

3 Spatial Models of Competition

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3.1 Introduction

Traditional models of competition usually assume well-mixed populations, neglecting the localized nature of interactions between organisms and their environment. Because each individual organism affects mostly its local neighborhood, organisms create spatial heterogeneity in the environment; because organisms respond to their local neighborhoods, this biotically generated heterogeneity provides opportunities for novel ecological strategies and multispecies coexistence. Abiotically generated heterogeneity can also foster coexistence on a small scale and may explain the distribution of species across geographic gradients. In this chapter we discuss how spatial aspects of competition can be captured in theoretical models and how they affect coexistence. Because spatial models of competition cover many disparate systems, we focus here on models of terrestrial plants and other sessile organisms, but we suspect many of the phenomena we discuss are more widely applicable.

Competition among sessile organisms is a more complicated process than competition in well-mixed systems as idealized by the laboratory chemostat (Chap. 2). In a chemostat, each cell interacts equally with every other cell, and these interactions are mediated by one or a few limiting resources (e.g. light, phosphorus, nitrogen). The cells in chemostats often have a simple life cycle: they reproduce and die continuously. Although terrestrial plants may also compete for only a few limiting resources, they interact locally with a few other individuals. Terrestrial plants also have more complicated life cycles: individuals originate as seeds, which must establish and grow into adults, which produce and disperse more seeds.

It is this complicated life cycle that makes competition between sessile organisms a hierarchical process. One can consider competition at two hierarchical levels: competition between individuals and competition between populations. Competition between individuals occurs when individuals decrease each other's growth and biomass by consuming shared limiting resources. Competition between populations occurs when competition

between individuals decreases the births or increases the deaths of individuals, so that the number of individuals of the competing species is decreased relative to their monoculture numbers. Competition between populations is more difficult to study because it occurs on a longer time scale and at a larger spatial scale, but it is ultimately more important because coexistence at the population level determines whether species will be found together in the field. Knowledge of how individual-level competition works is necessary but not sufficient to predict how species compete at the population level, because new processes such as seed production and dispersal also affect population-level competition. Mathematical models provide a way to integrate local interactions to understand population dynamics.

Different approaches have been taken to model the effect of local interactions on competition, each with its own strengths and weaknesses. Models can be stochastic or deterministic, continuous- or discrete-time. They can treat space explicitly, keeping track of actual locations in one-, two-, or three-dimensional coordinate systems, or implicitly, following only the percent cover of different species across the landscape. Explicitly spatial models can treat space either as continuous or discrete. Finally, different models measure species using different currencies: the number of individuals (the *population* approach), the proportion of habitat patches occupied (the *metapopulation* approach), or biomass (the *ecosystem* approach). There are close connections between some approaches such that a simpler approach is often attained as a limiting case of a more complex method. The choice of modelling approach depends on the questions the model is being used to answer and on the predisposition of the modeller. In Levin's apt metaphor (1992), the natural world is a high-dimensional cake through which models cut manageable low-dimensional slices. Some models are more useful than others, but none can capture the full richness of the natural world and still be comprehensible. We concentrate on relatively simple, general models that are at least partially analytically tractable. An alternative approach is to consider detailed simulation models tailored to specific systems, and to generalize based on the analysis of many such models. We focus on theoretical models because their transparency and simplicity can give insights into a broad range of systems, but this alternative approach provides another possible road to ecological insight.

In this chapter we examine a variety of simple spatial models of competition. In Sect. 3.2, we begin with implicitly spatial patch models, which discard spatial locations while retaining localized competitive interactions. We then look at a variety of explicitly spatial models (Sect. 3.3), which incorporate the actual location of organisms on the landscape. In Sect. 3.4, we discuss how these models are related and how they differ in their assumptions of various spatial scales. In Sect. 3.5, we summarize the findings of models that include extrinsic heterogeneity in the environment. In Sect. 3.6, we discuss how the spatial nature of competition affects coexistence, and in Sect. 3.7, we outline areas where further important work remains to be done.

3.2 Implicitly Spatial Models

Implicitly spatial models, also called pseudospacial (Bolker and Pacala 1997) or mean field models (Durrett and Levin 1994a,b), incorporate spatial variation in the presence or absence of individuals but do not account for the actual locations of these individuals. Patch occupancy models consider an effectively infinite number of patches coupled by global dispersal, each capable of supporting one or more species that compete for the same local resources. There are two possible interpretations of a “patch” (Tilman 1994). In the first, a patch holds one or a few individual plants that die and produce seeds; we scale from the interactions between individuals to the dynamics of populations. In the second, a patch holds local populations or communities that can go locally extinct and recolonize other patches; we scale from populations to metapopulations (Levins 1969; Hanski and Gilpin 1997). We will use the first interpretation of patches as holding individuals, but the resulting models are identical and the same conclusions can be reinterpreted in a metapopulation perspective. We discuss models that are continuous in time, but discrete-time models may be more appropriate for annual plants.

3.2.1 Single Species Model

If we consider only a single species, each patch may be in one of two states: empty (P_0 proportion) or occupied (P_1 proportion). Individuals die at rate m_1 , meaning that in any small time interval dt , the probability of death is $m_1 dt$. Individuals produce seeds at rate c_1 , that are then dispersed to another patch chosen at random. If this patch is occupied, the seed does not grow, but if the patch is empty, the seed establishes with probability e_1 . The change in occupied patches is determined by these two processes of death and birth, formalized in the following equation.

$$\frac{dP_1}{P_0} = e_1 c_1 P_1 P_0 - m_1 P_1$$

$$P_0 = 1 - P_1 \tag{1}$$

This model is known in the metapopulation literature as Levins’ model (Levins 1969). It is formally equivalent to logistic growth. The equilibrium density, $\hat{P}_1 = 1 - m_1/(e_1 c_1)$, increases with establishment probability, e_1 , and fecundity, c_1 , and decreases with mortality rate, m_1 . A species can persist alone when its effective colonization rate is greater than its mortality rate, $e_1 c_1 > m_1$. Notice that there are always $\hat{P}_0 = 1 - \hat{P}_1 = m_1/(e_1 c_1)$ proportion of sites left unoccupied.

3.2.2 Two Species Models

There have been many patch models of competition based on different assumptions of how individuals interact. Here we use a very general model of two species competition dating back to Slatkin (1974) as a common framework for examining these various simpler models. This general model of competition builds on Levins' model [Eq. (1)] in a straightforward way. Each patch may be empty (proportion P_0), occupied by an individual of either species 1 or species 2 alone (proportions P_1 and P_2), or occupied by individuals of both species (proportion P_{12}). Patches occupied by species i alone produce seeds at rate c_i . Patches occupied by both species produce species i seeds at rate c_{ij} . Seeds are dispersed globally. A seed of species i that lands on an empty patch establishes with probability e_i and one that lands on a patch occupied by species j establishes with probability e_{ij} . Species i dies at rate m_i when alone and at rate m_{ij} when locally co-occurring with species j . Figure 3.1 summarizes the transitions between states. These assumptions result in the following equations:

$$\begin{aligned} \frac{dP_1}{dt} &= e_1(c_1P_1 + c_{12}P_{12})P_0 - m_1P_1 - e_{21}(c_2P_2 + c_{21}P_{12})P_1 + m_{21}P_{12} \\ \frac{dP_2}{dt} &= e_2(c_2P_2 + c_{21}P_{12})P_0 - m_2P_2 - e_{12}(c_1P_1 + c_{12}P_{12})P_2 + m_{12}P_{12} \\ \frac{dP_{12}}{dt} &= e_{12}(c_1P_1 + c_{12}P_{12})P_2 + e_{21}(c_2P_2 + c_{21}P_{12})P_1 - (m_{12} + m_{21})P_{12} \\ P_0 &= 1 - P_1 - P_2 - P_{12} \end{aligned} \quad (2)$$

Competition can occur in three distinct ways (Levins and Culver 1971; Slatkin 1974; Bolker and Pacala 1997; Klausmeier 2001):

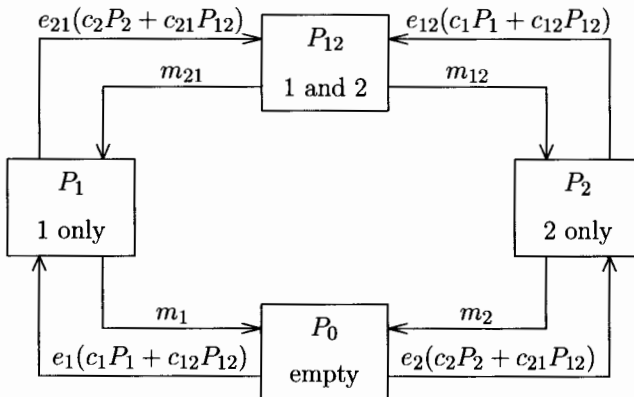


Fig. 3.1. State transition rates in the general two-species patch model, Eqs. (2)

- *Mortality competition*: increased mortality rate where individuals co-occur ($m_{ij} > m_i$)
- *Establishment competition*: decreased probability that a seed will successfully establish in a patch occupied by the other species ($e_{ij} < e_i$)
- *Fecundity competition*: decreased fecundity in jointly occupied patches ($c_{ij} < c_i$)

Any or all of these forms of competition may occur in the general framework of this model. This flexibility is both a blessing and curse. While the model can incorporate a variety of types of interaction, the range of possibilities makes fully exploring parameter space impossible and the equations are difficult to deal with algebraically (but see Taneyhill 2000, who uses advanced techniques from dynamical systems theory on the full model of Eqs. (2)). To reduce the model complexity, Levins and Culver (1971) assumed that the species are independently distributed, but in general, the assumption of independence is incorrect (Slatkin 1974), except in the case of pure fecundity competition (Klausmeier 2001). Instead of analyzing the full model, people have examined various ecologically motivated special cases. We summarize some of these informative special cases below.

