersal. This is also accompanied by an overall increase in species’ abundances compared with random dispersal. As with random dispersal, the predator-resistant inferior competitor’s dispersal has a disproportionately large effect on coexistence and species’ distributions compared to the dispersal effects of the predator or the predator-susceptible superior competitor.

3.5. Empirical Evidence of Spatial Foodweb Dynamics

There are only a handful of empirical investigations of spatial foodweb dynamics. I discuss these below.

3.5.1. Exploitative competition. A microcosm study of competitive interactions between protists (Fox 2007) shows that spatial mechanisms predicted by theory (emigration-mediated and source-sink) are insufficient to explain coexistence. [Although the study involved multiple consumer species competing for multiple resources, resource dynamics were ignored when investigating dispersal effects (Fox 2007).] Coexistence appears to additionally require dispersal-mediated changes in species’ traits such as competition coefficients and carrying capacities.

3.5.2. Apparent competition. The apparent competitive interaction between two species of bruchid beetles and their shared parasitoid, studied using a microcosm system (Bonsall et al. 2005), shows that larger metacommunities with limited (nearest-neighbor) dispersal increase the persistence of the three-species interaction. However, finite metacommunity size precludes long-term persistence. Limited dispersal and large metacommunity size are more important to metacommunity persistence than is habitat structure (Bull et al. 2006).

3.5.3. Predation. There have been two investigations of extinction-colonization dynamics when local niche partitioning occurs via a competition-predation trade-off. In the first study (Shurin & Allen 2001), theoretical predictions of predator-mediated coexistence facilitating a linear relationship between local and regional species diversity were supported by data on lake communities of phytoplankton, zooplankton, and fish. In the second study (Shurin 2000), which investigated predator and dispersal effects on zooplankton diversity, fish and insect predators increased the extinction of large-bodied zooplankton (putative superior competitors) and facilitated invasion by inferior competitors from the regional pool. In contrast, predators reduced local diversity when local pond communities were isolated from the regional pool, suggesting the importance of colonization in maintaining zooplankton diversity.
4. SYNTHESIS

The existing body of work on spatial foodweb dynamics highlights certain invariant properties that are preserved across foodweb modules, as well as emergent properties in the more complex modules that arise via the interplay between foodweb dynamics and spatial processes.

4.1. Invariant Properties

These are properties that arise in competitive and pairwise consumer-resource interactions, which are also preserved in the more complex foodweb modules considered here. I discuss invariant properties associated with both foodweb persistence and foodweb diversity.

4.1.1. Spatial mechanisms of foodweb persistence. The mechanisms that increase the persistence of pairwise consumer-resource interactions with fluctuating local dynamics (Section 2.3.2) can also operate in all foodweb modules regardless of complexity. As with pairwise interactions, these mechanisms require asynchronous dynamics and limited dispersal that preserve asynchrony.

4.1.2. Spatial mechanisms of foodweb diversity. The two spatial coexistence mechanisms that operate in purely competitive interactions also operate in all foodweb modules regardless of complexity. The first, emigration-mediated coexistence, operates in the absence of any spatial variation in the species’ $R^*$ and $P^*$ values. It requires the superior competitor (or apparent competitor) to be more vagile than the inferior competitor (or apparent competitor) in the case of exploitative and apparent competition, and the predator-resistant inferior competitor to be more vagile than the predator-susceptible superior competitor in the case of IGP and predation. It is robust to the type of spatial structure (implicit versus explicit) and the scale of dispersal (local versus global).

The second mechanism, source-sink coexistence, operates when there is spatial variation in the species’ $R^*$ and $P^*$ values, or, in the case of IGP and predation, when a local niche partitioning mechanism such as a competition-predation trade-off allows coexistence in at least some localities of the landscape. It requires that dispersal rates of all species be sufficiently low so as not to homogenize species’ differences in space but is otherwise robust to changes in spatial structure and dispersal scale.

4.2. Emergent Properties

These are properties that emerge in the more complex foodweb modules, which cannot be predicted from the spatial dynamics of purely competitive or pairwise consumer-resource interactions. I discuss emergent properties associated with both foodweb persistence and foodweb diversity.

4.2.1. Species-specific dispersal effects on asynchrony. In simple foodweb modules (e.g., exploitative and apparent competition), dispersal effects on population asynchrony, and hence long-term foodweb persistence, are the same as those predicted by the spatial dynamics of pairwise consumer-resource interactions. In tritrophic food chains and more complex foodwebs, dispersal effects depend on the trophic status of the species’ dispersing. In general, dispersal of species at upper trophic levels tends to synchronize dynamics and reduce long-term foodweb persistence, while dispersal of species at lower trophic levels tends to desynchronize dynamics and increase foodweb persistence. Importantly, these emergent effects arise when dispersal is nonrandom.
4.2.2. Keystone dispersers. Two lines of evidence suggest the existence of keystone dispersers, species whose dispersal has a disproportionately large effect on foodweb persistence and diversity. On the one hand, there are large-bodied consumers, more mobile than their resources, that link foodwebs in space through their foraging movements and dampen consumer-resource fluctuations through rapid behavioral responses such as predator switching. Such consumers can play a keystone role in increasing foodweb persistence. Consumer movement occurs on a much faster timescale than population dynamics and on a larger spatial scale than resource habitat distributions. Examples include communities with large vertebrate predators or herbivores (e.g., fish, birds, mammals) that feed on much smaller organisms (e.g., plankton, plants, invertebrates, small vertebrates). On the other hand, there are intermediate consumers, less efficient at procuring resources but more resistant to/tolerant of natural enemies, whose dispersal increases species coexistence and modifies species distributions. Such species can play a keystone role in increasing foodweb diversity. Movement occurs on the same or a slower timescale as local foodweb dynamics and on the same spatial scale as resources and predators. Examples include communities with small-bodied predators (parasites) that prey on (parasitize) organisms of the same or larger sizes (e.g., insects and aquatic invertebrates).

