

Competition in Spatial Habitats

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Early models describing local competition among species were interpreted as showing that two or more competing species could not coexist on a single resource (Lotka 1925; Volterra 1928). This was called the competitive exclusion principle, which was later generalized to the statement that n species could not coexist on fewer than n resources or limiting factors (e.g., MacArthur and Levins 1964; Levins 1968). When a single resource was explicitly included in such a model, the species formed a competitive hierarchy, with poorer competitors displaced as the resource was depleted by superior competitors (Tilman 1982).

The competitive exclusion principle immediately raised a paradox of diversity, however (Hutchinson 1961). A given habitat, such as a prairie or a lake, contains hundreds of species, but the number of limiting resources—nutrients, light, space, and so forth—is relatively small, likely fewer than a dozen. Resolving the paradox became a central issue in theoretical ecology. Early erroneous theoretical predictions about diversity arose from limited assumptions in classical competition models—including the assumption that the environment is homogeneous and perfectly well mixed. The early equations of competition had no explicit spatial coordinates (x, y, z) describing locations of individual organisms. Hutchinson conjectured that, among other things, relaxing this assumption would help resolve the paradox of diversity. The question addressed in this chapter is: How do predictions from ecological models of competition change when spatial structure is included?

Implicitly Spatial Formulations

As outlined in Chapter 1, space is implicitly included in metapopulation-like models (Levins 1969), with a dynamical variable $p(t)$ representing the portion of habitat sites occupied by an individual of the species at time t . A species is characterized by its mortality rate m and its colonization rate c :

$$\frac{dp}{dt} = cp(1 - p) - mp. \quad (8.1)$$

This basic formulation can be expanded into an abstract model for interspecific competition among individual plants (Tilman 1994):

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^i p_j \right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j. \quad (8.2)$$

Here p , c , and m have the same meaning as in Equation 8.1, except now they are indexed by species number i . In Equation 8.2, species are ranked by their competitive ability, as in a model of competition for a single resource, with species 1 being the best competitor. For historical reasons, it is convenient to call Equation 8.2 a metapopulation model, but it is important to keep in mind that in Equation 8.2 and throughout this chapter, we model individual organisms occupying individual sites, not groups of populations.

Colonization and mortality are explicit (through parameters c_i and m_i respectively), but the competitive hierarchy itself is implicit. The hierarchy results because the sums in Equation 8.2 include terms for superior competitors (those of lower index i) but exclude terms for inferior competitors (higher index i). In nonspatial models, only the best competitor, species 1, survives. Does the addition of implicit space change this exclusive survival of the best competitor and thus potentially resolve Hutchinson's paradox?

Tilman (1994) showed that under Equation 8.2, any number of species can stably coexist in an implicitly spatial homogeneous environment, even though the best competitor immediately displaces all others locally. Such coexistence requires both an interspecific trade-off in competitive ability versus dispersal ability and a limit to similarity of these traits. Although multispecies coexistence might seem paradoxical under such strict local displacement, it occurs because neither the best competitor nor any group of competitors can occupy all sites. Rather, at equilibrium, some proportion of sites will be empty, and there will be constant turnover in occupancy of all sites. Empty sites can be available "homes" for poor competitors if they are sufficiently good dispersers. In other words, coexistence occurs because local displacement by the best competitor is never permanent. No individual lives forever, and when an individual dies, its local site is free for colonization. If better competitors do not occupy all the available space—and according to Equation 8.2, they never can (Tilman 1994)—then there is always room for sufficiently mobile fugitives (e.g., Horn and MacArthur 1972; Armstrong 1976; Crawley 1990; Tilman 1994).

Thus arises a fundamental trade-off among competing species—the ability to hold a site (being a good competitor) versus the ability to get to a site (being a good colonizer), and this trade-off has been explored in several forms (MacArthur and Wilson 1967; Levin and Paine 1974; Werner and Platt 1976; Platt and Weis 1977; Tilman 1982, 1990, 1994). The trade-off can be as simple as energy allocated to roots traded for energy allocated to seeds. More energy to roots can mean better nutrient acquisition, and that makes a better competitor at a nutrient-limited site. More energy to seeds can mean more seeds, or more mobile seeds, or longer-lived seeds, and that makes a better colonizer. Trade-offs like this are both logically compelling and empirically observed (Tilman 1990).