3.2.2.1 Local Founder Control

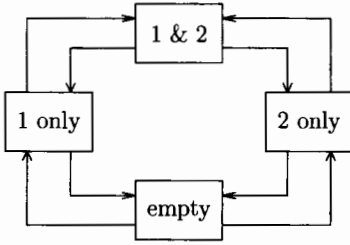
Local founder control is when an adult plant can prevent the establishment of seedlings in the same patch, thereby preempting the site. This may occur when individual plants compete for light, because light competition is asymmetric (Weiner 1990): the larger plant shades the smaller, but not vice versa. In this case, we set $e_{12} = e_{21} = 0$, to prevent establishment in already occupied patches. As a result, there are no jointly occupied patches ($P_{12} = 0$) and Eqs. (2) reduce to

$$\begin{aligned} \frac{dP_1}{dt} &= e_1 c_1 P_1 P_0 - m_1 P_1 \\ \frac{dP_2}{dt} &= e_2 c_2 P_2 P_0 - m_2 P_2 \\ P_0 &= 1 - P_1 - P_2 \end{aligned} \tag{3}$$

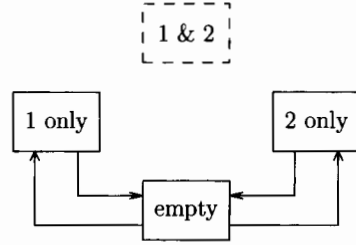
The model structure is shown in Fig. 3.2B.

This model is easily analyzed. The per capita growth rate of each species depends only on the amount of empty space, P_0 , which we can consider to be the single limiting resource. Since there is only one resource, we know that coexistence is impossible and that the species that reduces empty space the most will displace all others (Tilman 1982, Chap. 2). The amount of empty

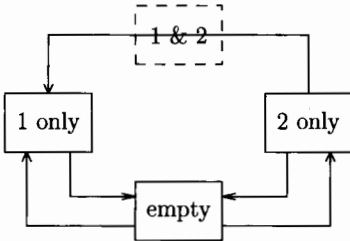
A) General model



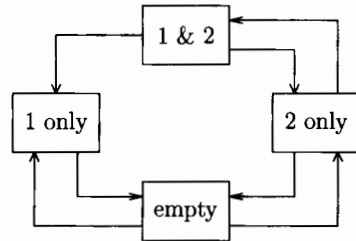
B) Local founder control



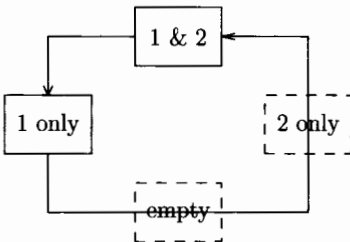
C) Hierarchical competition



D) 1 better than 2



E) Pure successional niche



F) Fecundity competition

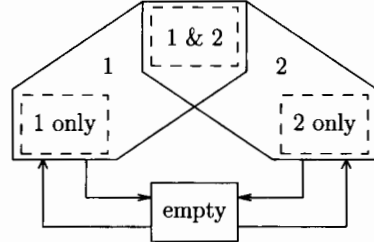


Fig. 3.2A–F. Schematic outline of different special cases. States represented by *dashed boxes* are empty

space a species leaves is $P_0^* = m_i / (e_i c_i)$, so a species can increase its competitive ability by decreasing its mortality rate m_i , increasing its fecundity rate c_i , or increasing its establishment probability e_i .

3.2.2.2 Hierarchical Competition

Suppose plants compete locally for a single soil nutrient, R . Resource competition theory shows that local coexistence is impossible and that species can be ranked according to their nutrient competitive abilities (Tilman 1982, Chap. 2). By convention, we let species 1 be the superior local competitor, and

species 2 be the inferior local competitor ($R_1^* < R_2^*$). We assume that local dynamics are instantaneous. Species 2 cannot establish in a site occupied by species 1 ($e_{21} = 0$), but species 2 does not inhibit species 1 from establishing ($e_{12} = e_1$). When a seed of species 1 establishes on a site occupied by species 2, species 1 immediately takes over the site. This means $m_{21} = \infty$. These assumptions imply that there are no jointly occupied sites ($P_{12} = 0$) and Eqs. (2) reduce to

$$\begin{aligned} \frac{dP_1}{dt} &= e_1 c_1 P_1 P_0 - m_1 P_1 + e_1 c_1 P_1 P_2 \\ \frac{dP_2}{dt} &= e_2 c_2 P_2 P_0 - m_2 P_2 - e_1 c_1 P_1 P_2 \\ P_0 &= 1 - P_1 - P_2 \end{aligned} \quad (4)$$

or equivalently,

$$\begin{aligned} \frac{dP_1}{dt} &= e_1 c_1 P_1 (1 - P_1) - m_1 P_1 \\ \frac{dP_2}{dt} &= e_2 c_2 P_2 (1 - P_1 - P_2) - m_2 P_2 - e_1 c_1 P_1 P_2 \end{aligned} \quad (5)$$

This hierarchical competition model was first studied by Hastings (1980), then later by Nee and May (1992), and Tilman (1994). The model structure is shown in Fig. 3.2C.

In this model, species 1 is not affected at all by species 2. In fact, the first equation of (5) is the single-species Levins' model, Eq. (1). The equilibrium density of the locally superior competitor, species 1, is $\hat{P}_1 = 1 - m_1/(e_1 c_1)$, regardless of the presence or absence of species 2. Although species 2 cannot coexist with species 1 within a patch, it can persist as a population if

$$e_2 c_2 > \frac{e_1 c_1 (e_1 c_1 - m_1 + m_2)}{m_1} \quad (6)$$

(Tilman 1994). Species 2 can persist if its effective colonization rate, $e_2 c_2$, is sufficiently higher than species 1's, or if its mortality rate, m_2 , is lower than species 1's (but only if the secondary condition $\hat{P}_1 < 0.5$ is met) (Tilman 1994). Coexistence of species 2 is made easier if species 1 is on a slower timescale ($e_1 c_1 - m_1$ small). The condition of $\hat{P}_1 < 0.5$ is not always met, so for simplicity most studies have assumed equal mortality rates m and assumed that species 2 has a higher effective colonization rate, $e_2 c_2$. In this case, the coexistence requirement for species 2 reduces to

$$e_2 c_2 > \frac{(e_1 c_2)^2}{m}. \quad (7)$$

Note that it does not suffice that species 2 is a slightly better colonizer than species 1; Eq. (7) shows that there is a finite limit to how similar species 2's colonization rate can be to species 1's to coexist (Fig. 3.3.D).

Equation (7) shows that coexistence is possible if the so-called *competition-colonization trade-off* between the ability to compete locally and the ability to effectively colonize empty patches exists. Such a trade-off has been observed in patterns of allocation of prairie plants (Tilman 1994). For coexistence to work, species 1 must not be able to reach all suitable sites; that is, it

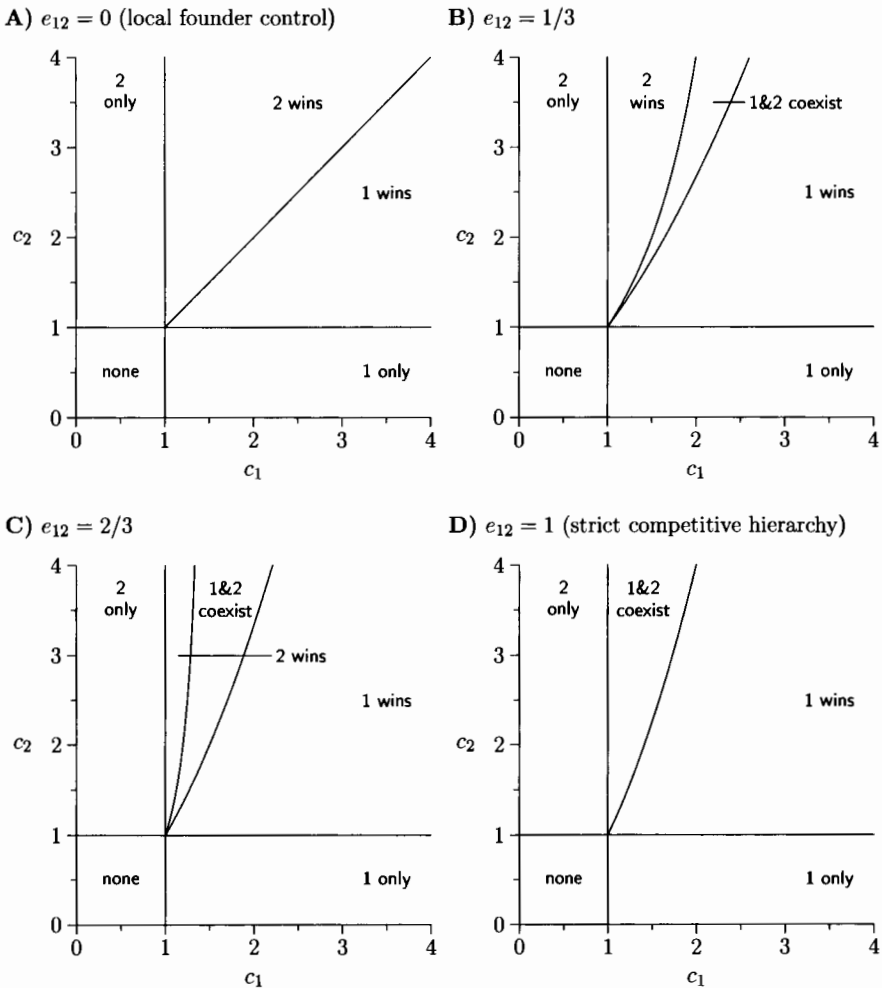


Fig. 3.3A–D. Outcome of competition with a competitive hierarchy of varying strictness as a function of fecundities. Other parameters: $e_{21} = 0$, $e_1 = e_2 = 1$, and $m_1 = m_2 = 1$. **A** $e_{12} = 0$, no hierarchy: local founder control as in Eqs. (3). Coexistence is impossible. **B** $e_{12} = 1/3$. **C** $e_{12} = 2/3$. **D** $e_{12} = e_1$, a strict competitive hierarchy as in Eqs. (4). Species 2 can never exclude species 1

must be recruitment limited. Species 2 represents a *fugitive species*, one that is inevitably displaced locally but persists by colonizing the empty patches left by species 1 (Hutchinson 1951). Because any number of species always leaves vacant space, a hyperfugitive species with a sufficiently high colonization rate can always persist, so there is no fixed limit to the number of species that may coexist in this model (Hastings 1980; Tilman 1994).

