

CHAPTER 2

The Effects of Spatial Processes on Two Species Interactions

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Introduction

Species interactions take place in a spatial context. That context affects organism encounters, yet the most common and familiar models in ecology ignore spatial processes and assume that interactions between groups of individuals, populations, and species are well represented by the interactions of the average individual. Here we will discuss the role of spatial processes in population and community dynamics with a focus on models that address the role of spatial processes in species coexistence and the maintenance of diversity. Recent interest in the role of spatial ecology has led to diverse literature on this topic (e.g., Caswell and Cohen 1991; Hanski 1997; Tilman and Kareiva 1997; Chesson 2000a; Holt 2002) that makes it impossible to summarize the full scope of this work in a single chapter. Instead, we will use illustrative examples that reveal the influence of space on coexistence in competition, mutualism, and consumer-resource interactions.

This chapter examines how spatial processes affect species diversity and the persistence of species interactions in general, not just at or near equilibrium. Often ecologists are interested in examining the factors affecting the coexistence or distribution of organisms in relation to particular other species or environmental factors. Equilibrium outcomes of spatial models may not provide the best answers for these questions. Many models display long periods of transient dynamics, in which populations and occupancies are not only not at equilibrium levels but are even on qualitatively different trajectories (Hastings and Higgins 1994; Ovaskainen and Hanski 2002; but see Labra et al. 2003). Over a given time period, these transient dynamics may dictate metapopulation occupancy and dynamics more accurately than will the equilibrium outcomes of spatial models (Holt 1992; Ruxton and Doebeli 1996). This is particularly true with metapopulations at high occupancy, which slows dynamics (Kinzig et al. 1999), and when spatial structure is combined with temporal heterogeneity (Gonzalez and Holt 2002). Temporal fluctuations may be on a time scale faster than the period required to reach equilibrium outcomes, so that spatial populations are always experiencing disturbances or always reacting to changing quality. Transient dynamics are ubiquitous in natural systems, and must be considered in understanding multispecies persistence and coexistence.

We begin with single species spatial models, which form the basis for multi-species models, then proceed through competitive, consumer-resource, and mutualism models. Because the literature we review is extensive and complex, we provide table 2.1 as a synoptic overview. Other perspectives on some of the topics we cover are provided in this volume by Holt and Hoopes in chapter 3, Mouquet et al. in chapter 10, and Chesson et al. in chapter 12.

Some pairwise species interactions do not fall neatly into any of the categories that we cover. The most notable of these is disease dynamics. Although consumer-resource models encompass many elements of spatial disease models, disease organisms experience hosts as separate (and heterogeneous) patches, thereby experiencing additional levels of spatial hierarchy (within individual hosts, among hosts, and among host populations) beyond the other systems that we discuss. Excellent reviews of spatial disease models include works by Sattenspiel and Simon (1988), Anderson and Christiansen (1989), Bolker and Grenfell (1995), Hess (1996), Lloyd and May (1996), Grenfell and Harwood (1997), Rhodes and Anderson (1997), Grenfell et al. (2001), Rodriguez and Torres-Sorando (2001), McCallum and Dobson (2002), and Park et al. (2002).

Spatial Models for Single Species

Models without Local Dynamics

One of the simplest spatial models for a single species is the patch-occupancy metapopulation formulation (Levins 1969, 1970), in which organisms exist in an infinite array of discrete populations or patches. The model assumes global dispersal, so that all patches are equally accessible from all other patches. It also assumes that patches have only two states, empty or occupied, and so ignores local population dynamics. The proportion of patches occupied at any time changes according to

$$\frac{dp}{dt} = cp(1-p) - mp, \quad 2.1$$

where p is the proportion of currently occupied patches, c is the rate at which empty patches are colonized, and m is the rate at which occupied patches go extinct. The nontrivial equilibrium occupancy, $p^* = 1 - m/c$, is globally stable when it is feasible, implying persistence if the colonization rate exceeds the extinction rate. Immediately after colonization, local population sizes are assumed to reach a carrying capacity so that continued dispersal has no effect on local dynamics. Dynamics within patches are, thus, assumed to happen on a faster time scale than dynamics among patches.

COMPARISON WITH NONSPATIAL MODELS

Because global dispersal creates a well-mixed system in which all patches are equally accessible, this metapopulation model is only implicitly spatial, meaning that patches are separate but there is no defined spatial distance among them. This model is analogous to a logistic model in which each patch represents a site occupied by a single individual (Gilpin and Hanski 1991; Caughley 1994; Amarasekare 1998a). Hence, factors that influence the persistence of a single population can have corresponding impacts on the persistence of a metapopulation. For example, metapopulations can experience demographic stochasticity and reduced probability of persistence at low occupancy (Stacey et al. 1997). Similarly, metapopulations can experience Allee effects in which a critical occupancy is required for colonization or persistence (Amarasekare 1998a). Harding and McNamara (2002) discuss a generalized Levins model with nonlinear extinction and colonization terms, comparable to incorporating nonlinear density dependence in local population models.

FACTORS AFFECTING PERSISTENCE

For a metapopulation to persist longer than a single local population, patches must act independently to a degree so that the entire metapopulation has a different extinction probability than a single population (Quinn and Hastings 1987), meaning that extinctions are not completely synchronized (Harrison and Quinn 1990). Equation 2.1 assumes that extinctions are independent among patches. In real-world systems or more complex models, synchrony is affected by both the degree of spatial correlation in the environment as well as dispersal distances and rates (figure 2.1; Hill et al. 2002; Ovaskainen et al. 2002). We will find that the synchrony of dynamics across space is an important subtheme as we add species interactions to our spatial models.

One of the simplest ways to include the factors that affect synchrony (isolation and correlation) is to use an incidence function model, which links patch-specific size (or quality) and isolation to extinction and colonization rates (Hanski 1994). Incidence function models are generally still patch occupancy models that do not follow local dynamics, and moreover they require an equilibrium between colonization and extinction. The assumption that patch size or quality matters in an incidence function model, however, is an implicit acknowledgment that emigration and immigration may be functions of population size and that population size may be affected by habitat quality.

Models with Local Dynamics

IMPLICIT SPACE

The simplest single species models that follow local dynamics in more than one local population do not include explicit spatial distances or heterogeneous

Table 2.1 An overview of the effects of adding spatial dynamics to different types of species interactions

