

Mathematical Challenges in Spatial Ecology

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The word *ecology* comes from the Greek *oikos*, which means “house”, and was coined by the German zoologist Ernst Haeckel in 1870. It is, according to the *Oxford English Dictionary*, the “branch of biology that deals with organisms’ relations to one another and to the physical environment in which they live.” Examples of such relations are predator-prey interactions and plants competing for resources. Such interactions may be influenced by demographic and environmental fluctuations and occur over a wide range of spatial and temporal scales.

Scientific curiosity by itself would be a sufficient impetus for studying ecology, but understanding species relations and interactions is not just an academic exercise: Humans rely on ecological services for purification of water and air, soil maintenance, pest control, waste management, nutrient recycling, and much more; these processes are controlled by complex interactions of species with each other and with the environment.

We are altering the environment at an unprecedented rate: foremost are land-use changes and invasions of nonnative species. These human-caused alterations of the environment disrupt the functioning of ecosystems, often with devastating consequences. For instance, land-use changes, such as the conversion of forests into agricultural land,

are often accompanied by soil erosion that affects water flow and nutrient recycling. There are numerous examples where species invasions drastically alter ecosystems: for instance, the water hyacinth, a plant native to the Amazon and considered one of the world’s worst invaders, now covers many lakes and rivers in the tropics. Land-use changes and species invasions are the two major causes of species extinctions: it is estimated that human activities have increased extinction rates by a factor of 100 to 1,000.

Both empirical work and theoretical work contribute to our understanding of how ecosystems function and to our ability to successfully manage and preserve them. Mathematicians can contribute to this understanding by collaborating with biologists on developing models, analyzing models, and relating theory to empirical work.

I will focus on one factor that has become increasingly prominent in theoretical and empirical ecological studies: namely, space (see Tilman and Kareiva, 1997). We live in a spatial world, and the spatial component of ecological interactions has been identified as an important factor in how ecological communities are shaped. Understanding the role of space is challenging both theoretically and empirically. Since it is impossible to cover all aspects of this area in a short article, I will concentrate on stochastic models in population ecology. After describing the most common types of spatial models, together with biological examples, I will conclude with some mathematical challenges in spatial ecology.

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The Role of Models in Ecology

Models in ecology serve a variety of purposes, which range from illustrating an idea to parameterizing a complex real-world situation. They are used to make general predictions, to guide management practices, and to provide a basis for the development of statistical tools and testable hypotheses.

Models that illustrate ideas are, for instance, Tilman's resource model (Tilman, 1982) and the Lotka-Volterra competition model. In Tilman's resource model, species compete for resources. In the case of competition for just one resource, the model predicts that the species with the lowest equilibrium resource requirement will outcompete all other species. Tilman and collaborators have tested the model in freshwater algae, for which silicate is the limiting resource, and in grasslands in Minnesota, where nitrogen is the major limiting resource. The Lotka-Volterra competition model, discussed in detail below, incorporates the observed reduction in the growth rates of two competing species as their densities increase. The model predicts that coexistence occurs if competition among individuals of the same species (*intraspecific* competition) is stronger than competition among individuals of different species (*interspecific* competition). In 1934, Gause tested this model in an experiment on competition between different species of paramecia (freshwater protozoans).

Making predictions in management situations requires more detailed and realistic models. Examples are models that investigate which areas need to be preserved to ensure persistence of an endangered species and models that predict how spatial planting patterns of a genetically modified crop affect the evolution of pathogen resistance. Realistic models are essential when experiments are not feasible or when either the temporal or the spatial scale over which predictions are sought is very large. For instance, predictions of the effect of an increase in carbon dioxide in the atmosphere on global climate and vegetation over the next one hundred years have to be aided by modeling: we can manipulate carbon dioxide levels only over short temporal and small spatial scales; models then extrapolate to the larger scale.