Hence the mere existence of spatial structure, acting through individual mortality and colonization, alters conclusions about the ultimate outcome of competition—local exclusion but regional coexistence—even when spatial structure is only

implicit. It is important to realize, however, that the early nonspatial models of competition are not strictly *incorrect*—they are simply *local*. They strictly apply only to a small local site, or to a perfectly well-mixed site, or to a site in which there is no limitation to colonization. Implicitly spatial formulations of competition take the conclusions of nonspatial models as premises, apply those premises to each point of space, then ask what conclusions follow for the entire region.

Explicitly Spatial Formulations

Explicitly spatial formulations give each organism a position demarked by some coordinates, and as a result, different points may have different characteristics—say, different nutrient levels or different light penetration (e.g., Pacala and Tilman 1994; Pickett and Cadenasso 1995). To apply the model of Equation 8.2 in explicitly spatial conditions, we use a spatial simulator with myriad sites for individual organisms, as described in Chapter 1. We have simulated numerous explicitly spatial cases, often involving altered habitat (Tilman, Lehman, and Yin 1997), and compared the results to analytical results derived for Equation 8.2. Our experience reveals two rather different results, depending on parameter values. On the one hand, many simulations of the explicitly spatial model readily approach the analytical implicitly spatial model as the size of the local neighborhood increases. This is true not just for qualitative behavior, but also for quantitative relationships among colonization rates, mortality rates, and species abundances (see Chapter 1). On the other hand, certain simulations diverge radically from predictions of the analytical model. The reason for the divergence sheds some light on the composition of communities. The single-species Equation 8.1, which applies to the best competitor, is a deterministic equation that assumes either an infinite habitat or infinitely subdivisible organisms. The explicitly spatial simulator is stochastic, both in colonization and mortality, and it uses of course a finite habitat. It thus should be a closer approximation to nature. We seek circumstances under which finitude and stochasticity cause the explicitly spatial formulation to behave differently from the implicitly spatial Equation 8.2.

Transient Behavior

Finite time is one point of departure of explicit simulations from analytical models. Models without spatial structure may reach an equilibrium relatively quickly, but spatial structure can greatly slow the timescale in competitive systems (Shmida and Ellner 1984; Hubbell and Foster 1986; Tilman 1994; Hurtt and Pacala 1995). For example, Equation 8.2, perturbed from equilibrium, can take thousands of simulated years to settle down (see figure 4 in Tilman 1994). During this equilibration, the composition of the community fluctuates widely; moreover, natural communities may be perturbed repeatedly and never settle down. This makes consideration of nonequilibrium behavior important in ecological systems (Byers, Hansell, and Madras 1992) and provides a good reason to examine the transient behavior of simulations.

Demographic Stochasticity

Finite space and a corresponding finite number of organisms is another point of departure of explicit simulations from analytical models. At its equilibrium of $\hat{p} = 1 - m/c$, Equation 8.1 has eigenvalue $\lambda = m - c$ (Tilman 1994), whose magnitude determines the strength of the force restoring the population to equilibrium after perturbation. The more negative the eigenvalue, the stronger is the restoring force; the closer the eigenvalue is to zero, the more nearly neutral is the system. Notice that the equilibrium abundance \hat{p} depends only on the *ratio* of m and c , whereas the restoring force λ depends on the *difference* between m and c . Thus a small difference between m and c may allow stochastic tendencies to knock the system away from equilibrium, overwhelming deterministic tendencies to draw it back.

When the difference between m and c is small, fluctuations in the population can be dramatic, often causing the population to drift to extinction in surprisingly short times. Consider two cases with the same equilibrium value but different eigenvalues. In the first case (Figure 8.1A), the habitat contains 198 sites, and the colonization rate is twice the mortality rate

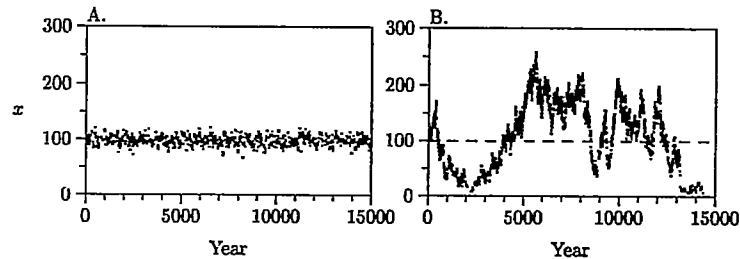


FIGURE 8.1. Effects of stochasticity on the best competitor. (A) Small oscillations in population with $m = 0.05$, $c = 0.1$, and $w = 198$ available habitat sites. The vertical axis is the number of individuals in the population; the horizontal axis is time. With these parameter values, the population remains near its equilibrium value of $(1 - m/c)w = 99$. (B) Wide swings in population with $m = 0.05$, $c = 0.050505$, and $w = 9,900$ available habitat sites. The vertical axis is the number of individuals in the population; the horizontal axis is time. The dashed line marks the equilibrium value $(1 - m/c)w = 99$.