Features of spatial dynamics	Simplest type of model	Examples	Comments
<i>Single species or noninteracting species</i> Asynchronous dynamics lead to a regional average occupancy despite local fluctuations, most basic statistical averaging	Patch occupancy (no local dynamics), spatially implicit	Levins 1969	<ul style="list-style-type: none"> Formally equivalent to the logistic equation at a regional level. Patches are independent and identical so that patch colonization and extinction probabilities are fixed. Population dynamic features, e.g., Allee effects and demographic stochasticity can be represented at a metapopulation scale.
Factors leading to asynchrony are explicit; statistical averaging	Patch occupancy, spatially implicit incidence function models	Hanski 1994	<ul style="list-style-type: none"> Recognize the importance of independence (asynchrony), or differences among patches in prolonging regional persistence time relative to population models; local dynamics are <i>statistically averaged</i> to give persistent regional dynamics. Between-patch differences act through influencing colonization and extinction probabilities, e.g., through population/patch size or quality.
Rescue effects, source-sink dynamics, pseudosink effects	Models with local population dynamics with implicit space	Hastings 1983; Comins and Noble 1985; Holt 1985; Watkinson and Sutherland 1995; Amarasekare 1998b; Amarasekare and Nisbet 2001	<ul style="list-style-type: none"> Local population sizes are explicitly represented. Variation in patch quality can promote source and sink dynamics with strong rescue effects, where sink populations are maintained by immigration. Immigration can create density-dependent reductions in local population growth (termed pseudosink effects by Watkinson and Sutherland 1985). Density independent emigration may cause declines in local population size.
Pattern formation/aggregation	Models with local population dynamics and explicit space.	Durrett and Levin 1994a, 1994b; Bolker and Pacala 1997	<ul style="list-style-type: none"> Local population dynamics coupled with larger scale dispersal can lead to pattern formation, and patterns can influence both local and regional dynamics.
<i>Competitive interactions</i> Competitive dominance, refuge effect or rescue effect	Spatially implicit models with habitat heterogeneity: (1) permanent habitat heterogeneity	Horn and MacArthur 1972; Comins and Noble 1985	<ul style="list-style-type: none"> Habitat heterogeneity can alter within-patch competitive ability so that different species are competitively dominant in different localities. Mechanism is equivalent to a refuge, which is more typically considered in predator-prey models.
Nonlinear, nonadditive responses to temporal heterogeneity	(2) Temporal habitat heterogeneity	Chesson and Warner 1981; Warner and Chesson 1985; Chesson 1994, 2000a	<ul style="list-style-type: none"> If habitat quality varies through time, coexistence is possible via a temporal <i>storage effect</i> if: <ul style="list-style-type: none"> i. long-lived life stages are present to permit survival through bad periods; and ii. species have different responses to environmental conditions so that maximum growth occurs at different times.
Nonlinear, nonadditive responses to spatial heterogeneity	(3) Spatial habitat heterogeneity	Chesson 1985, 2000a	<ul style="list-style-type: none"> Variation in density across space can allow species to persist in habitats where they are poor competitors through source and sink dynamics. This is termed the <i>spatial storage effect</i>. Source and sink dynamics, and the rescue/mass effects they entail are required and dispersal (across space) has the same function as long-lived life stages in the temporal storage effect (involving dispersal across time).
Competition-dispersal trade-off leading to regional equilibrium (statistical averaging)	Spatially implicit models for homogeneous habitats, with species' trade-offs	Levins and Culver 1971; Hastings 1978; Tilman 1994	<ul style="list-style-type: none"> A trade-off between competitive ability and dispersal ability can promote regional coexistence.

Table 2.1 continued

Features of spatial dynamics	Simplest type of model	Examples	Comments
Pattern formation / aggregation	Spatially explicit models for homogeneous habitats	Neuhauser 1998; Bolker and Pacala 1999; Law and Diekmann 2000	<ul style="list-style-type: none"> • Inferior competitors can repeatedly escape from competition by finding empty habitat not yet colonized by the superior competitor. • As habitat is destroyed superior competitors are lost first because of their poor dispersal abilities. • Clustering, associated with pattern formation, coupled with local interactions altered competitive effects and could change both local and regional competitive dominance. • At least three competitive strategies of space-use exist: tolerance (ability to resist invasion and take over space), dispersal, and exploitation (speed of utilizing space).
Competition-dispersal trade-off and pattern formation / aggregation	Models that combine competitive shifts in dominance (heterogeneous habitats) with species' trade-offs	Amarasekare and Nisbet 2001; Mouquet and Loreau 2002	<ul style="list-style-type: none"> • There are threshold levels of dispersal that allow species to coexist: If species dispersal is too high, then the advantage of niche partitioning is lost, whereas with too little dispersal, inferior competitors cannot survive.
<i>Consumer-resource interactions</i> Statistical averaging	Models with many independent interacting entities, e.g., multiple patches or explicit space with locally interacting individuals	Allen 1975; Crowley 1981; Reeve 1988; de Roos et al. 1991, 1998; McCauley et al. 1993, 1996; Wilson 1998	<ul style="list-style-type: none"> • Although local populations may fluctuate in density and are extinction-prone, regional population densities are relatively constant because of averaging population densities over fluctuating subpopulations. • Asynchrony is critical to the independence
Density dependence induced by dispersal: refuge effects, rescue effects, and source-sink dynamics	Models with patch heterogeneity	Crowley 1981; Sih 1987; Reeve 1988; Murdoch et al. 1992; Holt and Hassell 1993; Hochberg et al. 1996	<ul style="list-style-type: none"> • of the local populations across which the regional density is averaged. • Predator and prey dispersal can have different effects on synchrony. • Any supply of individuals from high- to low-density areas may promote density dependence (the refuge effect), which extends persistence through a rescue effect. • This process is similar to source-sink maintenance of inferior competitors in the competition models. • Local heterogeneity can be fixed or from spatiotemporal variation, as we found in spatial models of competition.
Nonlinear, nonadditive responses to heterogeneity	Patch, lattice, and reaction-diffusion models with spatial heterogeneity in densities and nonlinearities in predator-prey responses.	McCauley et al. 1996; De Roos et al. 1998; Gurney and Veitch 2000	<ul style="list-style-type: none"> • This feature is similar to a spatial storage effect (Chesson 1985, 1990; Warner and Chesson 1985). • Prey show strong patterning / aggregation in all models.
<i>Mutualistic interactions</i> Nonlinear, nonadditive responses to heterogeneity	Obligate mutualisms with implicit space	Hutson et al. 1985; Hastings and Wolin 1989	<ul style="list-style-type: none"> • Mutualistic effects that vary nonlinearly spatially allow obligate mutualists to span a broader range of densities and still persist; this is similar to a spatial storage effect.
Spatial heterogeneities, refuge or rescue effects, density dependence induced by dispersal	Facultative mutualisms	Addicott 1981; Ringel et al. 1996	<ul style="list-style-type: none"> • Facultative mutualists improve the quality of habitat where they coexist, leading to spatial heterogeneities and mass effects that always increase the persistence of two species interactions. • A mutualist as a third species can alter the balance of competition or consumer-resource interactions and can create the spatial heterogeneities listed in previous sections of the table.

Note: The table lists the spatially dynamic features that emerge from models and includes only the models that exemplify these features.

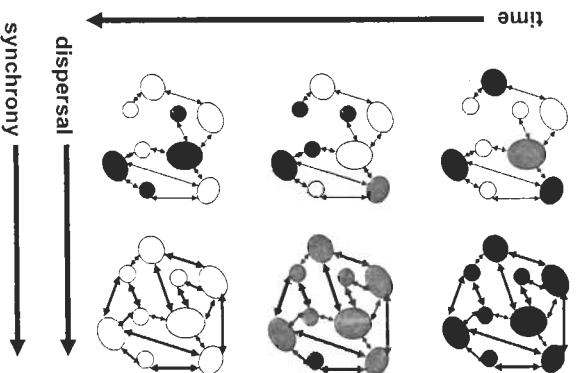


Figure 2.1 Relationship between dispersal and synchrony in metacommunities. Each row of figures represents a metacommunity through three successive temporal snapshots. Different colors represent different species combinations, resulting in different local communities. Arrow thickness represents dispersal rate. Note that the top row has more dispersal between patches as well as higher rates of dispersal. Synchrony of local communities is higher in the top metacommunity than in the bottom metacommunity.

habitats. Differences in local population sizes allow these models to reveal rescue effects and costs of dispersal (Brown and Kodric-Brown 1977; Amarasekare 1998b). A *rescue effect* occurs if emigrants from high population density patches prevent low population density patches from declining to extinction (table 1.1). Rescue effects in homogeneous habitats are only possible if dynamics are asynchronous (Doebeli 1995).