Models can help to design experiments, to test hypotheses, and to develop new hypotheses and ideas. New ideas may contradict long-held views and spur new research to resolve controversies; conflicting hypotheses may coexist until a synthesis is reached. Models are not the ultimate judge in resolving controversies, but they do play an important role in investigating consequences of alternative hypotheses. To illustrate this point, I will briefly discuss a long-standing controversy in ecology: namely, whether a more diverse community is more stable, a question that has consequences for the effects of species loss.

In the 1950s, Elton and MacArthur promoted the idea that a more diverse community is more stable. Their conclusion was based on a combination of verbal models and observations from natural and agricultural systems. Their idea was accepted until the 1970s, when Robert May investigated mathematical models of randomly assembled communities that showed a decrease in stability with diversity—just the opposite of the conclusion of Elton and MacArthur. Although May emphasized that there was no paradox, since his randomly assembled communities may not resemble natural systems, the stability-diversity hypothesis was no longer believed to be universally true. May's contribution demonstrated that mathematical reasons alone do not suffice and that biological reasons need to be sought to understand the relationship between diversity and stability. At that time there was a marked lack of empirical evidence for or against the hypothesis; moreover, the word "stability" was used in different ways, making comparisons between different statements difficult. Over the last ten years the stability-diversity debate has been revived, and several empirical and theoretical studies have been published that argue either side. New empirical results and new insights from models that address conflicting hypotheses might ultimately resolve the debate.

Modeling in Spatial Ecology—a Brief History

Mathematical models have played an important role throughout the history of ecology. Early examples are population growth models such as exponential growth, which Thomas Malthus used in 1798 to argue the consequences of unrestricted population growth, and logistic growth, which was developed by Pierre-François Verhulst in 1835 to model density-dependent population growth and used by Raymond Pearl and Lowell J. Reed in the 1920s to predict the future population size of the U.S. The 1920s also saw the development of mathematical models of multispecies interactions, notably the predator-prey and competition models of Alfred J. Lotka and Vito Volterra.

Before the 1970s ecological population modelers typically used ordinary differential equations, seeking equilibria and analyzing stability. The early models provided important insights, such as when species can stably coexist and when predator and prey densities oscillate over time.

A common feature of these early models is that the interactions were based on the *mass-action law*, an approach that has its conceptual foundation in modeling chemical reactions. When the reactants are well mixed and have to collide in order to react, the mass-action law says that the collision rate (hence the reaction rate) is proportional to the product of the concentrations of the reacting molecules.

In many ecological situations, however, the assumption of being well mixed does not hold, and a spatial model with local interactions is more appropriate and can result in predictions that differ from the well-mixed case. The two most frequently quoted and now classical studies that point to the central role of spatial subdivision are Andrewartha and Birch's 1954 observations of insect populations that became frequently extinct but persisted globally due to recolonization from local populations, and Huffaker's 1958 laboratory experiment with a predator-prey system of two mites, one that feeds on oranges (*Eotetranychus sexmaculatus*) and the other a predatory mite (*Typhlodromus occidentalis*) that attacks *E. sexmaculatus*. Huffaker set up an array of oranges and rubber balls with different levels of spatial complexity that controlled dispersal and demonstrated that a complex, spatially heterogeneous array promoted coexistence, whereas coexistence was impossible in simpler, spatially homogeneous arrays. Mathematical models later confirmed that spatial subdivision is important for the persistence of populations.

Some of the early models include space implicitly, such as the *Levins model* (Levins, 1969), discussed below, which uses the framework of ordinary differential equations to describe the dynamics of a population in a spatially subdivided habitat. Populations may go extinct in patches and may subsequently be recolonized from other occupied patches. Space is implicit in this framework in the sense that recolonization is equally likely from all occupied patches, regardless of their locations. Models that include space explicitly, such as reaction-diffusion equations, were employed by Skellam in the 1950s to describe the invasion of species; they are of the same type as Fisher's 1937 model for the spread of a novel allele. Though these models include space, they still do not allow for spatial correlations, since local populations are effectively infinite.