($m = 0.05$, $c = 0.10$). That makes $\hat{p} = 1 - m/c = \frac{1}{2}$, so the equilibrium is $\frac{1}{2} \times 198 = 99$ sites occupied. In the second case (Figure 8.1B), the habitat contains 9,900 sites, and the colonization rate is only slightly greater than the mortality rate ($m = 0.05$, $c = 0.050505\dots$). That makes $\hat{p} = 1 - m/c = \frac{1}{100}$, so the equilibrium is $\frac{1}{100} \times 9,900 = 99$ sites. The two cases have the same equilibrium site occupancy, but have markedly different dynamical behavior (Figure 8.1A,B), owing to the difference in eigenvalues. Trajectories in the first case (Figure 8.1A) appear to be locked in a narrow band around the equilibrium. In contrast, trajectories in the second case (Figure 8.1B) visit values far from equilibrium and consequently often drift to extinction. The time to extinction varies enormously—in many cases it is less than five hundred years, in rarer cases more than thirty thousand years.

Effect on the Competitive Hierarchy

Coexistence in these models occurs because individual mortality leaves open sites and limited random dispersal can never consistently fill all open sites. The best competitor sees a relatively simple environment; it can colonize any site not

already occupied by a member of its own species. In these models, the only stochasticity in its dynamics arises from mortality and colonization of its own species, as just described. The second competitor is affected not only by stochasticity in its own mortality and its own colonization, but it can also be displaced by stochastic colonization of the best competitor, and it may find sites opened by stochastic mortality of the best competitor. Thus stochastic effects are greater for the second competitor, and these effects compound throughout the competitive hierarchy (Figure 8.2B).

This compounding of stochasticity, together with stochasticity accompanying small differences between colonization and mortality, opens the question of whether simple competitive interactions within a local site will lead to predictable community structures at the regional level, as they always do in the implicitly spatial model, or whether ecological drift can overwhelm competitive interactions and lead to communities that seem to depend on random forces for their structure. Hurtt and Pacala (1995) show that in a model of spatial heterogeneity with strong local competition and strong recruitment limitation, but without a strict competitive hierarchy, drift can overwhelm, and they stress that this possibility helps reconcile the apparently contradictory observations of strong interactions in competitive experiments (e.g., Tilman 1982, 1988) and communities that are difficult to distinguish from chance assemblages of species (Hubbell and Foster 1986). Our work suggests that such stochasticity has its greatest effects on inferior competitors, especially those with low equilibrium abundances, but that even superior competitors of low abundances are not immune.

Let us illustrate this idea with the models under discussion, which have a strict hierarchy of competitive exclusion locally and a uniform homogeneous environment. Suppose the implicitly spatial model 8.2 is infused with many species of specified parameters and initial abundances. Then given those parameters and abundances, the ultimate community is predetermined, for this implicitly spatial model has no stochasticity. It may take a long time, and abundances of various species may

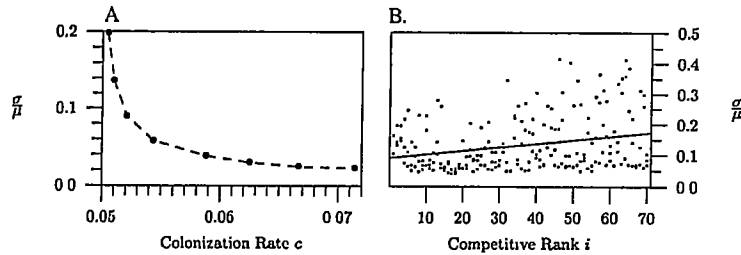


FIGURE 8.2. Variation in abundance from year to year. (A) Results for the best competitor in a stochastic version of Equation 8.2. Mortality is constant at $m = 0.05$, and the habitat contains 9,900 habitable sites. Each point was derived by starting a simulation at the corresponding equilibrium $(1 - m/c)$, running the simulation for one hundred years, and repeating the process for one hundred simulations. The population values at the beginning of each year were then used to compute the mean population and its standard deviation, and thence the coefficient of variation, which appears on the vertical axis. (B) Increase in stochasticity through the competitive hierarchy. Each point is the coefficient of variation through time derived from one of several explicitly spatial simulations with seventy species competing. Parameters are the same as those of Figure 8.3, except these results simulate continuous time.

rise and fall in transitory successional patterns, but the same final community will always result (Tilman 1994).