Armstrong (1976) relaxed the assumption of an absolute competitive hierarchy by letting e_{12} , the probability that a seed of the superior competitor displaces an adult of the inferior competitor, vary between 0 and e_1 :

$$\begin{aligned}\frac{dP_1}{dt} &= e_1 c_1 P_1 P_0 - m_1 P_1 + e_{12} c_1 P_1 P_2 \\ \frac{dP_2}{dt} &= e_2 c_2 P_2 P_0 - m_2 P_2 - e_{12} c_1 P_1 P_2 \\ P_0 &= 1 - P_1 - P_2\end{aligned}\tag{8}$$

This model interpolates between the case of local founder control given by Eqs. (3) when $e_{12} = 0$ and the case of an absolute competitive hierarchy given by Eqs. (4) when $e_{12} = e_1$. Species 2 now exerts a negative influence on species 1 at the population level, even though it is still an inferior local competitor.

The criterion for species 2 to invade a monoculture of species 1 is

$$e_2 c_2 > \frac{e_1 c_1}{m} \left[m + e_{12} c_1 \left(1 - \frac{m}{e_1 c_1} \right) \right],\tag{9}$$

and the criterion for species 1 to invade a monoculture of species 2 is

$$e_1 c_1 > \frac{e_1 c_2}{m} \left[m - e_{12} c_1 \left(1 - \frac{m}{e_2 c_2} \right) \right].\tag{10}$$

Equation (10) shows that an inferior local competitor can regionally exclude a superior local competitor if the assumption of an absolute competitive hierarchy is relaxed. Figure 3.3 uses these criteria to determine the outcome of competition as a function of the fecundity of both species. As discussed above (Sect. 3.2.2.1), when there is local founder control, the most fecund species displaces the other and coexistence is impossible (Fig. 3.3A). As the competitive hierarchy becomes more strict (e_{12} increases), the region of coexistence gets larger at the expense of the region where species 2 displaces species 1 (Fig. 3.3B, C). For an absolute competitive hierarchy, coexistence is easiest and species 2 can never displace species 1 (Fig. 3.3D).

Starting from the local scale where species 1 is the superior competitor, we see that species 2 persists regionally due to its superior ability to colonize empty sites. In the previous section (Sect. 3.2.2.1) we saw that when it is

impossible for a seedling to displace an adult, species cannot coexist and the best colonizer (species 2) dominates. Starting from the regional scale where species 2 is the superior competitor due to its higher fecundity (Sect. 3.2.2.1), we see that species 1 persists through its ability to take sites away from species 2. This dual perspective highlights that species coexistence is a two-way relationship that requires each species to excel at some point along its life-cycle: trade-offs are necessary (Tilman 1990). Because terrestrial plants have more complex life-cycles than simpler organisms such as phytoplankton (see Sect. 3.1), they have novel opportunities for coexistence.

3.2.2.3 Non-instantaneous Displacement and the Successional Niche

One of the most extreme oversimplifications of the hierarchical competition model described above is its assumption of instantaneous displacement of inferior competitors by superior competitors. Retaining the assumption of a strict competitive hierarchy, Pacala and Rees (1998) relaxed the assumption of instantaneous local dynamics. They augmented the hierarchical competition model [Eq. (4)] with two additional states: patches containing both species and patches containing the superior competitor that are still invulnerable by the inferior competitor. To keep within our framework of Eqs. (2), we will not track patches of the superior competitor susceptible to invasion by the inferior competitor, but will allow for transient local co-occurrence during local competitive exclusion. The essential assumptions of this model are $e_{21} = 0$, $\infty > m_{21} > m_2$, $m_{12} = m_1$, and $c_{21} = c_2$. For simplicity, we will follow Pacala and Rees (1998) in also assuming $e_{12} = e_1$ and $c_{12} = c_1$ so that species 1 remains completely unaffected by species 2, but these additional assumptions are not particularly well-founded, because the presence of an inferior competitor should negatively impact the superior competitor to some degree.

$$\frac{dP_1}{dt} = e_1 c_1 (P_1 + P_{12}) P_0 - m_1 P_1 + m_{21} P_{12}$$

$$\frac{dP_2}{dt} = e_2 c_2 (P_2 + P_{12}) P_0 - m_2 P_2 - e_1 c_1 (P_1 + P_{12}) P_2 + m_1 P_{12}$$

$$\frac{dP_{12}}{dt} = e_1 c_1 (P_1 + P_{12}) P_2 - (m_1 + m_{21}) P_{12}$$

$$P_0 = 1 - P_1 - P_2 - P_{12} \quad (11)$$

Overall, these assumptions are similar to those of the hierarchical competition model, except the death rate of the inferior competitor in jointly occupied patches, m_{21} , is not considered to be infinite (see Fig. 3.2D).

Since species 1 is assumed to be completely unaffected by species 2, the question of coexistence is reduced to the question of species 2's persistence. Assuming $m_1 = m_2 = m$, it can be shown using an invasibility argument that species 2 can persist when

$$e_2 c_2 > \frac{(e_1 c_1)^2}{m} \cdot \frac{m_{21} + m^2 / (e_1 c_1)}{m_{21} + e_1 c_1}. \quad (12)$$

Pacala and Rees (1998) derived a similar criterion for their model. Since the second fraction on the right hand side of Eq. (12) approaches 1 as m_{21} approaches infinity, the coexistence criterion Eq. (12) approaches that of the hierarchical model of Eq. (7). It becomes easier for species 2 to persist as the rate it is displaced from jointly occupied patches, m_{21} , decreases.

However, it is not clear that coexistence will always become easier when the inferior competitor can locally coexist with the superior competitor, because of the unlikely assumption that species 1 is completely unaffected by species 2. If the inevitable effects of species 2 on species 1 were included, species 1 may be regionally excluded, and it is likely that coexistence of both species would be made more difficult, as Armstrong (1976) found.

Pacala and Rees (1998) used a model similar to that in Eqs. (11) to examine an alternative mechanism by which an inferior competitor can coexist with a superior competitor, which they called the *successional niche*. The essential trade-off is between growth rate within patches and local competitive ability so that an inferior competitor with a greater growth rate can take advantage of a recently colonized patch while the slower-growing superior competitor is not yet mature. This trade-off is similar to the gleaner-opportunist trade-off that can allow coexistence in nonspatial models of competition in a fluctuating environment (Grover 1997; Litchman and Klausmeier 2001).

To isolate the influence of the successional niche on coexistence, Pacala and Rees (1998) eliminated the influence of any competition-colonization trade-off by setting all $c = \infty$, removing recruitment limitation of both species. Assuming that both species have infinite colonization rates eliminates both empty patches and patches occupied only by species 2 ($P_0 = 0$ and $P_2 = 0$). Equations (11) then reduce to one independent equation,

$$\begin{aligned} \frac{dP_{12}}{dt} &= m_1 P_1 - m_{21} P_{12} \\ P_1 &= 1 - P_{12} \end{aligned} \quad (13)$$

(Pacala and Rees 1998) (see Fig. 3.2E). In this model, a recently vacated site is immediately colonized by both species. Species 2 enjoys a period of local dominance due to its faster growth rate, but is eventually displaced by species 1, the superior local competitor. When species 1 dies, this cycle begins again. Coexistence in this model is inevitable, with species 1 present in all patches, and species 2 found in $\hat{P}_{12} = m_{21} / (m_{21} + m_1)$ proportion (Pacala and Rees 1998).

3.2.2.4 Fecundity Competition

The previous models have assumed that local competition is so strong that local coexistence is impossible. However, individual plants may be able to coexist within a patch by a number of mechanisms, such as different phenologies or rooting depths, or regulation by species-specific natural enemies (Chap. 7). Here we assume weak competition so that species can stably coexist within patches. Following Klausmeier (2001), we assume $e_{12} = e_1$, $e_{21} = e_2$, $m_{12} = m_1$, and $m_{21} = m_2$, so that neither establishment nor mortality is affected by the presence of a competitor, as would be expected if individuals can locally coexist. Competition occurs only through a reduction in seed production, so $c_{12} \leq c_1$ and $c_{21} \leq c_2$. This represents pure fecundity competition. The quantity c_{ij}/c_i measures how much species j changes species i 's fecundity where they locally co-occur.

Under these assumptions, the distributions of species 1 and 2 become independent as time tends to infinity (Klausmeier 2001). This means that the probability of finding species 1 in a patch is not affected by the presence or absence of species 2. Independence implies that $P_{12} = (P_1 + P_{12})(P_2 + P_{12})$ so we need to keep track of only the total occupancies of species 1, $p_1 = P_1 + P_{12}$, and species 2, $p_2 = P_2 + P_{12}$. Levins and Culver (1971) also assumed independence for the general model, but this assumption usually does not hold (Slatkin 1974): pure fecundity competition is the unusual special case in which the distributions are independent. The equations governing the total occupancy of both species are

$$\begin{aligned} \frac{dp_1}{dt} &= e_1(c_{11}p_1(1-p_2) + c_{12}p_1p_2)(1-p_1) - m_1p_1 \\ \frac{dp_2}{dt} &= e_2(c_{22}p_2(1-p_1) + c_{21}p_1p_2)(1-p_2) - m_2p_2 \end{aligned} \quad (14)$$

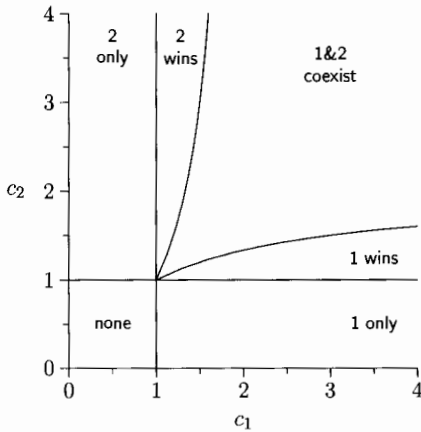
(Klausmeier 2001) (see Fig. 3.2F).