With differences in patch quality, however, a broader range of dynamics appears even with implicit space (Hastings 1983; Comins and Noble 1985; Amarasekare and Nisbet 2001). Coupling habitats with different qualities can lead to source-sink dynamics (Holt 1985; Pulliam 1988; Pulliam and Danielson 1991). Strictly speaking, *sources* are areas in which species experience positive population growth, and *sinks* are areas in which they experience negative population growth at all densities; populations in sinks are only maintained by immigration from source areas (Holt 1985; Pulliam 1988). With strong mass effects (Shmida and Ellner 1984; see table 1.1 for a definition), such that immigration exceeds emigration, populations can be held above carrying capacity in lower quality areas even if this area is strictly speaking a source (Holt 1983, 1985). Without immigra-

tion, populations decline in these elevated areas, but not to extinction. This makes it hard to tell sources from sinks in practice (Walkinson and Sutherland 1995). For the purposes of this chapter, the term *source-sink* denotes a class of models that examine movement of individuals from high quality to low quality areas with effects on local population dynamics.

If patches differ in quality, rescue effects are more likely; for example immigration from source patches may rescue sink patches. Such rescue effects explain some of the stabilizing influence of habitat heterogeneity in spatial predator-prey models (Crowley 1981; Holyoak and Lawler 1996). Movement from high quality to low quality areas also has associated costs (Amarasekare 1998b). Individuals may die while dispersing or end up in lower habitat quality. For organisms free to move and capture resources according to their availability (i.e., populations with ideal-free distributions; Fretwell and Lucas 1970), individuals are only found in areas of low habitat quality when moving suboptimally (Hastings 1983; Holt 1985), meaning that they do not select habitats to maximize their individual fitness (Delibes, Ferreras, et al. 2001; Delibes, Gaona, et al. 2001b). Species cannot necessarily optimize their fitness, however, because they cannot always cue in on habitat factors that differentiate between high and low habitat quality (Pulliam and Danielson 1991). Source-sink models have received wide attention in conservation circles because they demonstrate that the addition of low quality habitat can increase the regional abundance of a species by maintaining individuals not only in high quality areas but also in low quality areas where they would not otherwise survive (Hoopes and Harrison 1998). For a single species in a temporally invariant environment, however, sink habitat only increases population persistence and abundance if populations do not have an ideal free distribution; population increases only occur when individuals disperse passively or use low-quality habitat exclusively after high-quality habitat is depleted (Holt 1985; McPeck and Holt 1992; Donahue et al. 2003). In the latter case sink habitats do not drain reproductive individuals away from areas where they can contribute to population growth. When organisms cannot distinguish between habitats, dispersal into low-quality or sink habitat can decrease population abundance and persistence (Holt 1985; Donovan and Thompson 2001; Gundersen et al. 2001). We will see later that this trend extends to multispecies models where dispersal does not always increase community stability or diversity if it overexposes rare populations to increased predation or competition or decreased facilitation.

EXPLICIT SPACE

Single-species models that include explicit space range from extremely detailed spatially explicit population models (SEPMs) based on empirical spatial and movement data to much more general reaction-diffusion models that combine basic population growth equations (reaction) with diffusive movement (diffusion). SEPMs offer excellent predictive abilities about specific habitats but are

computationally intensive and difficult to analyze (Pacala et al. 1996). Their use has increased with recent computational advances. Reaction-diffusion models are well developed and tractable but include nonzero rates of infinite dispersal and may not reflect realistic movement patterns (Okubo 1980). Despite these simplifications, reaction-diffusion models are the basis of many advances in spatial ecology and are still essential in the field.

Models with explicit space include the range of behavior found in spatially implicit models but with a greater range of impediments or aids to movement. Rescue effects are less frequent because immigrants cannot come from infinite distances. In this way, spatially explicit models with local dynamics are somewhat parallel to incidence functions in patch occupancy models; where incidence functions make some patches more or less likely to be occupied, explicit space in models with local dynamics increases the differences between population sizes and makes some populations more likely to be rescued than others.

These differences can induce heterogeneities in homogeneous habitats. Models with explicit local interactions—meaning models in which population dynamics are followed explicitly at scales smaller than the dispersal distance—frequently lead to pattern formation (Durrett and Levin 1994b). For example, lattice formulations, which follow populations or individuals distributed across a grid of spatial habitats are followed in discrete time, lead to clustering of individuals (Durrett and Levin 1994a). Similarly, point-process models, which examine populations in continuous space (point) and follow the dynamics (process) of population density in continuous time, also can lead to clustering pattern formation (Bolker and Pacala 1997). Although the habitat is homogeneous, these emergent patterns are themselves spatial heterogeneities. As with implicit space models, heterogeneities, including spatial patterns, can alter the persistence of interacting species in models with explicit space (De Roos et al. 1998; Bolker and Pacala 1999; Gurney and Veitch 2000).

Spatial Competition Models

Spatial models of competition generally address the maintenance of diversity by examining equilibrium conditions for species coexistence, or nonequilibrium conditions for the persistence of two or more competitors (Hastings 1980; Tilman 1980, 1994; Chesson 1985, 2000a; Pacala 1986). The use of the term *coexistence* is somewhat confusing in the literature because it can refer to coexistence within a locality or an entire region. Here we use it to mean coexistence within a region regardless of whether coexistence is possible in individual localities (Amarasekare and Nisbet 2001; Mouquet et al. 2002).

Spatial competition models often use as a reference point the expected outcomes of Lotka-Volterra models of direct competition. For example, adding space to models of competition can allow inferior competitors to persist (Hastings

1980; Tilman et al. 1994; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002), can shift relative dominance as local abundances change (Bolker and Pacala 1999; Loreau and Mouquet 1999), and can lead to the exclusion of competitive dominants (Law and Dieckmann 2000). Here we will only summarize some of the major spatial processes responsible for these shifts. A more thorough review of spatial competition models is provided by Mouquet et al. in chapter 10.

Although there are several mechanisms that can maintain species diversity (see Chesson [2000b] for an excellent review), the two most common mechanisms in spatial models are (1) habitat heterogeneity that shifts the local balance of competition so that different species are competitively dominant in different localities, and (2) a trade-off between competitive ability and dispersal ability (figure 2.2). The first mechanism basically offers a refuge (Horn and MacArthur 1972; Comins and Noble 1985); this refuge need not be constant in space but can emerge from environmental fluctuations in either space or time (Chesson 1985, 2000a; Warner and Chesson 1985). In the second mechanism, inferior competitors repeatedly escape from competition by finding empty habitat not yet colonized by the superior competitor (Levins and Culver 1971; Hastings 1978; Tilman 1994). These two mechanisms sound remarkably similar when stated this way. The biological concepts underpinning the two ideas approach each other, but there is a fundamental difference in the model formulation for a shift in competitive superiority (first mechanism) and a constant chase (second mechanism). We will first detail models that rely on habitat heterogeneity to maintain diversity, then examine models with a trade-off between competitive ability and dispersal ability, and finally discuss ways in which these two mechanisms can interact.