Keystone dispersers are likely to have a significant impact on both natural and managed ecosystems. For instance, the success of marine reserves may depend crucially on large-bodied predators whose foraging movements encompass both protected and unprotected areas. Similarly, the control of invasive pests may depend crucially on whether pests are better resource competitors, or more resistant to native predators and parasites, than their native counterparts.

5. FUTURE DIRECTIONS

5.1. Theoretical

Most theory on spatial foodweb dynamics has focused on a particular aspect of spatial dynamics in a specific foodweb module (Table 2). Very few studies have attempted a comparative analysis of different types of spatial mechanisms across a given foodweb module, or of a given spatial mechanism across different types of foodweb modules. There is a great need for such a comparative analyses, particularly along the axes of dispersal scale (local versus global), dispersal mode (random versus nonrandom), and environmental heterogeneity (spatial versus temporal). Investigations of the heterogeneity axis are particularly needed, given that virtually all existing studies consider permanent spatial heterogeneity in a temporally constant environment.

The work on spatial coupling of foodwebs brings to light an important phenomenon that is largely ignored in studies of metacommunity dynamics: Spatial scales of dispersal are not necessarily the same for species occupying different trophic levels. Analyzing metacommunity dynamics with different spatial scales of dispersal for consumers and resources provides a means of developing a comparative framework with dispersal at different temporal scales (e.g., dispersal associated with foraging versus demographic processes) and spatial scales (e.g., scales of resource versus consumer dispersal).

A third important future direction is to investigate the robustness of the keystone disperser phenomenon. There are two aspects of the problem to analyze. The first is a comparative analysis of spatial coupling versus metacommunity dynamics to establish whether consumers at upper trophic levels play a keystone role even when dispersal occurs on the same timescale as local foodweb dynamics. In other words, is the keystone role of large, mobile consumers dependent on consumer movement associated with behavioral rather than demographic processes? The second aspect of the problem is to investigate the robustness of the dispersal asymmetries observed in
the IGP and predation modules to increases in foodweb complexity and metacommunity size. Does the dispersal of inferior competitors that are resistant to/tolerant of predation continue to play a keystone role when foodwebs contain multiple species at each trophic level and constitute metacommunities with a large number of local communities?

It is vitally important that theoretical results be presented in ways that facilitate empirical testing. For instance, comparative predictions on several axes such as local niche partitioning (absent versus present), magnitude of dispersal (low versus high), and mobility of interacting species (resources versus consumers versus predators) are particularly helpful when one is designing experimental or observational studies to test spatial mechanisms. It is equally important to cast model outcomes in terms of easily measurable attributes such as species’ distributions as a function of spatial heterogeneity (e.g., abundance-productivity relationships) and species’ associations in space (e.g., interspecific segregation versus aggregation).

5.2. Empirical

Given the scant empirical evidence of spatial effects in foodwebs, the first step is to test the key spatial mechanisms in microcosm studies. Progress is already being made in this direction (e.g., Cadotte et al. 2006, Donahue et al. 2003, Fox 2007, Holyoak & Lawler 2005). The more challenging next step is to test predictions in field systems. This involves a stepwise procedure. The first step is to establish local foodweb properties: (a) the types of species interactions, (b) the nature of local dynamics (e.g., fluctuating versus nonfluctuating), (c) local niche partitioning mechanisms (e.g., life history trade-offs), and (d) the outcome of local dynamics (e.g., local extinctions versus persistence). The second step involves characterizing spatial properties. How are species interactions distributed in space? Do species within a trophic level coexist everywhere, or are there localities that favor certain species? The third step involves quantifying dispersal traits. Do interacting species differ in their mobility, and if so, which species are more mobile? Is dispersal random or dependent on particular cues (e.g., density, resource productivity)? Techniques such as mark-recapture, radio telemetry, or molecular markers could be used to quantify the magnitude and the directionality of dispersal. The fourth, and most challenging, step involves assessing dispersal effects on local and metacommunity dynamics. Do highly isolated communities (natural or experimental) exhibit different local dynamics than more connected ones? Do local communities with greater/lesser connectivity exhibit greater/lesser variability in abundances? On the metacommunity scale, what is the relationship between local and regional diversity for different community modules?

The key to making empirical progress is in using multiple sources of information to test comparative predictions. To the extent that it is feasible, experiments or observational studies that simultaneously test multiple hypotheses will be the most informative. Mechanistic models that can be parameterized for specific communities can simplify experimental designs by eliminating mechanisms that are inconsistent with the species’ biology and predicting the outcomes of the mechanisms that are likely to operate.

6. CONCLUDING REMARKS

This review attempts to synthesize current knowledge of spatial foodweb dynamics into a framework that can both identify new theoretical directions as well as facilitate empirical investigations. It utilizes two major axes, foodweb complexity and type of movement, along which the theory can be organized. The attempt to find common themes and generalities reveals that our knowledge of spatial foodweb dynamics is not only sketchy but also fragmented. This makes it difficult
to develop predictions that are amenable to empirical testing. These limitations underscore the importance of a more systematic analysis of spatial dynamics across different foodweb types. It is only through such a comparative analysis that we can achieve a greater integration of theory and data in spatial community ecology.

**DISCLOSURE STATEMENT**

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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