The condition for species i to invade a monoculture of species j is

$$\frac{e_i c_i}{m_i} > \frac{1}{(c_{ij}/c_i)(I?m_j/(e_j c_j)) + m_j/(e_j c_j)}. \quad (15)$$

Figure 3.4 uses Eq. (15) to illustrate the outcome of competition between two species. In Fig. 3.4A, each species reduces the fecundity of the other to half ($c_{ij}/c_i = 0.5$); in Fig. 3.4B, species 1 has a larger effect on species 2's fecundity than species 2 has on species 1's ($c_{12}/c_1 = 0.8$, $c_{21}/c_2 = 0.2$). In both cases, local coexistence translates into regional coexistence if both species have sufficient fecundity c_i so that they are not recruitment limited. It is only when a species becomes recruitment limited (c only slightly larger than m) that pure fecun-

A) $c_{12} = 0.5c_1, c_{21} = 0.5c_2$



B) $c_{12} = 0.8c_1, c_{21} = 0.2c_2$

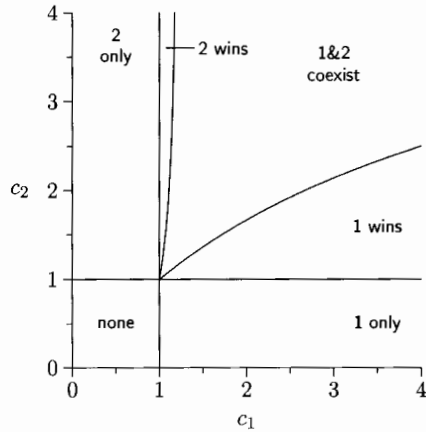


Fig. 3.4A,B. Outcome of fecundity competition as a function of fecundities. Other parameters: $e_1 = e_2 = 1$ and $m_1 = m_2 = 1$. **A** Equal competitors. **B** Species 1 is a better local competitor than species 2

dity competition can result in its competitive exclusion at the population level.

3.2.2.5 Competition and Facilitation

One of the advantages of the general model of Eqs. (2) is that it can incorporate a range of interactions between individuals. For example, in harsh environments, adult plants can act as nurse plants that facilitate the establishment of seedlings of other species beneath them (Aguiar and Sala 1994). However, when two adults share the same site, they compete. Considering species 1 to be the nurse, we let $e_{21} > e_2$ so that species 2 can establish more easily under an adult of species 1. We also let $m_{12} > m_1, m_{21} > m_2, c_{12} < c_1,$ and $c_{21} < c_2$ so that individuals experience both mortality and fecundity competition.

Figure 3.5 shows the combined patch occupancy of both species as the colonization rate of the nurse plant species 1 is increased. For small values of c_1 , the abundance of both species increases with c_1 , indicating net positive interactions at the population level. However, for larger values of c_1 , species 2 declines while species 1 increases with increased c_1 , indicating net negative interactions at the population level. Thus this model can integrate various individual level interactions to predict population level responses.

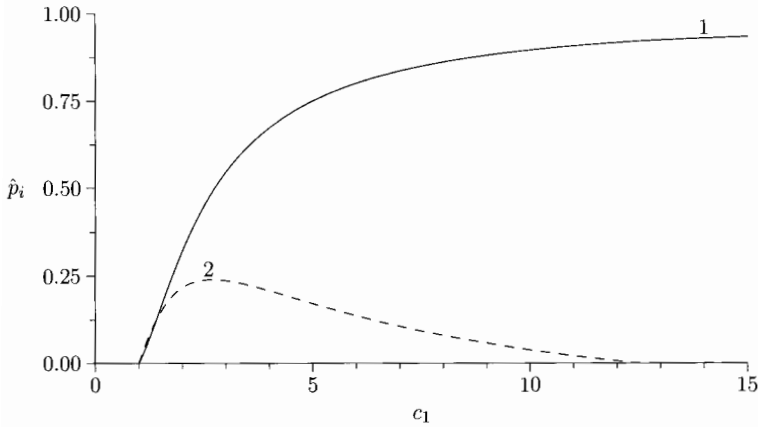


Fig. 3.5. Interplay of competition and facilitation. Equilibrium total patch occupancy of species 1 (solid), $\hat{p}_1 = \hat{p}_1 + \hat{p}_{12}$, and species 2 (dashed), $\hat{p}_2 = \hat{p}_2 + \hat{p}_{12}$ versus the fecundity of species 1. Species 2 is driven extinct for $c_1 > 12.5$. Other parameters used: $c_2 = 1$, $m_1 = m_2 = 1$, $e_{12} = 1$, $e_{21} = 10$, $m_{12} = 2$, $m_{21} = 6$, $c_{12} = 0.5c_1$, $c_{21} = 0.5$

3.2.3 Conclusions

Advantages: Patch occupancy models are flexible, in that they can incorporate competition at various stages of the life-cycle of a plant. Because they are formulated as familiar ordinary differential equations, they are also the most easily analyzed spatial models.

Insights: Patch occupancy models can be used to determine how the three possible outcomes of local competition (founder control, competitive exclusion, and coexistence) scale up to the population level. With local founder control (Sect. 3.2.2.1), coexistence at the population level is impossible. With local competitive exclusion (Sects. 3.2.2.2, 3.2.2.3), coexistence at the population level is possible if the locally inferior competitor is a superior colonizer (Hastings 1980; Nee and May 1992; Tilman 1994) or a faster grower (Pacala and Rees 1998). Finally, when species can locally coexist (Sect. 3.2.2.4), coexistence at the population level follows as long as both species have sufficient fecundity to prevent recruitment limitation (Levins and Culver 1971; Klausmeier 2001).

Limitations: Patch occupancy models achieve their simplicity by neglecting the actual location of organisms on the landscape. They confound dispersal distance and fecundity into the “colonization rate” parameter (Holmes and Wilson 1998; Klausmeier 1998). They cannot account for endogenous small-scale heterogeneity due to local dispersal or large-scale heterogeneity in the environment (Klausmeier 1998). Except in limiting cases that assume instantaneous displacement, the relationship of patch occupancy models to

mechanistic models of local competition is ad hoc, modelling deterministic processes such as local competitive displacement as stochastic processes (Johnson 2000).

3.3 Explicitly Spatial Models

Explicitly spatial models are those that track the actual location of organisms in the landscape. Such models address questions that are unanswerable by implicitly spatial models, but this extra detail complicates model analysis. Here we give an overview of three types of explicitly spatial models (interacting particle systems, point processes, and reaction-diffusion equations), and two techniques to simplify their analysis (pair approximation and moment methods).

3.3.1 Interacting Particle Systems

Interacting particle systems, or stochastic cellular automata, are explicitly spatial stochastic processes, recently introduced to ecology (Durrett and Levin 1994a, b). In these models, patches are given actual locations, often arranged on a one- or two-dimensional square lattice (Durrett and Levin 1994a). Dispersal distance can now be incorporated, as short as to neighboring sites only or as long as global. Often, in the limit of long dispersal, the dynamics of interacting particle systems converge to the dynamics of an analogous patch model, referred to as the *mean field* model. However, when dispersal is short-range, small-scale heterogeneity can arise, changing the quantitative and sometimes qualitative behavior of the system. Here we discuss some well-known examples analogous to some of patch models of Sect. 3.2.

3.3.1.1 Contact Process

The contact process is the particle system analogue of Levins' model (Durrett and Levin 1994a). When dispersal is local, individuals are more clustered than random (Fig. 3.6), so that a neighbor of an occupied site is more likely to be also occupied than a site chosen at random. This clustering lowers the rate of successful colonization because seeds are more likely to be wasted on already occupied sites, lowering the equilibrium density and increasing the minimum colonization rate that allows persistence. For example, for the two-dimensional contact process with dispersal to the nearest four neighboring sites, the criterion for persistence is approximately $e_1 c_1 > 1.65 m_1$, compared to $e_1 c_1 > m_1$ for Levins' model. This value is determined by simulations.

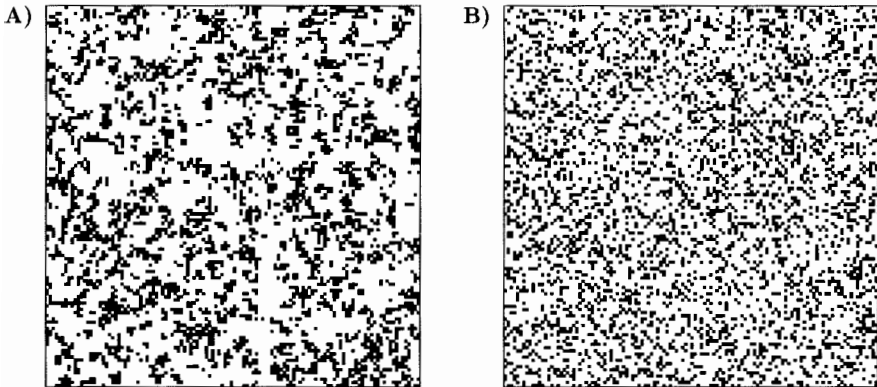


Fig. 3.6A,B. Spatial distribution of plants with patch occupancy $P \approx 0.25$. A Clustered distribution from the nearest-neighbor contact process ($c = 1$, $m = 0.55$). B Random distribution

3.3.1.2 Competing Contact Processes and the Voter Model

Now consider the particle system analogue to the patch model with local founder control (Sect. 3.2.2.1). When both species disperse the same distance, and have equal mortality rates, the species with the greater fecundity outcompetes the other (Neuhauser 1992; Durrett and Neuhauser 1997); it is conjectured that this result generalizes to the species with the greatest $e_1 c_1 / m_1$ outcompetes the other as in the mean field model of Eqs. (3). Little is known rigorously about cases with different dispersal distances, but it is conjectured that competitive exclusion is the rule in one and two dimensions (C. Neuhauser, pers. comm.).