Heterogeneous Habitats and Switches in Competitive Dominance

A simple way to allow two species to coexist in a region is to have the region include qualitatively different habitats in which each species specializes so that there is niche differentiation. Intuitively, if species switch competitive superiority with habitat type, then a region can support as many species as there are habitat types as long as each species can maintain a balance of births and deaths (or extinctions and recolonizations) within its preferred habitat (Horn and MacArthur 1972). If the quality of a spatially uniform environment changes through time, then species may partition dominance through time in a similar way, allowing multiple species to coexist (Grubb 1977; Sale 1977; Chesson and Warner 1981; Comins and Noble 1985). This has been called the “storage effect” because species with long-lived life stages and overlapping generations can store up the benefit from good years by reproducing in positive conditions and surviving through negative conditions (Chesson and Warner 1981; Warner and Chesson 1985; Chesson 1994). Species need to have different responses to variation so that there are species-specific responses to the environment that allow niche partitioning (Chesson 2000a). The storage effect requires subadditivity, in which the

covariance between competitive processes and the environment decreases with density (Chesson and Huntly 1989; Chesson 1990, 1994). This means that, with a range of densities and environments, a species experiences lower competitive effects on average than if all the individuals were at the mean density and experiencing the mean environment and level of competition. This effect arises from Jensen's inequality, which states that the mean of a decelerating function (come down, 2nd derivative negative) is less than the function at the mean (Ruel and Ayres 1999; see also figure 12.1 and box 12.2). For populations spread across space

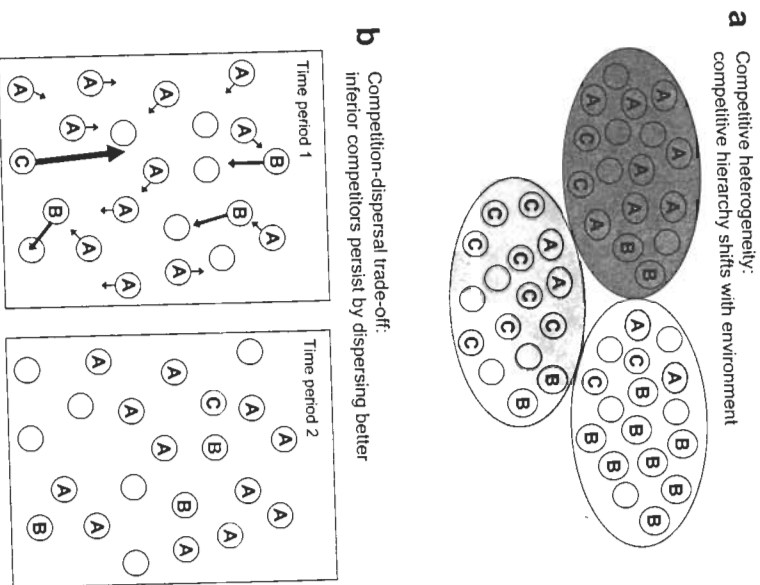


Figure 2.2 Regional competitive coexistence through (a) heterogeneity in the competitive hierarchy or (b) a competition-dispersal trade-off. Species can coexist regionally through either competitive spatial mechanism. Circles represent local communities with A, B, and C representing different species or community types. In the top panel (a) different colors represent different habitat types. Each species competes best in a particular habitat type, and all three species persist in the system. Note that each species is also found, through source-sink dynamics, in habitats in which it is an inferior competitor. In the lower panel (b) arrows represent dispersal, with arrow size depicting dispersal distance and rate. Locally, species A outcompetes species B, which outcompetes species C; however inferior competitors disperse better and persist in the system.

this systematic difference from the behavior expected from mean conditions can be extremely important for persistence. Jensen's inequality and the nonadditive responses to heterogeneity that result from it not only play a role in competitive coexistence in the storage effect but also play a role in spatial consumer resource and mutualism models.

Chesson (1985, 2000a) has pointed out that storage effects can also be spatial, meaning that species survive in habitats where they are extremely poor competitors because the environment is favorable for them in other patches. Spatial storage effects are, in fact, more likely than temporal storage effects, as they can come from pure spatial variation as well as from spatiotemporal variation, which affects different parts of the environment at different times (Chesson 1985). As with the source-sink effect described in the single species section above, maintenance in low quality areas results from mass effects, or movement of individuals from high quality areas (see also Mouquet et al., chapter 10; Chesson et al., chapter 12; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002).

Homogeneous Habitats and a Competition Colonization Trade-off

When there is no location in which the competitive hierarchy switches, poor competitors can nonetheless survive by dispersing to take advantage of empty habitat. The competition-dispersal trade-off appears most frequently in patch occupancy models similar to the metapopulation approach in equation 2.1 (e.g., Levins and Culver 1971; Hastings 1980; Nee and May 1992; Tilman 1994; Mouquet and Loreau 2002). These models generally assume hierarchical competition, meaning that species have fixed competitive rankings. When a superior species colonizes a site occupied by an inferior competitor, the latter is supplanted. Sites available for colonization, therefore, consist of all sites not occupied by the species itself or a superior competitor. The dynamics of the i th species can be represented as

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^i p_j \right) - m_i p_i - \left(\sum_{j=1}^{i-1} c_j p_j p_i \right). \quad 2.2$$

Here p_i is the fraction of the habitat occupied by species i , c_i and m_i are the colonization rate and extinction rate, respectively, of species i , and the competitive superiority of species decreases with increasing i . Patches can be occupied by single individuals or populations. This model permits an infinite number of species to potentially coexist, provided inferior local competitors are superior at reaching empty patches, and may explain how multiple species can coexist on a single limiting resource (Hastings 1980; Tilman 1994). The “ R^* -rule” in resource competition suggests that—on a single limiting resource—only the species that can reach the resource to the lowest level while maintaining a positive growth rate could survive (Tilman 1980, 1982). More generally, nonspatial models suggest

that the equilibrium number of species in closed habitats should match the number of limiting resources. Patch occupancy models help to bridge the discrepancy between R^* predictions and the diversity found in real communities by considering the effect of space on species interactions.

Note that space is still implicit in models like equation 2.2, meaning that there are no explicit distances between patches or sizes of patches. Adler and Mosquera (2000) have pointed out that models without explicit space but with interference competition and frequency dependence also predict a potentially infinite number of coexisting competitors. Note that a spatially implicit model is similar to Adler and Mosquera's nonspatial model with frequency dependence because both models look at the proportion of a system in particular states (2000). In patch occupancy models the states are the occupying species, and in frequency dependent models the states are the competing species.

Models based on equation 2.2 offer qualitative insight into the identity of coexisting species. The competitive hierarchy dictates dispersal requirements for coexisting inferior competitors. Competitive dominants always leave a portion of the habitat unoccupied, leaving room for an inferior competitor to invade, but only an inferior competitor with high colonization rates is capable of finding and using the vacant habitat (Horn and MacArthur 1972; Hastings 1980; Tilman 1994). Taking these insights to more quantitative levels can be misleading, though, because superior competitors can always invade, regardless of their dispersal rates (Kinzig et al. 1999). Some researchers have derived quantitative expressions for limits to similarity of competing species by looking at expressions for successive invaders based on the invasion criteria from equation 2.2 (Pacala and Tilman 1994; Tilman 1994). These quantitative predictions are not reliable because, as superior competitors invade, they change the amount of unoccupied habitat and the subsequent quantitative dispersal requirements for coexistence of inferior competitors (Horn and MacArthur 1972; Kinzig et al. 1999).

These patch occupancy models for competition shed light on relative species abundance and the effects of habitat alteration, fragmentation, or destruction (Hastings 1980; Nee and May 1992; Tilman et al. 1994). As habitat quality declines or habitats are destroyed, superior competitors with lower dispersal rates should suffer more than inferior competitors that are better at dispersal (Tilman et al. 1994). The models suggest that, because of competitive release, weedy species may increase in abundance in disturbed habitats (Nee and May 1992); diversity (Hastings 1980) and extinction probabilities (Tilman et al. 1994; Huxel and Hastings 1998, 1999) may be hard to predict with initial loss of superior competitors (Tilman et al. 1994). These qualitative insights are instructive, but models based on equation 2.2 may not provide appropriate tools for examining specific outcomes at high diversity levels because in that region the dynamics are so slow as to be pathological (meaning they lead to internal inconsistencies or contradictions of model assumptions; Kinzig et al. 1999).