On the other hand, suppose identical parameters and initial abundances are applied to the corresponding explicitly spatial model with hexagonal cells described earlier. Will species abundances match the analytical predictions? The answer depends on parameters. With a community of a few abundant species (Figures 8.3A–C), species abundances may differ somewhat from the analytical predictions, but they will be roughly the same from trial to trial. In contrast, with a community of many species, none abundant (Figures 8.3D–F), species may coexist, but with little quantitative correspondence to the analytical model. In each trial a different community can arise, its composition depending on initial distributions of organisms and on chance mortality and colonization as the community develops. Thus implicit spatial structure can be sufficient to explain regional coexistence of species that cannot coexist locally, but explicit spatial structure helps to resolve the appar-

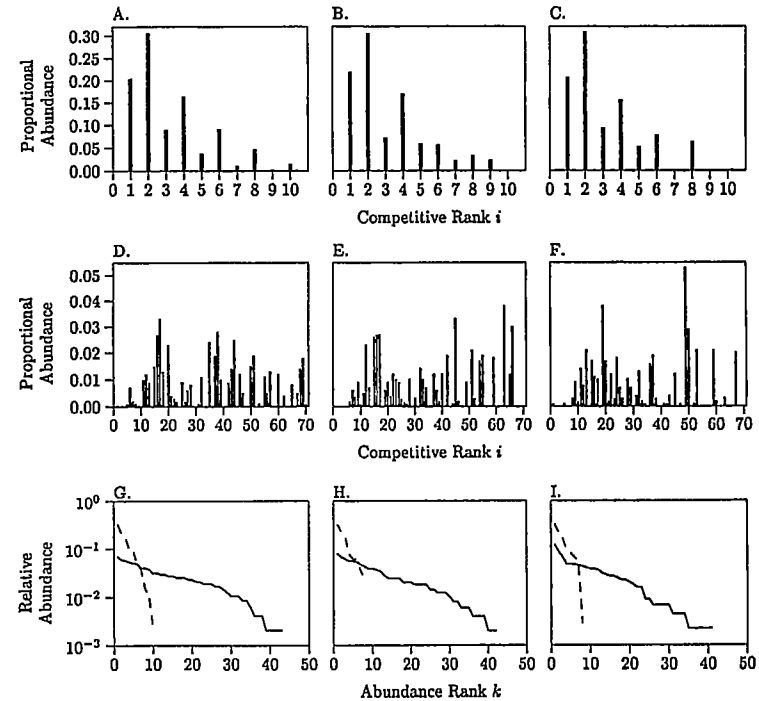


FIGURE 8.3. Community composition in an explicitly spatial analog of Equation 8.2. In A–F, the horizontal axis represents species, ranked in competitive order from the best competitor ($i = 1$) to the poorest ($i = 10$ or $i = 70$). The vertical axis represents P_i after a thousand years. Species competed in a 100×99 hexagonal array with absorbing boundaries, with dispersal once per year to the sixty hexagonal cells in four adjacent rings. Mortality was $m_i = 0.05$ for all species, and colonization was $c_i = m_i / (1 - z)^{2i-1}$, with $z = 0.3$ for parts A–C, and $z = 0.01$ for parts D–F. (A, B, C) Three typical cases with ten species competing and with the best competitors in high abundance. The composition of the communities is roughly the same from case to case for these parameter values. (D, E, F) Three typical cases with seventy species competing and with all competitors in low abundance. Of seventy species initially, approximately forty-three survived a thousand years—a different set in each case. (G, H, I) Dominance-diversity curves for communities A–F. The horizontal axis represents surviving species, ranked in order of abundance. The vertical axis is abundance. Dashed lines represent the communities directly above in A–C; solid lines represent those in D–F. The different communities in A–C have similar curves, as do those in D–F, and these curves are not unlike those of some natural communities (Hubbell 1997).

ent contradiction between local determinism versus regional stochasticity. Community composition can be strongly influenced by history and chance despite strong local deterministic dynamics (Hubbell 1979; Shmida and Ellner 1984; Hurtt and Pacala 1995), especially for highly diverse communities in which the dominant competitors are rare.