One well understood special case of the competing contact process is the voter model (Durrett and Levin 1994a). This is the case when both species have the same parameters and colonization rates are infinite, leaving no empty sites. In the voter model in one and two dimensions, species segregate into monospecific patches that continue to grow indefinitely. In a finite habitat, the asymptotic state consists of only one species. Neuhauser (1992) showed that these results extend to the case with equal, but noninfinite colonization rates. Coexistence is possible in three or higher dimensions, but this is not relevant to competition among sessile organisms, which typically inhabit two dimensions.

3.3.1.3 Hierarchical Competition

The particle system analogue to the patch model with hierarchical competition (Sect. 3.2.2.2) has also been extensively studied. Durrett and Swindle (1991) and Durrett and Schinazi (1993) showed that the dynamics of the particle system approach that of the mean field model of Eqs. (4) as the dispersal range increases. Holmes and Wilson (1998) considered the case with differing dispersal distances. They found that long-range dispersal can allow an inferior competitor to coexist with a locally dispersing superior competitor, even if the inferior competitor has an equal or lower fecundity. However, the conditions for this to occur are narrow.

3.3.1.4 Conclusions

Advantages: The main strength of interacting particle systems is that they can account for local dynamics. They are easy to simulate on a computer. S3 is a freely available program by Ted Cox and Rick Durrett that can simulate all of the interacting particle systems we discuss. It can be found on the internet at <http://gumby.syr.edu> and works on UNIX systems.

Insights: Local dispersal can lead to the clumped distribution of plants. This clumped distribution can make persistence more difficult and affect the outcome of interspecific competition.

Limitations: Except in the limit of long-range dispersal, it is hard to prove results rigorously, and one can be misled by merely watching simulations. In nature individuals do not live on lattices, so parameterization and quantitative predictions are not easy.

For further reading: See the reviews of Durrett and Levin (1994a, b) and Durrett (1999).

3.3.2 Point Process Models

Point processes, or neighborhood models, are similar to interacting particle systems in that they are explicitly spatial stochastic models. The main difference is that they do not restrict individuals to live on a lattice, but rather give individuals a location in continuous space (Fig. 3.7). Competition integrates the density of con- and heterospecifics over a local neighborhood to affect vital rates, and seeds are dispersed in a dispersal neighborhood (Pacala and Silander 1985; Bolker and Pacala 1997, 1999). Each of these neighborhoods can be any size or weighted according to any density function, so the system's natural spatial scales can be included. As with particle systems, biotic interac-

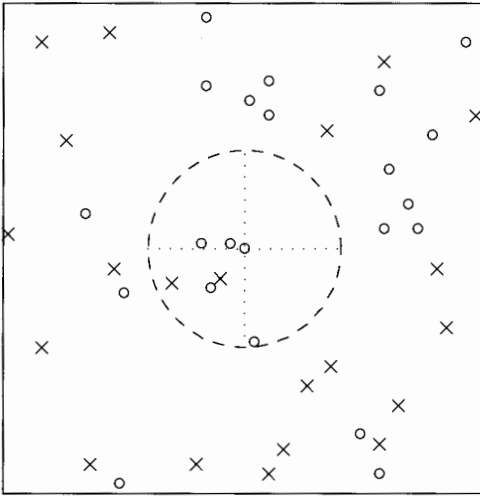


Fig. 3.7. In neighborhood models, discrete individuals inhabit continuous space and experience only their local neighborhoods

tions can cause non-random spatial patterns, which feed back on the growth rates of populations. Mathematical analysis is difficult except in limiting cases.

Advantages: The main strengths of point process models are that they have few unnatural assumptions and can be parameterized with field data on individuals and then used to predict population and community dynamics. Pacala and co-workers have implemented this research program for annuals (theory: Pacala and Silander 1985; Pacala 1986a, b; field test: Pacala and Silander 1990) and temperate forests (theory: Pacala et al. 1993; field test: Pacala et al. 1996).

Insights: Models parameterized with field data can make accurate quantitative predictions about population and community dynamics (Pacala and Silander 1990; Pacala et al. 1996).

Limitations: Analysis relies on simulation or complicated mathematical approximations (see Sect. 3.3.3 below).

3.3.3 Pair Approximation and Moment Methods

Pair approximations and *moment methods* are not types of models per se. Instead they are approximations that attempt to capture some of the effects of the small-scale spatial heterogeneity that arises in interacting particle systems and point processes, respectively. Both types of approximations are most accurate when dispersal or interaction ranges are relatively large and become less accurate as these ranges decrease (Bolker and Pacala 1999).

Pair approximations track not only the global occupancy of patches, but also the local occupancy, deriving equations for the probability that a neighboring site is occupied conditioned on a focal site being occupied (Harada 1999; Iwasa 2000; Satō and Iwasa 2000). With local dispersal, successful colonization depends on the local density, which can differ from the global density due to clumping, providing a feedback from local density to global density. Pair approximation more closely captures the dynamics of the nearest-neighbor contact process than the mean-field Levins' model.

Second-order moment methods supplement equations for the mean density of organisms with equations for the spatial covariance at all distances (Bolker and Pacala 1997, 1999; Bolker et al. 2000; Law and Dieckmann 2000). At any distance this spatial covariance can be positive, indicating a clumped distribution, negative, indicating a regular distribution, or zero, indicating a random distribution. Local dispersal promotes a clumped distribution whereas local competition promotes a regular distribution (Bolker and Pacala 1997). With two species, the covariance between species can indicate spatial segregation of the population. Analysis of a neighborhood competition model using moment equations shows that the outcome of competition may depend on the scale of interaction and dispersal, and that sometime short-range dispersal is advantageous (Bolker and Pacala 1999).

Advantages: Pair approximations and moment methods provide a deterministic framework for incorporating the effects of nonrandom spatial distributions; thus these effects can be determined by solving a set of equations once instead of running many replicate simulations to average out stochastic fluctuations.

Limitations: As approximations, these methods are not strictly accurate and rigorous justification for the approximations do not exist. The resulting equations are complicated and difficult to analyze without a computer in all but the simplest cases.

3.3.4 Reaction-Diffusion Models

Reaction-diffusion equations have a long history in theoretical ecology (Skellam 1951; Holmes et al. 1994). We include related integrodifference (Kot and Schaffer 1986; Neubert et al. 1995; Allen et al. 1996) and integrodifferential (Klausmeier 1998) equations in this category. These models arise in two ways. Traditionally, they have been derived as spatial extensions of nonspatial models by simply appending a diffusion term to simulate random movement of organisms (Holmes et al. 1994; Klausmeier 1999). They can also be derived as limiting cases of interacting particle systems. Reaction-diffusion equations result when individuals move rapidly (Durrett and Neuhauser 1994) and integrodifferential equations result when individuals disperse over long distances (Swindle 1990).

A single species reaction-diffusion equation takes the form

$$\frac{\partial n}{\partial t} = f(n) + D\Delta n \quad (16)$$

[change in density at a location] = [births and deaths] + [dispersal]

where n is a function of time, t , as well as one, two, or three spatial dimensions. Here, the change in organisms at a given location, $\partial n/\partial t$, consists of local births and deaths, $f(n)$, and passive dispersal, modelled by the diffusion term, $D\Delta n$. The model is completed by a set of boundary conditions describing what happens at the edges of the system. Multiple species models are similar. For example, a reaction-diffusion model of Lotka-Volterra competition between two species is

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= r_1 n_1 \left(1 - \frac{n_1}{K_1} - \alpha \frac{n_2}{K_1} \right) + D_1 \Delta n_1 \\ \frac{\partial n_2}{\partial t} &= r_2 n_2 \left(1 - \beta \frac{n_1}{K_2} - \frac{n_2}{K_2} \right) + D_2 \Delta n_2 \end{aligned} \quad (17)$$

In other words, the simplest reaction-diffusion models simply add a diffusion term to the analogous nonspatial model.

Reaction-diffusion equations are well-suited to dealing with large-scale heterogeneity, both in the abiotic environment and in population densities. We discuss the use of reaction-diffusion equations with environmental heterogeneity in Sect. 3.5.1. One common way that large-scale biotic heterogeneity can arise in population densities, albeit transiently, is during the process of invasion. Reaction-diffusion equations show that when a competitor is locally introduced to a new habitat, competition occurs by a travelling wave that moves at an asymptotically constant speed when dispersal is local (Fig. 3.8A–C). When the invader and resident can locally coexist, the travelling wave of the invader advances, leaving the coexisting populations behind it. When the invader locally outcompetes the resident, the travelling wave of the invader replaces the resident with the invader. Okubo et al. (1989) used such a model to examine the displacement of the red squirrel by the introduced grey squirrel in Britain, and Allen et al. (1996) developed a similar model appropriate for annual plants. When the resident outcompetes the invader, the invader fails to spread and no travelling wave occurs. Finally, when the local dynamics predict founder control, one species dominates, displacing the other from the habitat, unless its initial population is too small or the habitat is sufficiently nonconvex (Mimura et al. 1991). Competition by travelling waves slows dynamics, replacing the exponential rates found in nonspatial models (Fig. 3.8E) with linear rates (Fig. 3.8D).