Models with Explicit Space

Models with explicit space allow researchers to examine the effects of extremely local interactions and pattern formation, as discussed in the section on single species models, and may be particularly useful for examining questions with an applied twist (e.g., effects of habitat destruction on coexistence). In a cellular automata model, Neuhauser (1998) found that local interactions altered competitive effects and could change both local and regional competitive dominance. The proximity of neighbors affected the strength of interactions and led to superior competitors excluding inferior competitors from their immediate vicinity. Habitat destruction did not necessarily affect superior competitors more, and actual outcomes depended on the spatial structure imposed by species interactions.

Other competition models with explicit spatial structure have also found that local interactions and pattern formation can change regional dominance. In a spatially continuous model with a homogeneous environment, Law and Diekmann (2000) used moment closure to examine the effects of local dispersal and competition. Unlike neighborhood competition models, which assume a uniform distribution of competitive effects over some local distance (Pacala 1986), the moment-closure approach allows a probability distribution or kernel of dispersal and competitive effects (Bolker and Pacala 1997, 1999; Law and Diekmann 2000). Law and Diekmann found that an inferior competitor with superior dispersal could actually regionally exclude a superior competitor. As the superior competitor eliminated the inferior competitor from its local vicinity, the two species formed clusters: the superior competitor suffered from increased intraspecific competition while the inferior competitor escaped from interspecific effects (Law and Diekmann 2000).

Bolker and Pacala (1999) used a similar moment closure approach to isolate the spatial and competitive trade-offs that contribute to coexistence. They identified three mechanisms involved in competitive use of space: (1) tolerance, which in their definition ranged from the ability to take over occupied space to the ability to resist encroachment, (2) dispersal, which in this definition described the distance moved, and (3) exploitation, which involved the speed with which an organism could actually make use of space to reproduce. Although most models separate tolerance from the other two mechanisms, most spatially implicit models combine the second and third mechanisms into a single process. The explicit spatial structure of the model allowed the authors to separate the ability to reach habitat (dispersal) from the ability to reproduce (exploitation). In patch dynamic models, colonization combines both finding empty localities and instantly reaching carrying capacity in the colonized area (Hanski 1983). Bolker and Pacala found that coupling long-range dispersal with exploitation was unlikely to maintain inferior competitors in the system unless superior competitors were far more clumped than empirically demonstrated for plant species (1999). Instead, they

found that strategies combining short dispersal with either high exploitation or tolerance allowed coexistence. Short dispersal and resistance to competitors created what they called a “phalanx effect” in which clusters of conspecifics experienced lower competition. One might expect this dynamic from a species able to change its competitive regime through allelopathy or other processes that affect conspecifics less than heterospecifics (Bolker and Pacala 1997). Although individuals in the phalanx might individually be inferior competitors, when aggregated in clusters they could limit the effects of the superior competitor and change the balance of interspecific and intraspecific competition (Bolker and Pacala 1997). Note that combining both exploitation and the phalanx effect would create a superior competitor.

Similar clustering effects appear in cellular automata models, which follow local interactions in discrete space (Molofsky 1994; Molofsky et al. 2001). Despite a homogeneous environment, organisms in cellular automata models create spatial patterns that alter the quality of local habitats or competitive neighborhoods, just as we saw in spatially explicit models for single species. Consideration of pattern formation in models for competing species shows that, as spatial structure becomes more explicit, spatial processes increasingly affect and in turn are affected by species interactions.

Interaction between Competition-Dispersal Trade-offs and Heterogeneity Induced Shifts in Dominance

As spatial structure in model formulations increases, the two basic mechanisms for competitive coexistence in effect interact. Our initial discussion of heterogeneity in the spatial or temporal environment pointed out that average competitive values may change with spatial or temporal fluctuations, allowing switches in local or short-term competitive dominance and the maintenance of multiple species in a region (Warner and Chesson 1985). With a competition-dispersal trade-off, the competitive hierarchy is fixed so such switches are not possible; yet models that look at this trade-off in explicit space with local interactions find that the average competitive effect actually experienced by individuals across the landscape can be altered by spatial patterns that form in response to this competition-dispersal trade-off. Models that attempt to examine the effects of both habitat heterogeneity and trade-offs have found that there are threshold levels of dispersal that allow species to coexist (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). If species dispersal is too high, then the advantage of niche partitioning is lost. With too little dispersal, inferior competitors cannot survive. A similar threshold is apparent in Bolker and Pacala’s explicit space model, where high levels of dispersal of the inferior competitor did not generally promote coexistence (1999). In chapter 10, Mouquet et al. more thoroughly review models combining source-sink dynamics and life history trade-offs.

Spatial Consumer-Resource Models

Nonspatial consumer-resource models with living resources tend to be unstable, meaning that one or both species goes extinct or both species oscillate. This lack of stability affects persistence and the maintenance of diversity. Nonspatial predator-prey models have generally been based on either a Lotka-Volterra formulation in continuous time (Lotka 1925; Volterra 1926a, 1926b, 1931) or a Nicholson-Bailey formulation in discrete time (Nicholson 1933; Nicholson and Bailey 1935). The most basic nonspatial formulations of each model include only the two interacting species; neither model leads to local stability without the addition of direct density dependence in some fashion (May 1976). The Lotka-Volterra model leads to neutral stability in which populations do not return to equilibrium after a perturbation, but instead oscillate around the equilibrium with amplitude cycle set by the amplitude of the perturbation. The Nicholson-Bailey model produces diverging oscillations until one species goes extinct (May 1976). Stabilizing factors for both models include the addition of a carrying capacity or density dependence for either or both species and an immune stage or age class for the prey (which acts as a refuge; Murdoch and Oaten 1975; Kuno 1987). In the Lotka-Volterra formulation the addition of a Type III functional response in the predator also offers the prey a refuge at low density (Murdoch and Oaten 1975). In the Nicholson-Bailey formulation, adding a negative binomial attack rate, which simulates aggregation in the predator attacks, helps to stabilize the model by offering prey a partial refuge away from clumps of predators (May 1978). We will show that some of the spatial factors that stabilize spatial predator-prey models and assist persistence mimic the same features required for stability in these nonspatial models.

Because of their inherent instability, consumer-resource interactions have received considerable attention from theoreticians and have a broader response to spatial processes than other two-species models. To avoid unnecessary complexity, we focus on stabilizing features of spatial processes in two-species predator-prey models. Following Briggs and Hoopes (2004), we have classified spatial processes that stabilize dynamics into three categories: (1) spatial averaging of fluctuations, frequently referred to as “statistical stability” (De Roos et al. 1991; McCauley et al. 1993, 1996), (2) density dependence induced by dispersal (Murdoch et al. 2003), and (3) nonadditive, nonlinear responses to heterogeneity in densities (Briggs and Hoopes 2004). These three mechanisms are not completely independent, and many models combine aspects of more than one of them. Below we provide an explanation of each mechanism and some examples. We do not specifically discuss spatially explicit versus spatially implicit formulations as we did for single species and competitive models because such divisions do not as accurately divide model outcomes as they do in the other models. The first and

third stabilizing mechanisms below are found more frequently in spatially explicit formulations, but all three stabilizing mechanisms can be found in both implicit and explicit spatial models. There are a number of good reviews of spatial consumer-resource models available for the reader wanting more depth on this subject (Murdoch and Oaten 1975; Briggs and Hoopes 2004; Murdoch et al. 2003).