Patterns

With local dispersal and local interactions, spatial patterns form. Local competition and local colonization cause populations to become aggregated with the passage of time (Vance 1984; Pacala 1986a). Consider the best competitor. No other species displaces it from the sites it occupies, so its distribution is influenced only by its own mortality and its own patterns of colonization. Because a propagule is more likely to colonize a nearby site, local concentrations and local bare spots arise in the distribution of the population over space (Figure 8.4).

The same processes of local colonization apply to competitors of all rank, but for poorer competitors there is an additional effect. The second competitor has its own intrinsic tendency to aggregate, due to local colonization, but in addition, the environment it "perceives" is already aggregated. In other words, because the population of the best competitor is aggregated, it follows that the sites unoccupied by the best competitor are also aggregated, or at least not random. These unoccupied sites are the only places available to the second competitor for colonization. Thus the second competitor tends to aggregate in an area that is already nonrandom and hence becomes more aggregated than the best competitor. This tendency toward aggregation increases down the competitive hierarchy, rapidly reaching an asymptotic value (Figure 8.5).

More Realistic Population Dynamics

A final question concerns whether the conclusions depend upon the greatly abstracted local dynamics, or whether they continue to hold as local dynamics are made more realistic. For example, the metapopulation models discussed assume that local growth and competitive displacement are instantane-

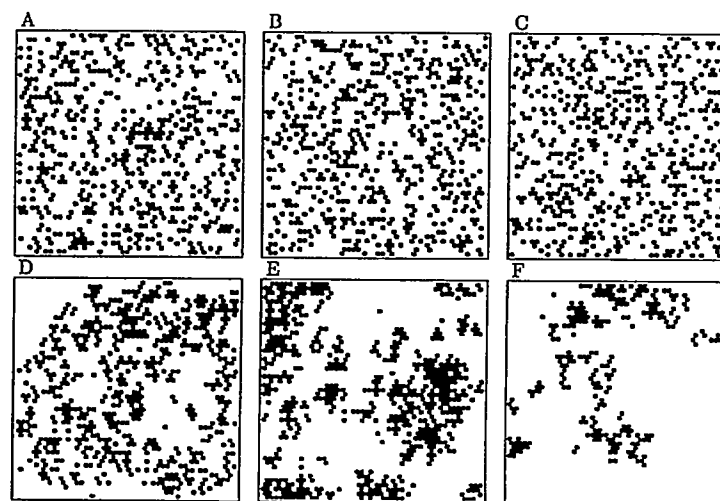


FIGURE 8.4. Aggregation developing with time. (A, B, C) Random distributions at $t = 0$ for the best three competitors in an explicitly spatial metapopulation model with local dispersal. The habitat contains 2,950 individual sites arranged in a hexagonal lattice. Dots show sites occupied by individual plants. (D, E, F) Distribution at $t = 5,000$. The best competitor (D) is clustered compared to the initial random distribution. The second competitor (E) and the third competitor (F) are more clustered still, because they are restricted to the already-clustered sites not occupied by better competitors. Level of clustering approaches an asymptote.

neous, but reproduction is continuous. However, for a vast array of plant and animal species, seed production or birth is an episodic event often synchronized with the seasons, whereas growth and competitive displacement occur gradually throughout the year. Thus, in reality, reproduction is better modeled as instantaneous and discrete, while growth and competitive displacement are better modeled as continuous.