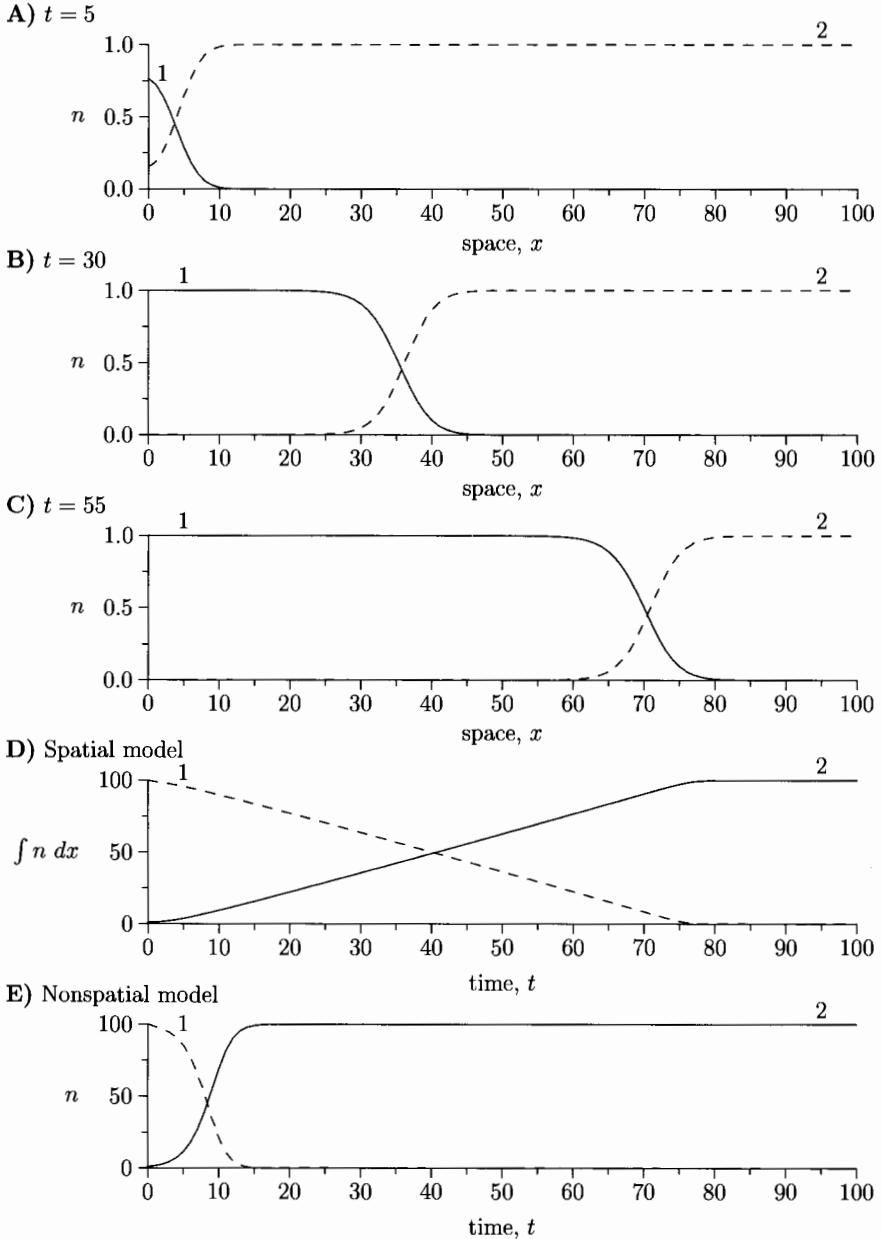


Fig. 3.8A-E. A reaction-diffusion Lotka-Volterra competition model, where species 1 displaces species 2. $r_1 = r_2 = 1, K_1 = K_2 = 1, D_1 = D_2 = 1, \alpha = 1/2, \beta = 2$. **A-C** Snapshots of the spatial distribution of both species at $t = 5, t = 30$, and $t = 55$. When species 1 is introduced at $x = 0$, it displaces species 2 through a travelling wave. **D** Total density of species 1 and 2 throughout the habitat. Competitive exclusion happens linearly with time. **E** Total density of species 1 and 2 in the corresponding nonspatial model; competitive exclusion occurs more rapidly

Advantages: There is an extensive literature on reaction-diffusion equations providing useful mathematical techniques (Okubo 1980; Murray 1989; Holmes et al. 1994). These models can easily incorporate large-scale heterogeneity (see Sect. 3.5.1).

Insights: Competition in a homogeneous environment can occur by a travelling wave, slowing competitive exclusion. Coexistence of species with local founder control is impossible unless the habitat has a nonconvex shape.

Limitations: Like patch models, these models average out small-scale heterogeneity.

3.4. Comparing and Connecting Methods

We have looked at a variety of different approaches to modelling competition in a spatial environment. Here we highlight the connections between these different approaches and discuss their implicit assumptions. The most encompassing approach is that of neighborhood models (Sect. 3.3.2), with their ability to include any mode of competition, arbitrary interaction and dispersal ranges, and environmental heterogeneity. This makes them most easily connected with empirical data. Unfortunately, in the general case they are analytically intractable and must be investigated by computationally intensive stochastic simulations. Simplification is possible when the intrinsic spatial scales involved are sufficiently different, leading to more manageable models (Fig. 3.9).

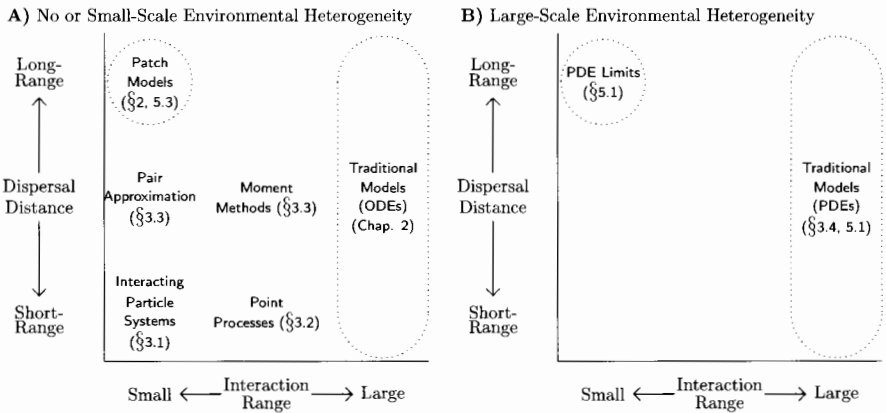


Fig. 3.9A,B. Overview of different modelling approaches. ODEs=ordinary differential equations, PDEs=partial differential equations. **A** No or small-scale environmental heterogeneity. **B** Large-scale environmental heterogeneity.

First, assume no large-scale heterogeneity, either in the underlying environment or in the population densities (Fig. 3.9A). When individuals have large interaction ranges (Fig. 3.10A), each individual experiences the mean density of all species and traditional nonspatial models (Chap. 2) are applicable (Pacala and Levin 1997). Even though nonrandom spatial patterns may exist, they have no effect on population dynamics if each individual averages over an area larger than the scale of pattern formation. When individuals have small interaction ranges (Fig. 3.10B–D), interacting particle systems (Sect.

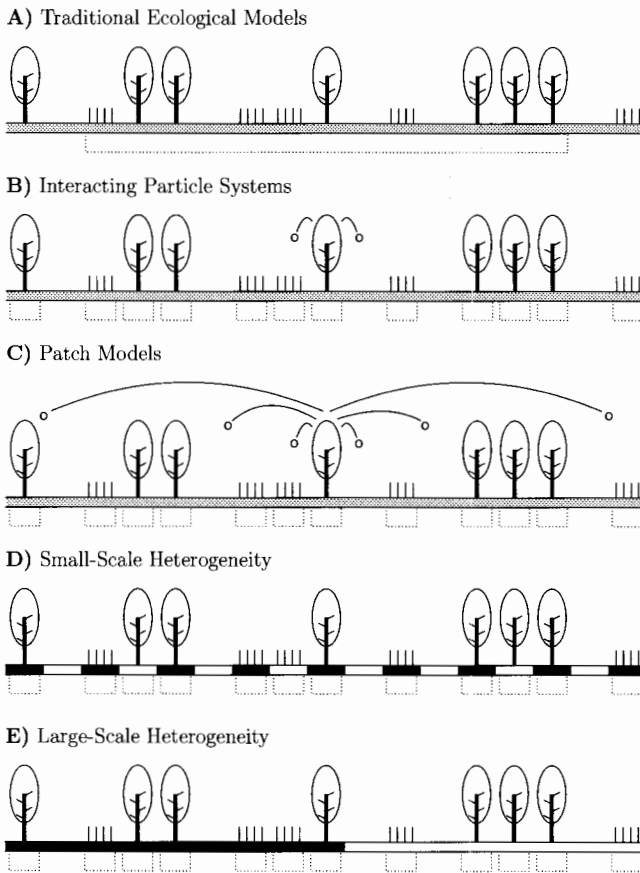


Fig. 3.10A–E. Assumptions about spatial scales inherent in different modelling approaches. Underlying heterogeneity in the environment is shown in the strip directly under the plants. Dotted zones underneath plants show the area over which an individual experiences the environment. **A** Traditional ecological models (Chap. 2) assume that individuals interact with many others. **B** Interacting particle systems (Sect. 3.3.1) can assume local interactions and local dispersal. **C** Patch models (Sect. 3.2) assume local interactions but long-range dispersal. **D** Small-scale heterogeneity of a similar size to the interaction range can be incorporated into patch models (Sect. 3.5.3). **E** Large-scale heterogeneity can be modelled using reaction-diffusion or integrodifferential equations (Sect. 3.5.1)

3.3.1) are applicable, and when dispersal is long-range as well, patch models (Sect. 3.2, 3.5.3) are appropriate (Durrett and Levin 1994b). For long-range dispersal with intermediate-sized interaction ranges, Poisson limits can be applied (Durrett and Levin 1994; Pacala and Levin 1997). When mean field models begin to fail for smaller neighborhood sizes, pair approximation and moment methods (Sect. 3.3.3) can account for the emergent small-scale spatial structure and its effects on dynamics. Bolker and Pacala (1997, 1999) suggest that mean field models are sufficient for neighborhoods of more than 100 individuals (which may apply to many grasslands), moment methods work for neighborhoods of 10–100 individuals, and both fail for smaller neighborhoods.