Statistical Stability, Homogeneous Space

The first of these mechanisms, spatial averaging or statistical stability (De Roos et al. 1991), is seen most frequently in models with many patches or a lattice with local interactions (Allen 1975; De Roos et al. 1991, 1998; McCauley et al. 1996; Wilson 1998). In these models, although local patches may continue to fluctuate, regional population densities are relatively constant. This constancy comes from averaging population densities over fluctuating subpopulations. This mechanism does not require homogeneous space, but it can be swamped by the other two mechanisms in models with heterogeneous space. In models with explicit space there is a characteristic spatial scale below which local dynamics continue to fluctuate as in isolated, nonspatial predator-prey models and there is often pattern formation that induces spatial heterogeneities (De Roos et al. 1991; McCauley et al. 1993, 1996; Wilson et al. 1993). In patch models with small numbers of identical patches, this sort of statistical stability generally requires patches in out-of-phase limit cycles (Adler 1993; Jansen 2001). With more patches, patch models can have more variability in patch densities because the law of large numbers still leads to relatively constant average regional densities (Allen 1975; Crowley 1981). In order for regional densities to remain fairly constant, local populations must fluctuate asynchronously, which generally requires low to intermediate levels of dispersal (Allen 1975; Crowley 1981; De Roos et al. 1991; Adler 1993; but see Jansen 2001). Predator and prey dispersal can have different effects (McCauley et al. 1993), but this result comes partially from heterogeneities in local interactions, which is part of the third mechanism discussed below.

Density Dependence Induced by Dispersal: Heterogeneities in Space or Initial Conditions

The second stabilizing mechanism can come from any of a number of different spatial processes that result in density dependence in local dynamics. The simplest of these processes is a refuge or a constant number of dispersers (Crowley 1981; Sih 1987; Reeve 1988). As local densities vary, this movement leads to smaller changes in large populations and larger changes in small populations, resulting in density dependence that usually stabilizes local dynamics (Holt 1993; Briggs and Hoopes 2004; Murdoch et al. 2003), though immigration can at times be destabilizing (Holt 2002). Heterogeneities in initial conditions can lead to density dependent interactions in a similar fashion although very specific dispersal parameters are required to maintain such heterogeneities (Crowley 1981). A

propagule pool can similarly cause local density dependence. If all dispersers move into a pool from which they are evenly distributed, then immigration is higher per capita in low density patches than in high density patches (Weisser et al. 1997). Similarly, a time lag in dispersal—which is somewhat like a temporal dispersal pool—can be stabilizing as it disconnects dispersal from local dynamics (Gourley and Britton 1996; Neubert et al. 2002). Density dependence can also come from constant per capita immigration or emigration rates among heterogeneous patches (Crowley 1981; Holt 1984; Murdoch et al. 1992; Holt and Hassell 1993; Hochberg et al. 1996). This process is similar to source-sink maintenance of inferior competitors in the competition models. Local heterogeneity can be fixed or from spatiotemporal variation, as we found in spatial models of competition (Crowley 1981). Predation that is focused on areas where prey have high growth rates can be particularly stabilizing (Holt 1993; Holt and Hassell 1993). Conversely, as in the competition and single-species models, any dispersal that overemphasizes areas where populations are doing poorly will destabilize the dynamics and reduce persistence (Murdoch et al. 1992; Holt and Hassell 1993). For example, if predators aggregate too well on prey, they can synchronize patches and destabilize dynamics (Murdoch et al. 1992).

Nonlinear, Nonadditive Responses to Heterogeneity

The third stabilizing mechanism comes only with spatial heterogeneity in densities and nonlinearities in predator-prey responses. This feature is similar to a spatial storage effect (Chesson 1985, 1990; Warner and Chesson 1985) in that prey benefit more in areas where they are at high density than they lose in areas where they are at low density; this nonlinearity leads to subadditivity of density and predation effects (figure 12.1; box 12.2; Chesson 1990). The predators, therefore, still control the prey but without the overcompensation effects that would cause cycles. This sort of effect has been demonstrated with patch models (De Roos et al. 1998), lattice models (McCauley et al. 1996), and reaction-diffusion models (Gurney and Veitch 2000). In all of these models prey show distinct spatial patterns. In the patch model example, predators with a Type II functional response were spread evenly across the patches; prey dispersal combined with the nonlinear predator functional response led to some patches devoid of prey and others at high density (De Roos et al. 1998). In the individual-based lattice model example, predator functional responses were nonlinear because of age-structure: adult and juvenile predators had similar attack rates, but juveniles did not reproduce (McCauley et al. 1996). Local dispersal of juveniles led to prey clustering, creating necessary spatial heterogeneities; this clustering combined with the nonlinear predation stabilized the system and increased persistence (McCauley et al. 1996). In the reaction-diffusion model, Gurney and Veitch (2000) found that low predator dispersal and immobile prey could form spiral waves in a continuous model and clusters in a discrete analogue; with Rosenzweig-MacArthur predation

(Rosenzweig and MacArthur 1963), both spatial patterns could stabilize the system.

Combining the Three Stabilizing Mechanisms

These three stabilizing mechanisms in consumer-resource interactions are not independent and may not only act together but even be indistinguishable in both models and empirical systems. For example, the formation of stable spatial patterns promotes statistical stability, creates differences in local densities that can lead to density dependent dispersal, and creates heterogeneities that may interact with predator nonlinearities. In many models in which spatial patterns do not stabilize dynamics, they nonetheless lead to increased persistence (Hassell et al. 1991; Comins et al. 1992; Rohani et al. 1996; Gurney et al. 1998). Note that transient dynamics can contribute to persistence (Hastings 2001). This is particularly true for statistical stability, which is basically a series of very local systems with transient dynamics that are constantly buffered by the transient dynamics of their neighbors. On the other hand, models with all of these mechanisms may lead to extinction, cycling, or complex dynamics. No mechanism guarantees stability. Instead each mechanism *can* promote stability and persistence, given appropriate model structure, rates and modes of dispersal, and system size. The functional form of predator responses and prey growth can strongly affect model outcomes (Rohani and Ruxton 1999) with differences between comparable discrete and continuous models (Wilson 1996, 1998; Gurney and Veitch 2000). Dispersal is equally crucial. Too much can synchronize systems so that dynamics are similar to those of nonspatial models (Crowley 1981; Adler 1993; McCauley et al. 1993; Doebeli 1995), and too little dispersal can fail to separate dynamics enough (McCauley et al. 1993; Jansen 2001). The size of the system and boundary conditions can affect spatial pattern formation and stability (Wilson 1996; Donaldson and Nisbet 1999), and in small systems even or odd numbers of patches can affect the ability to attain out of phase limit cycles (Adler 1993). We have here only provided a brief outline or explanation and one or two examples. There are also examples of similar models with slightly different combinations of functional responses or dispersal distances that lead to very different outcomes. However, we suggest that any system that is stable or persists will include one of these three mechanisms.