We can install discrete reproduction with gradual growth and competition by considering a continuous-time differential equation at each site. Individuals increase or decrease in biomass according to the amount of limiting resource available, and the resource increases or decreases according to the amount consumed and the amount resupplied. To make this

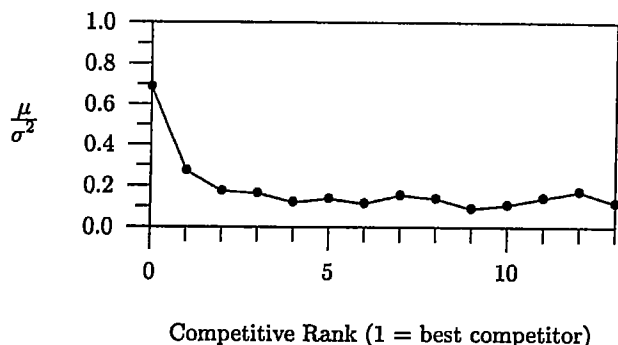


FIGURE 8.5. Random spatial distribution versus competitive rank. Spatial distribution of competing species in an explicitly spatial metapopulation model with local dispersal in a habitat of 100×99 hexagonal sites. The horizontal axis shows the position on the competitive hierarchy, with the best competitor numbered 1. Number 0 represents uninhabited sites. The vertical axis is a simple index of randomness (μ/σ^2) averaged over all spatial scales from 2×2 through 33×33 . Deviations from unity indicate nonrandom spatial distributions. (Note that values of unity in this index do not imply randomness; Hurlbert 1990.) Randomness decreases for the first few competitors, then reaches a noisy asymptote (see Figure 8.4).

precise, we apply a specific model of resource competition (Appendix 8.1) to each hexagonal site, keeping mortality and colonization as before.

The competitors at a site interact only through the resource. The equations establish an implicit competitive hierarchy through resource values. Each species i has a characteristic level of resource called R_i^* below which its population cannot survive, but above which its population grows. The species with the lowest R_i^* displaces all others by driving the nutrient level at the site below the level at which other species can survive or invade (Tilman 1982).

Equation 8.2 entails two key assumptions: (1) A species is displaced immediately when propagules from a better competitor arrive, and (2) a species is unable to survive or invade a given site if a species higher in the competitive hierarchy is already present. In contrast, for a more realistic model, the

effect of invasion by a better competitor is delayed. A better competitor can invade immediately, for the resource level maintained at the site by the poorer competitor is sufficient for the better competitor to grow. However, the better competitor displaces the poorer competitor only by reducing the resource, following Equation 8.4. This takes time. Thus, increased local dynamical realism means a delay in competitive displacement.

Second, when a better competitor dies, the resource level can recover and allow poorer competitors to invade. But it recovers as a dynamical variable, following Equation 8.3. This also takes time. Thus, increased local dynamical realism also means a delay in recolonization, at least for species low on the competitive hierarchy (i.e., the poorer competitors).

The net effect of the first of these alterations is to favor poorer competitors, while the net effect of the second is to favor better competitors. How the two balance depends on the recovery rate of the resource, the resource supply point, and the difference among species in minimal resource requirements. Figure 8.6 shows a numerical result for an environment approximated by discrete cells in a hexagonal grid. The two species coexist, but species 2 is more widespread than it would be in the corresponding nonresource model.

EVOLUTION AND A LONGER TIMESCALE

The slowing of the timescale in competitive systems with spatial structure may make it important to consider evolutionary effects. Vanderlaan and Hogeweg (1995), for example, found that certain theoretical predator and prey species can persist indefinitely when allowed to evolve, but become extinct if evolution is blocked. In all the competitive models described thus far, evolution has been blocked—characteristics of each species are fixed parameters. What can be expected at long timescales when parameters are allowed to evolve? To address this question, we examine a simple formulation of phenotypic evolution. Our phenotypic trait of interest is the position of each species along an R^* -dispersal axis, which is defined by assuming a positive correlation between R^* and dispersal ability (and a trade-off between dispersal and competitive ability,

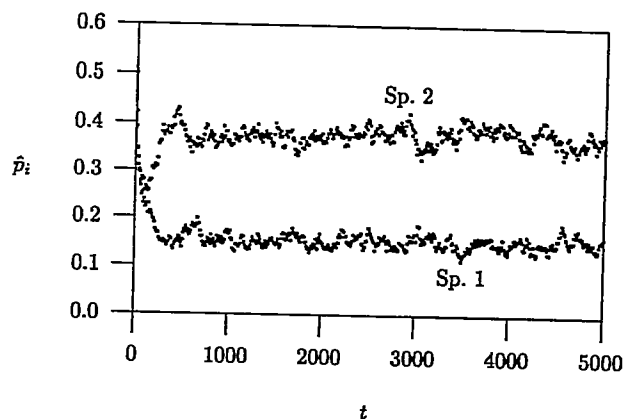


FIGURE 8.6. Coexistence of two species growing continuously and reproducing discretely while explicitly competing for a single resource. In each hexagonal cell, species compete for a single resource according to Equation 8.3. The horizontal axis is time; the vertical axis is portion of sites occupied. Colonization and mortality are such that, in the explicitly spatial analog of Equation 8.2, species 1 would occupy more sites than species 2. However, because of increased dynamical realism, including delayed displacement of species 2 by species 1, species 2 is more prevalent. Without space, species 2 would be extinct.