Now, consider large-scale heterogeneity (Fig. 3.9B). This could be due to heterogeneity in the underlying environment (Fig. 3.10E), self-organized, or due to an on-going invasion (Fig. 3.8A–C). In all these cases, reaction-diffusion or related models (Sect. 3.3.4) are useful because they can capture this large-scale variation without being burdened by small-scale detail. When interactions are localized and dispersal is long-range compared to the interaction range, but short-range compared to the scale of the heterogeneity, integrodifferential equations are a valid limit (Swindle 1990). Klausmeier (1998) used this limit to investigate the effect of habitat loss on competing species when one large remnant tract of habitat remained. Reaction-diffusion equations derived as spatial analogues of traditional nonspatial models have been used to study pattern formation (Levin and Segel 1976; Klausmeier 1999), ecological invasions (Okubo et al. 1989; Shigesada and Kawasaki 1997), and competition in heterogeneous environments (Pacala and Roughgarden 1982; Ali and Cosner 1995). Second-order moment methods are ill-suited in all these cases because sharp interfaces occur, leading to non-negligible third spatial moments, which are assumed to be zero by these moment methods (Bolker and Pacala 1997, 1999). However, Ellner and Sasaki (1998) have recently modified pair-approximation methods to work at the front of an invasion, so perhaps moment methods can be similarly modified.

Figure 3.9 provides a rough map of the domains of applicability of these different modelling approaches. The natural history of the system being modelled should guide the choice of modelling frameworks. This choice also depends on whether the goal is quantitative prediction or qualitative understanding of generic phenomena. In the case of quantitative prediction, neighborhood models can't be beat, but because watching a simulation unfold can be nearly as baffling as observing the real system, simpler models allow for more understanding. In summary, each of these modelling approaches has its own niche and they should continue to coexist in the ecological literature indefinitely.

3.5 Underlying Spatial Heterogeneity

All of the models we have discussed so far assume that the underlying environment is perfectly homogeneous; the only source of spatial heterogeneity is from the distribution of the organisms. Yet, abiotic heterogeneity is ubiquitous in natural systems and may provide opportunities for the coexistence of competitors if there is a trade-off between competitive abilities in different types of habitat. Tilman (1982) proposed that continuous spatial variation in the ratio of supply rates of two essential resources could allow an essentially unlimited number of species to stably coexist (see also Chap. 2). A similar argument could be made for spatial variation in any factor that determines the outcome of local competition, as long as each species has some part of the habitat where it can persist. This argument is quite general, made without reference to any particular type of system. It is also purely verbal; no mathematics translates the local-scale interactions into rigorous population level conclusions. One would like to know more: is coexistence due to spatial heterogeneity actually possible? how does it depend on the details of local competition (see Sect. 3.2)? and what is the effect of the spatial scale and arrangement of different patch types? Below we look at different approaches to answer these questions.

3.5.1 Reaction-Diffusion Models

Pacala and Roughgarden (1982) considered the situation in which two species inhabit a one-dimensional continuous habitat, compete according to a Lotka-Volterra formulation and disperse by diffusion. The habitat is broken into two pieces, with lengths L_1 and L_2 . The competitive parameters depend on the patch type. They focused on the question of invasion and considered three cases: (1) one part of the habitat is favorable (the invader can either coexist with or displace the resident) and the other part is unfavorable (the invader is displaced); (2) both parts of the habitat are favorable; and (3) both parts of the habitat are unfavorable. In the first case, successful invasion depends on the size of the favorable patch relative to the invader's dispersal rate. If the favorable part of the habitat is too small, the invader cannot coexist with the resident. The invader may persist by decreasing its dispersal rate. This is our first indication that the existence of some favorable environment for each species does not guarantee coexistence; the favorable habitat must be large enough. In the second case, invasion may be impossible despite the fact that the invader can grow in both patches. This can occur when the invader disperses more than the resident. In the third case, invasion may be possible even if neither patch is favorable to the invader. This can occur when the resident disperses too much and the invader disperses sufficiently less than a threshold. Recently

Cantrell and Cosner (1998) explained these two counterintuitive results in terms of how dispersal leads to nonlinear averaging of the environmental conditions.

3.5.2 Neighborhood Models

Pacala (1987) extended his neighborhood models of competition (Sect. 3.3.2) to include abiotic environmental heterogeneity. As with the reaction-diffusion models described above (Sect. 3.5.1), favorable patches must be sufficiently large compared to the mean dispersal distance for heterogeneity to allow coexistence. This holds for arbitrary number of competing species. He also found that the scale of environmental heterogeneity that allows coexistence may depend on the size of the competitive neighborhood.

3.5.3 Patch Models in Heterogeneous Environments

Suppose the environmental heterogeneity is fine-scale (Fig. 3.8D). If dispersal distances are sufficiently large, patch models can be used to understand the influence of heterogeneity on the outcome of competition between two species and the assembly of many species communities. Even with the assumption of global dispersal, competition in heterogeneous environments is a complicated process that theoreticians have barely begun to investigate. Establishment probabilities, fecundities, and mortality rates can all depend on patch type, as can the effect of competition, which itself can manifest itself in three ways (Sect. 3.2.2).

Other researchers (Pacala and Tilman 1994; Hurtt and Pacala 1995) have used discrete-time patch models to study competition in a heterogeneous environment. We will present some results from a related continuous-time model we are developing (Klausmeier and Tilman, in prep.) that is easier to analyze but gives similar results. Following others, we assume that only the competitive interactions may depend on the patch type, while all other parameters are constant across different patch types. We will also initially follow the assumption that local competition follows a strict hierarchy (as in Sect. 3.2.2.2), but that the ordering of the species depends on the patch type. For instance, the local competitive ability as summarized by R^* may depend on the patch type. If each species has a different optimal patch type, x_{opt} , the competitive hierarchy may depend on the patch type (Fig. 3.11).

Assuming instantaneous competitive displacement, so that each patch is occupied by at most one individual, we arrive at the following equations for two species:

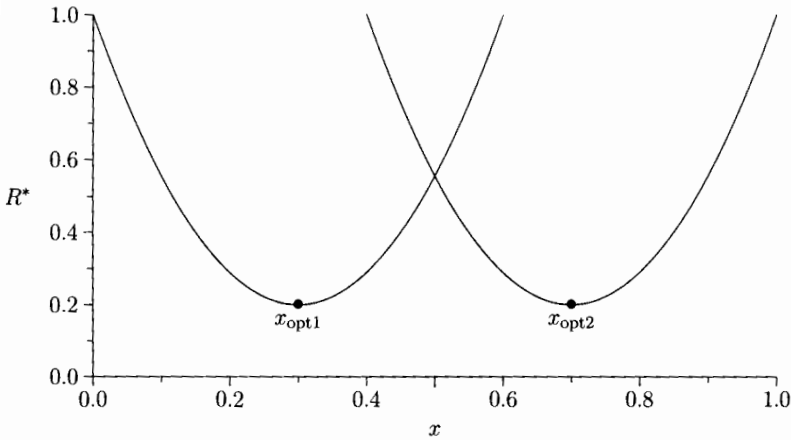


Fig. 3.11. Competitive ability (R^*) of two species with differing optimal patch types (x_{opt}) as a function of patch type, x . The species with the lowest $R^*(x)$ is the best competitors in patch type x

$$\begin{aligned} \frac{\partial P_1(x,t)}{\partial t} &= c_1 \int_0^1 P_1(x',t) dx' (1 - P_1(x,t) - e_{12}(x) P_2(x,t)) - m P_1(x,t) \\ &\quad - c_2 \int_0^1 P_2(x',t) dx' e_{21}(x) P_1(x,t) \\ \frac{\partial P_2(x,t)}{\partial t} &= c_2 \int_0^1 P_2(x',t) dx' (1 - P_2(x,t) - e_{21}(x) P_1(x,t)) - m P_2(x,t) \\ &\quad - c_1 \int_0^1 P_1(x',t) dx' e_{12}(x) P_2(x,t) \end{aligned} \tag{18}$$

where $e_{12}(x) = 1$ and $e_{21}(x) = 0$ if species 1 outcompetes species 2 in patch type x and $e_{12}(x) = 0$ and $e_{21}(x) = 1$ if species 2 outcompetes species 1. We further assume $e_1 = e_2 = 1$.

Let H_i be the proportion of the habitat where species i is the superior competitor. It can be shown (Klausmeier and Tilman, in prep.) that the condition for species 2 to invade a monoculture of species 1 is

$$H_2 > \frac{c_1^2 m - c_2 m^2}{c_1^2 c_2 - c_2 m^2} \tag{19}$$

In the case when species 2 is an inferior competitor everywhere ($H_2 = 0$), this condition reduces to $c_2 > c_1^2/m$, and when species 2 is the superior competitor everywhere ($H_2 = 1$), it reduces to $c_2 > m$; both of these results accord with the simple model of hierarchical competition in a homogeneous environment we discussed earlier (Sect. 3.2.2.2).