Spatial Mutualism Models

Although mutualistic interactions appear to be common in nature (Crepet 1983; Boucher 1985; Schwartz and Hoeksema 1998), there are far fewer models that address the population dynamic consequences of mutualisms than there are for competition or predation (Wolfin 1985; Bronstein 1994). Simple models suggest that mutualistic interactions are unstable with a tendency toward extinction and unbounded population growth; however obligate and facultative mutualisms

display different dynamics (May 1974; Vandermeer and Boucher 1978). Obligate mutualisms are those in which each partner requires the other for survival. Examples include some plant-pollinator systems, such as figs with fig wasps and yuccas with yucca moths (Bronstein 1988; Pellmyr and Huth 1994), mycorrhizae and some plant species (Hoeksema and Bruna 2000); and coelenterates and zooxanthellae (Goreau et al. 1979). Facultative mutualisms are those in which each partner can survive without the other. Plants with multiple dispersal pathways and pollinating insects with a range of food resources are good examples of facultative mutualists. Because there are fewer mutualism models, let alone spatial mutualism models, we briefly summarize nonspatial models, examine the effects of spatially implicit processes on obligate mutualisms, and then extend these results qualitatively to facultative mutualisms.

Nonspatial Mutualism Models

The simplest models of obligate mutualisms generally consist of Lotka-Volterra competition equations with positive, rather than negative, constant interaction coefficients to indicate linear, positive effects from species interactions (Gause and Witt 1935; Vandermeer and Boucher 1978). These models often assume a negative or zero carrying capacity to meet the assumption that the two species do not survive in the absence of the other. As with competition models, these mutualism models produce intersecting linear isoclines. The intersection of the isoclines is an unstable equilibrium point with a tendency toward extinction below the equilibrium point and limitless growth above it, an unrealistic prediction that has hampered the study of mutualisms in communities. Nonlinear interaction coefficients between the two species (e.g., saturating benefits, DeAngelis et al. 1986) though, can give curved isoclines (figure 2.3); when these isoclines intersect so that there are two interior equilibria (i.e., the curves create an eye by crossing twice), the second intersection is a locally stable equilibrium, and the species persists as long as densities stay above the lower intersection or saddle equilibrium point (May 1976; Vandermeer and Boucher 1978; DeAngelis et al. 1986). Because these more realistic models predict that both mutualistic partners go extinct when densities drop below this threshold lower equilibrium point, they suggest that obligate mutualisms should only persist in relatively stable environments where population densities are unlikely to experience extreme reductions (May 1974; Travis and Post 1979). Other researchers have suggested that the diversity of obligate mutualists in nature indicates instead that these models fail to capture the full range of factors affecting the population dynamics of mutualists (Heithaus et al. 1980; Boucher et al. 1982; Wolfin 1985; Ringel et al. 1996).

Models of facultative mutualisms are far easier to stabilize than obligate mutualisms (Wolfin and Lawlor 1984; Wolfin 1985). Because facultative partners can survive without the other species, their populations grow when small and do not tend toward extinction at low densities (Vandermeer and Boucher 1978; Travis

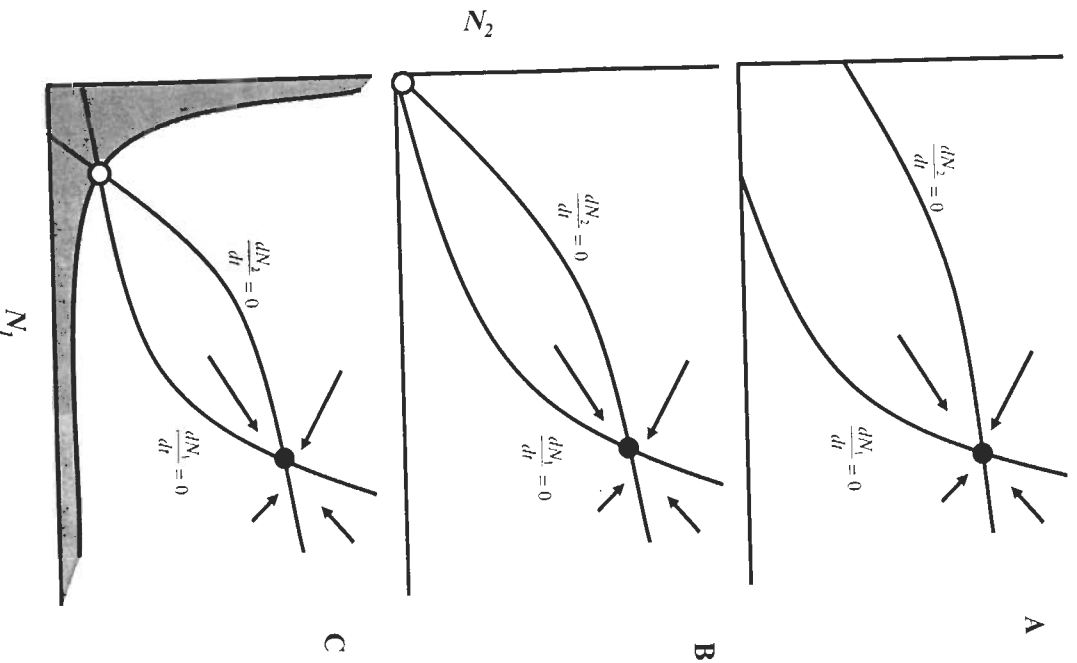


Figure 2.3. Isoclines and equilibria for (A) facultative and (B, C) obligate mutualists. Facultative mutualisms can be very stable although obligate mutualisms may not be. Solid circles represent stable equilibria and open circles represent unstable equilibria. In panel A each species can exist without the other, making the species facultative mutualists. Notice that each species exists at a higher density with its mutualistic partner than alone. In panels B and C, the two species can only exist in the presence of the other, making them obligate mutualists. In panel C the unstable equilibrium is a saddle point with a stable manifold that acts as a threshold. At densities below this manifold (in the shaded region) the species cannot persist (after Vandemeer and Boucher 1978; Dean 1983).

and Post 1979; Wolin and Lawlor 1984). Mutualistic effects may also be incorporated in multiple ways in models of facultative mutualisms. For example, the presence of a facultative mutualistic partner may increase carrying capacities or alter the speed at which populations approach carrying capacity (Dean 1983; Wolin 1985; Wright 1989). The effects of facultative mutualists can also vary with the density of either partner (Wolin and Lawlor 1984). In general mutualistic effects at low density or decreasing with density lead to stable equilibria (Dean 1983; Wolin and Lawlor 1984; Wright 1989); however all facultative mutualisms, even those that do not contain stable equilibria, increase the persistence of the mutualistic partners (Boucher et al. 1982; Wolin 1985).

Adding Space to Models of Obligate Mutualism

One of the missing factors of realism in obligate mutualism models is spatial structure. Hutson et al. (1985) point out that nonspatial approaches to modeling obligate mutualisms assume that populations are so evenly spread across an environment that modeling average dynamics is equivalent to modeling complete dynamics. If, instead, one assumes that populations are spread out across space with different densities in different locations, then drops in local population density will not necessarily take even an obligate mutualist below a threshold density (Hutson et al. 1985). In fact, if one can describe density across linear space with a function, then all points above that function should be dynamically equivalent to average population densities that uniformly approach a stable equilibrium point (figure 2.4; Hutson et al. 1985). There should be, therefore, a vast array of distributions for which the spatial mutualistic interaction is extremely resilient to perturbations (Hutson et al. 1985). Similarly, Hastings and Wolin (1989) examined a structured population model to look at obligate mutualists in spatial subpopulations. The model is an age-structured model in which local density is assumed to increase with patch age (time since colonization). If extinction rates decrease with density, then there is an equilibrium distribution of numbers within patches, and all equilibria are stable (Hastings and Wolin 1989). This outcome is similar to the dynamic equilibrium found in patch occupancy single species and competition models in which local occupancy may vary but the fraction of occupied patches is constant. This outcome is also similar to the statistical averaging found in consumer-resource models with increased persistence or regional stability arising from statistical stability. Space, therefore, can stabilize models of obligate mutualisms. These spatial models suggest not only that obligate mutualisms may persist in nature, but also that the consideration of spatial structure may be particularly important in community dynamics involving such mutualists.