since low R^* corresponds to competitive superiority). This composite trait can be described by the parameter x_i . We assume that a large proportion $\alpha \approx 1$ of offspring possess the parental parameter value x_i , but a small proportion $(1 - \alpha)/2$ possess parameter value $x_i + \epsilon$, and the same proportion $(1 - \alpha)/2$ possess parameter value $x_i - \epsilon$, where ϵ is a small increment. In the infinitesimal limit, this kind of phenotypic evolution becomes simply diffusion in the parameter space (Appendix 8.2).

Solutions through Time

Figure 8.7 shows a particular numerical solution when parameters are able to evolve. The parameter x that evolves represents R^* , which establishes the competitive hierarchy—the lower the R^* , the better the competitor. Colonization increases with x , which corresponds to a competition-colonization trade-off. Mortality is the same for all phenotypes.

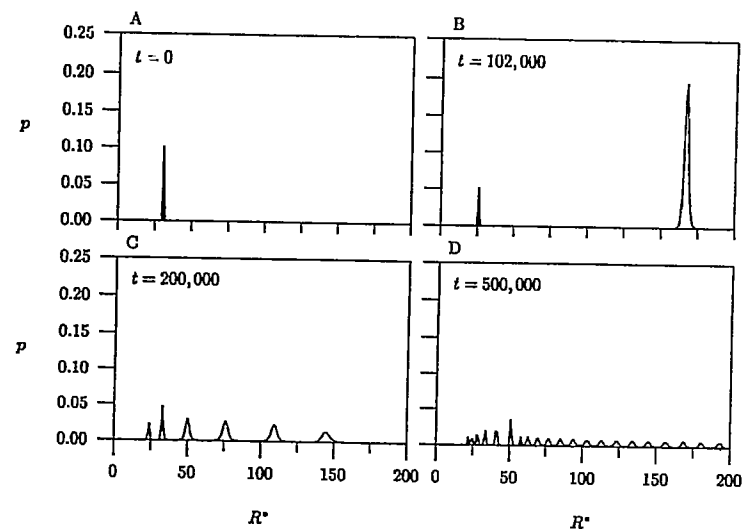


FIGURE 8.7. Patterns in phenotype space at intermediate times. The horizontal axis is the phenotypic variable x , which represents R^* , or competitive rank, and which is positively correlated with dispersal ability. The vertical axis represents abundance of the corresponding phenotype in the region. (A) At $t = 0$, a single phenotype is seeded. (B) By $t = 102,000$, original phenotype has evolved to lower R^* , its abundance has decreased, and a weedy species has risen to high levels. (C) At $t = 200,000$, six distinct peaks appear along the phenotype axis, representing six different coexisting species. (D) By $t = 500,000$, species have become more tightly packed, with about twenty species coexisting. This process continues until species are packed to the limits allowed by the dynamics of the system.

The system starts with a single late-successional phenotype of low, but not minimal, R^* . Phenotypic diffusion generates all phenotypes at exceedingly low population levels. Individuals of the initial phenotype spawn offspring of higher R^* and higher colonization rate, which tend to be outcompeted by their parents, and also offspring of lower R^* and lower colonization rate, which tend to displace their parents. Thus the colonization rate tends to decrease. After sufficient time, the initial species approaches its physiological limits, and its evolution

slows. There is a peak in the phenotype space at the lower limit of the colonization rate (Figure 8.7A). Now a weedy species with high R^* and high colonization rate arises sympatrically (Figure 8.7B) and, with passing time, evolves to be less weedy by the same mechanism that reduced the colonization rate of the initial species. This process continues, with more and more species arising, each weedy at first but each growing less so with time.

Early in the process, even though any phenotype is possible, the phenotypes present are separated by large gaps in the phenotype space. Continuous phenotypic variation has been organized under the force of competition into clusters of phenotypes. With the passage of time, the clusters become more and more closely packed. Yet for much of the time, the clusters remain unsaturated, as real communities may be (e.g., Cornell and Lawton 1992).