When species have the same fecundity, c , and differ only in their optimal patch type, x_{opt} , the invasion criterion of Eq. (19) reduces to

$$H_2 > \frac{m}{c+m}. \quad (20)$$

This represents a critical amount of habitat in which species 2 must dominate in order to coexist at the population scale. Species can stably coexist even if they have close to identical optimal patch types (e.g. $x_{\text{opt}1} = 0.49$ and $x_{\text{opt}2} = 0.51$). This occurs because no matter how similar the species are, they still divide the habitat in two halves in which different species dominate, permitting their stable coexistence (see also Abrams 1996).

3.5.4 Conclusions

Environmental spatial heterogeneity has the potential to support many coexisting competitors, but the relationship between environmental heterogeneity and diversity is not straightforward. One recurrent theme of different models is that of critical patch sizes, in which the amount of habitat where a species can locally persist must exceed some minimum threshold in order for the species to persist across the landscape. Diversity is highest in the idealized case in which every species has some part of the habitat where it is the superior competitor and each species can reach and remain in its favored habitat. In addition to landscape features, the details of local competition between individuals affect the diversity of the community.

3.6. Competition and Coexistence

We have seen that accounting for space, implicitly or explicitly, can fundamentally alter the outcome of competition, potentially changing competitive exclusion into coexistence. Here we discuss the role of space on two forms of coexistence, stable and neutral. By *stable coexistence*, we mean the ability of species to invade the community consisting of all other coexisting species. By *neutral coexistence*, we mean the coexistence of identical species that are the same in all aspects of their ecology: they require the same resources, which they attain with equal ability, they share the same natural enemies, and they experience the same density-independent disturbances. The difference between stable coexistence and neutral coexistence is that stably coexisting species have a deterministic tendency to recover from low densities, while neutrally coexisting species do not; the densities of stably coexisting species are attracted to an equilibrium, a limit cycle, or a strange attractor, while the

densities of neutrally coexisting species vary randomly and without any central tendency.

The coexistence of species with the competition-colonization trade-off (Sects. 3.2.2.2 and 3.3.1.3), of species with the competition-successional niche trade-off (Sect. 3.2.2.3), and of species with differing optimal patch types (Sect. 3.5.3) are all examples of stable coexistence, because each species can invade a monoculture of the other. In each case, coexistence can be thought of as resulting from spatial heterogeneity that serves to segregate the competitors. In the cases of the competition-colonization and competition-successional niche trade-offs, an inferior competitor can persist by using the sites devoid of adult superior competitors. In the case of underlying spatial heterogeneity, each species specializes on a particular type of patch, which also decreases direct competition and permits stable coexistence.

Biotically generated spatial heterogeneity can not allow the stable coexistence of identical competitors. At equilibrium, the growth rate of a species in monoculture is zero. It follows that the invasion rate of an identical species would be the same: zero. Stable coexistence requires a positive invasion rate for both species, so therefore identical species cannot stably coexist. Since local dispersal can cause intraspecific clumping and interspecific segregation (Sects. 3.3.1, 3.3.3), one might think that these explicitly spatial phenomena could stabilize otherwise neutral competitors. However, using pair approximation or moment equations to calculate the invasion rate of a rare species into a monoculture of an identical species shows otherwise: the positive effects of resident clumping and interspecific segregation are completely negated by the negative effect of invader clumping. We concur with Chesson, who asserted a “need for niches” in order to explain stable coexistence (Chesson 1991).

The effect of explicit space on neutral coexistence is less clear. Explicit space can slow the time competitive exclusion takes. This occurs when a superior competitor displaces an inferior competitor (Sect. 3.3.4), when similar species show founder control (Gandhi et al. 1998), and when identical species compete according to the voter model in one or two dimensions (Sect. 3.3.1.2). It could be that the spatial effect of slow exclusion, balanced with immigration or speciation, could help explain competitive biodiversity (Hubbell 2001).

Spatial effects can also change local coexistence into global exclusion. In the case of fecundity competition (Sect. 3.2.2.4), the effect of competition on fecundity can push a marginally persisting species extinct regionally, even when individuals can coexist locally (Klausmeier 2001) (Fig. 3.4). In the case of competition in a heterogeneous landscape (Sect. 3.5.1), regional coexistence can depend delicately on the rate of dispersal (Pacala and Roughgarden 1982). If a species disperses too much, it may not be able to remain within its favored habitat type and therefore be excluded.

Including space in models of competition certainly complicates matters, but in itself does not explain species coexistence. Spatial effects can also tip

the balance of competition from coexistence to exclusion. For space to allow stable coexistence, species must have trade-offs in their life-history strategies or environmental requirements. Explicit space can slow the rate of competitive exclusion, which may make neutral coexistence through the balance of speciation and extinction more plausible.

3.7. Future Directions

Although we now understand some of the ways in which the spatial distribution of individuals affects the outcome of competition, much remains unknown. Here we speculate on some avenues of inquiry that may provide further insights into how spatial dynamics affect competition and coexistence.

3.7.1 More Work on Environmental Heterogeneity

The models described in Sect. 3.5 have only begun treating the problem of environmental heterogeneity. Some open areas for future work follow.

- The models we have considered either have simple geometries (Sect. 3.5.1) or ignore the location of patches altogether (Sect. 3.5.3). How does the spatial arrangement of different patch types affect how organisms experience heterogeneity? Is short- or long-range dispersal advantageous in a heterogeneous landscape?
- The patch models that have been studied (Sect. 3.5.3) assume local competitive hierarchies and that only competitive ranking depends on patch type. Competition sets the realized niche of each species, but each species has an unlimited fundamental niche. Competition of species with varying fundamental niches could be studied by letting establishment probabilities and mortality rates vary also with patch type.
- Species in heterogeneous habitats may differ not only in their optimal patch type, but also in their overall competitive ability and their degree of specialization. We (Klausmeier and Tilman, in prep.) have begun analysis of a model including both a trade-off in optimal patch type and between overall competitive ability and fecundity. Another useful study would address the trade-off between habitat generalists and specialists.

3.7.2 Combining Population and Ecosystem Perspectives

As we mentioned in the introduction (Sect. 3.1), one may measure a population in terms of numbers of individuals (a population perspective) or in terms

of biomass (an ecosystem perspective). The neighborhood and patch models we have examined are examples of population approaches, whereas resource-consumer models (Tilman 1982, Chap. 2), with their explicit incorporation of limiting nutrients, are examples of ecosystem approaches. Population approaches incorporate the discrete nature of individuals and can be interfaced with life-history theory; nutrient-based ecosystem approaches can accommodate the variation in biomass between individuals and can be interfaced with ecosystem ecology and physiological studies on nutrient uptake and nutrient use efficiency. Linking these two approaches would be a significant step in unifying the study of plant competition. Huston and DeAngelis (1994) provide an initial step in this direction.

Only when individuals of a population are all identical in biomass and nutrient content can one move between these two approaches by merely applying a constant biomass-to-individual conversion factor. In general, both measures of populations as individuals and populations as biomass will need to be included in models. One approach is the simulation model, which can incorporate any level of biological detail. Unfortunately, it can be difficult to understand the dynamics of simulation models and fully explore the large parameter space.

Another approach is to derive a structured population model (Metz and Diekmann 1986; Hastings and Wolin 1989; Gyllenberg et al. 1997). These models track the density of patches of all values of state variables (density of each species and amount of resource) using partial differential equations in a manner similar to the McKendrick-Von Foerster model from demography. The advantages of this formulation are that it is easier to solve numerically than the large set of ordinary differential equations described above, it eliminates the noise of demographic stochasticity, and it may be partially analytically tractable.

3.7.3 Competition for Light Among Terrestrial Plants

Although competition for light among phytoplankton is becoming better understood theoretically (Britton and Timm 1993; Huisman and Weissing 1994, 1995; Litchman and Klausmeier 2001; Klausmeier and Litchman 2001; Diehl 2002; Chap. 7), the theory of competition for light among terrestrial plants is still poorly developed, except in forest simulation models (e.g. Shugart 1984; Pacala et al. 1996). Understanding light competition among terrestrial plants is complicated by the asymmetric nature of light: taller plants shade shorter ones, but not vice versa. This necessitates the inclusion of size structure and the vertical spatial dimension.

Tilman (1988) used a program called ALLOCATE to simulate competition for soil nutrients and light. Species were defined by their allocation to stems, roots, and leaves. The model produced successional patterns, culminating in

the dominance of a single species. Reynolds and Pacala (1993) analyzed a simplified version that includes only allocation to roots and leaves, to determine the identity of the initial dominant and the eventual winner of competition (see also Vincent and Vincent 1996). This analytically tractable version makes the important point that competition can depend on initial densities (founder control) but is essentially a model of local competition between individuals. It takes an ecosystem approach, neglecting the spatial variation caused by the discrete nature of individuals, as well as neglecting the size structure. Inclusion of either or both of these additional factors may make interesting predictions of how local interactions scale up to produce population and community dynamics.

3.7.4 Evolution and Community Assembly

Most models of competition determine the outcome of the interaction between two fixed species. Because the traits of the species that are allowed to interact are fixed, these models cannot fully answer the question of what types of species, out of all possible species, will make up a particular community. Recent advances in the theory of community assembly and evolutionary ecology (Brown and Vincent 1992; Geritz et al. 1998; Abrams 2001) based on evolutionary game theory make it possible to understand how ecological communities become organized over ecological and evolutionary time.

The models presented in this chapter can provide a credible ecological basis for understanding the evolution of traits such as competitive ability, fecundity, mortality, dispersal distance, and habitat specialization. Initial investigations along these lines include the evolution of seed size (Geritz 1995, Geritz et al. 1999), limited dispersal (Dockery et al. 1998), allocation to vegetative propagation versus propagation by seed (Harada 1999), and competitive ability versus fecundity (May and Nowak 1994; Lehman and Tilman 1997; Kinzig et al. 1999). Given the rich dynamic possibilities of spatial competition, this approach to community assembly is just beginning to uncover the rules by which ecological communities are assembled in both ecological and evolutionary time.

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