Adding Space to Models of Facultative Mutualism

Because even nonspatial models suggest that facultative mutualisms not only persist in nature but can increase the persistence of each species beyond their indi-

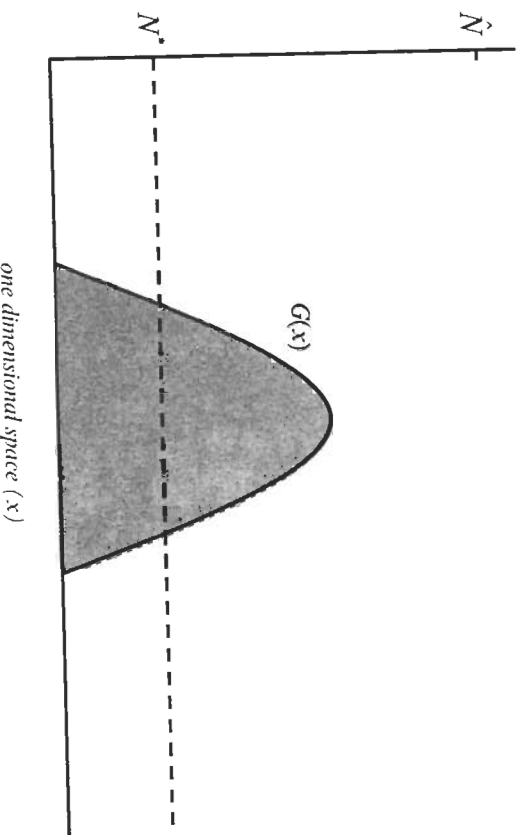


Figure 2.4. One dimensional spatial representation of an obligate mutualist. Obligate mutualisms may be far more stable in space than nonspatial models suggest. The density of each species in figure 2.3 could be represented in one dimensional space. If the species were uniformly distributed across space, then at the unstable equilibrium the density at each point x would be N^* , and any density below the dashed line would bring the interaction below the threshold stable manifold in figure 2.3C, leading to the extinction of the two obligate mutualists. As suggested by Hutson et al. (1985), though, a variety of potential functions, $G(x)$, could describe the distribution of the species in space. As long as $N(x)$ is greater than $G(x)$, meaning the distribution does not lie in the shaded region, the species should head toward the stable equilibrium, and the mutualists should persist. This result suggests that obligate mutualists can persist despite very low densities in some areas, and that these interactions might be quite stable.

vidual expected persistence time, spatial models of facultative mutualisms offer more insight into the mechanisms of single-species spatial persistence or spatial processes in multispecies models. The nonuniform distribution of a facultative mutualist can create higher quality habitats that lead to mass effects for focal single species. Similarly, mutualists can stabilize larger community dynamics and food web modules by creating habitat heterogeneity that shifts the balance of competition and allows inferior competitors to persist or that offers a refuge from predators (Heithaus et al. 1980; Addicott 1981; Boucher et al. 1982; Ringel et al. 1996). Mutualisms are not always direct interactions and are not always without costs; they represent one end of a continuum of interactions from predatory or parasitic to facilitative (Abrams and Matsuda 1996; Abrams et al. 1998). Many researchers have pointed out the likelihood of evolution of mutualistic interaction from parasitic ones (Axelrod and Hamilton 1981; Toff and Karter 1990; Nee 2000; Bronstein 2001; Westerbergh and Westerbergh 2001), and many empirical and

modeling studies have examined interactions that vary spatially or temporally from positive to negative (Vandermeer et al. 1985; Dodds 1988; Abrams and Matsuda 1996; Ringel et al. 1996; Abrams et al. 1998). The stabilizing influence of mutualistic interactions, therefore, may be extremely common and hard to detect in communities, and mutualists may play an important and poorly understood role in metacommunity dynamics.

Conclusion

This chapter has outlined some basic spatial processes in models of two species interactions, with an emphasis on key features that help to increase stability or persistence in single and two-species models. The first feature is asynchrony in local dynamics, particularly in models with homogeneous space. This feature is crucial for single species models but is also important in statistical averaging found in competition-dispersal trade-off competitive models, statistical stability in consumer resource models, and the stable distribution of population abundances found in Hastings and Wolin's spatially structured mutualism model (1989).

With heterogeneity in habitat quality, the potential for persistent interactions or communities increases by creating refuges or disparities in habitat quality that increase differences in local population abundances. With dispersal these disparities lead to mass effects that allow rescue effects and source-sink dynamics in single species and competitive models, and create induced density-dependent stability in predator-prey interactions. Facultative mutualistic interactions can increase such spatial heterogeneities and contribute to the persistence not only of the mutualistic partners but also of their predators.

Spatial heterogeneity and nonlinearities in response to that heterogeneity can also increase persistence in all three types of two-species models. Nonlinear, non-additive responses to other species can create thresholds as well as relative spatial refuges. They can interact with spatial or temporal heterogeneity to change average regional parameter values from those expected for a mean environment as in temporal and spatial storage effects in competitive interactions, nonlinear stabilization in predator-prey interactions, and the potential maintenance of obligate mutualists with nonuniform distributions.

As discussed in the consumer-resource section, these mechanisms can interact and are not always completely separable. Pattern formation in homogeneous landscapes creates heterogeneities that influence persistence, so that organisms in homogeneous landscapes may experience not only statistical averaging but also mass effects from local changes in habitat quality due to altered interaction strengths or barriers to dispersal. Also, if interacting species disperse at different scales or use different resources, they may experience very different environments, even so far as one species perceiving a homogeneous environment while the other perceives a heterogeneous one. This is frequently the case in predator-prey models.

We have emphasized modeling approaches that highlight the maintenance of diversity, yet community dynamics can just as frequently be affected by spatial responses to species interactions that limit or reduce diversity. As we have discussed in each section, a balance between too little and too much dispersal is important in order to maintain asynchrony between local communities. At higher levels of dispersal, spatial subdivision disappears and the stabilizing or persistence increasing effects of spatial processes may be diluted or may disappear altogether. Facultative mutualisms, for example, may decrease persistence of other species by increasing abundance and dispersal between local communities so that synchrony increases (Ringel et al. 1996). Dispersal in heterogeneous landscapes can permit exclusion that otherwise would not be observed, and at times even destabilize predator-prey interactions.

With all formulations the addition of space can stabilize dynamics, increase persistence of species, and offer some explanations for the maintenance of species diversity. These spatial dynamics are crucial to metacommunities. We will see in the next chapter that additional interacting species add heterogeneity and can distinctly alter dynamics as we discussed briefly in regard to mutualistic interactions. Additional species may alter local habitat quality leading to variation in spatial effects that may allow inferior competitors in one area to dominate in another, that may offer alternative prey resources or shelter from predation, or that may facilitate growth or reproduction in ways that alter the outcomes of other species interactions. As with space, species interactions can have both facilitative and negative effects. In many cases the addition of species or interactions to the models we have outlined may destabilize stable interactions or may change spatial or temporal heterogeneity just enough to remove a fugitive species from the system and lead to reductions in local and metacommunity diversity.

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