What exactly is the force that forms the phenotypic peaks in this evolving competitive system? A clue lies in the limiting similarity already known in competitive systems (May 1981; Pacala and Tilman 1994; Hurtt and Pacala 1995), and specifically known for the immutable version of this system (Tilman 1994). Assuming mortality does not vary among species, then to coexist, the second competitor must have a higher colonization rate than the best competitor. But an arbitrarily higher colonization rate will not do. The colonization rate must be higher by a minimum amount, that amount determined by characteristics of the best competitor (Tilman 1994). When parameters are immutable, limiting similarity excludes certain species from the region. But when parameters can evolve, limiting similarity leads to the origin of species, that is, to sympatric speciation of hundreds of species.

We have explored evolution only in implicitly spatial competition models, and only under the simple mechanism of phenotypic inheritance with a direct trade-off between competitive ability and dispersal. The results raise many questions, and additional work is needed to determine their generality and robustness, especially the effect of random walks to extinction of rare phenotypes, of explicit genetics, and of explicit space.

SUMMARY

Implicit spatial structure, coupled with trade-offs in species dispersal and competitive traits, promotes coexistence among competing species that would otherwise be subject to competitive exclusion. Coexistence continues as spatial structure is made more explicit and as local population dynamics are made more realistic. Added realism leads to new phenomena, such as spatial patterning and increasing stochasticity down the competitive hierarchy. Explicit spatial structure coupled with stochasticity helps explain the apparent discrepancy between observations of strong competition at the fine scale and random assemblages of species at the community scale. Implicit spatial structure, interacting with phenotypic mutation and competitive dynamics, can organize a continuous array of phenotypes into discrete species-like sympatric clusters. In all these cases, the dynamics of competition over a spatial habitat can be dramatically different from the corresponding dynamics in each local site.

APPENDIXES

Appendix 8.1: Resource Competition

The following single-resource model is from Tilman (1990):

$$\begin{aligned} \frac{dR}{dt} &= \alpha(R_0 - R) - \sum_{i=1}^n Q_i f_i(R) B_i \\ \frac{dB_i}{dt} &= [f_i(R) - m_i] B_i \\ f_i(R) &= r_i \frac{R}{R + K_i} \end{aligned} \quad (8.3)$$

Here $R = R(t)$ is the amount of resource in the environment at time t , $B_i = B_i(t)$ is the biomass of species i at time t , Q_i is a resource-to-biomass conversion coefficient, $f_i(R)$ is the growth function for species i , r_i is the maximum growth rate of

species i with unlimited resource, K_i is a half-saturation constant of the growth function, R_0 is the supply point of the resource, and α is the supply rate of the resource. In this model, if species i is alone in occupying the site, the resource will be drawn down to a level

$$R_i^* = \frac{K_i}{r_i/m_i - 1}. \quad (8.4)$$

Appendix 8.2: Phenotypic Diffusion

Instead of species with fixed parameters $x_1, x_2, x_3, \dots, x_n$, we have in the infinite limit an unlimited number of potential “species” in a continuous parameter space $x \in \mathbf{R}^+$. Using implicit spatial structure, we replace the discrete species indices $i = 1, 2, 3, \dots$ of Equation 8.2 with a continuous variable x , where x is simply the R^* value of the represented phenotype, and where x varies continuously across all positive values representing all possible species:

$$\begin{aligned} \frac{\partial p}{\partial t} = & c(x)p(x, t) \left[1 - \int_a^x p(u, t) du \right] \\ & - m(x)p(x, t) - p(x, t) \int_a^x c(u)p(u, t) du + \mu \frac{\partial^2 p}{\partial x^2}. \end{aligned} \quad (8.5)$$

The point $x = a$ represents the lowest R^* of any species physiologically possible. The colonization function $c(x)$ and the mortality function $m(x)$ are algebraic and typically increase with x ; μ is a constant.

This is an integro-differential reaction-diffusion equation. The first three terms make up the reaction term, which models population growth and competition over the entire spatial region for species with $R^* = x$. The fourth term $\mu \partial^2 p / \partial x^2$ is the diffusion term, which models inheritance, abstractly repre-

senting heredity, mutation, and recombination without addressing a precise genetic system. Patterns that develop in x are clusters of phenotypes, not spatial patterns.

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