In the late 1960s and early 1970s, F. Spitzer in the United States and R. L. Dobrushin in the Soviet Union began to develop a framework for spatial stochastic models known as *interacting particle systems*. These are stochastic processes that evolve on the d -dimensional integer lattice. Each site on the lattice is in one of a finite or countable number of different states, and sites change their states according to rules that depend on the states of neighboring sites. Originally, interacting particle systems were motivated by attempts to describe phenomena in physics, but it soon became evident that this framework is useful in biology. Some of these models can be viewed as spatial generalizations of classical ecological models such as the logistic model and the Lotka-Volterra competition model.

During the 1970s the availability of computers greatly expanded the use of spatial models in

ecology. Although spatial ecology today is still dominated by theoretical investigations, empirical studies that explore the role of space are becoming more common due to technological advances that allow the recording of exact spatial locations.

The Mathematical Framework of Spatial Models in Ecology

Demographic models are the fundamental building blocks of models in population and community ecology. The simplest demographic models are deterministic ones based on ordinary differential equations. I will use the logistic model as an example to introduce the different modeling frameworks. *Logistic growth* was introduced by Verhulst as a model for population growth with negative density dependence. Namely, if $N(t)$ denotes the population size at time t , then

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right),$$

where r and K are positive parameters; r is the *intrinsic rate of growth*, which is the maximum per capita growth rate; and K is the *carrying capacity*, which is the nonzero equilibrium population size.

The easiest way to include space in the logistic model is the *metapopulation* framework in which an infinite number of sites are linked by migration. In the original formulation all sites are equally accessible, and we say that migration is *global* (the more general framework is discussed below); this model is *spatially implicit*, since no explicit spatial distances between sites are included.

The analogue of the logistic model in the metapopulation framework is the *Levins model*. Namely, if $u(t)$ denotes the fraction of occupied sites, then

$$\frac{du}{dt} = \lambda u(1 - u) - u.$$

The colonization rate is equal to the parameter λ times the product of the fraction of occupied sites and the fraction of vacant sites. Time is scaled so that the rate at which sites become vacant equals 1, and a nontrivial equilibrium exists if λ is greater than 1. Deterministic models with global dispersal, called *mean-field models*, originated in physics. The idea is to replace complicated local interactions by an "effective field" produced by all other particles and to use the mass-action law to describe the dynamics.

Models at the next level of complexity explicitly include distances between sites. The simplest examples are reaction-diffusion equations, such as *Fisher's equation*, which was introduced to ecology by Skellam. It describes logistic growth in an explicitly spatial setting by

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + \lambda u(1 - u) - u,$$

where $u = u(x, t)$ is the population density at location x at time t . The parameter D is called the *diffusion coefficient*, and the reaction term $\lambda u(1 - u) - u$ has the same interpretation as in the Levins model.

Closely related to reaction-diffusion equations are integro-differential equations. The analogue of Fisher's equation in this framework is

$$\frac{\partial u(x, t)}{\partial t} = -u(x, t) + \lambda(1 - u(x, t)) \int k(x, y)u(y, t) dy.$$

The function $k(x, y)$ is a probability density that describes colonization of a vacant site at x from an occupied site at y ; it usually depends only on the distance between x and y .

Finally, interacting particle systems allow the inclusion of local interactions. As mentioned above, an interacting particle system is a stochastic process with state space $E^{\mathbf{Z}^d}$, where E is some finite (or countably infinite) set. The state at time t is a configuration that assigns each site in \mathbf{Z}^d a value in E . The dynamics of the model are described by *rate functions* that indicate how a site changes its state based on the current states of sites in a local neighborhood. The rate functions define exponentially distributed times, and we say that a change occurs at rate μ if the waiting time T for this event is exponentially distributed with mean $1/\mu$, that is, $P(T > t) = e^{-\mu t}$. The interacting-particle analogue of logistic growth in space is the *contact process* (see Liggett, 1985). In this model each site on the d -dimensional integer lattice is either vacant (state 0) or occupied (state 1). A site becomes occupied at a rate equal to λ times the fraction of occupied sites within a given neighborhood (for instance, all sites within distance R), and an occupied site becomes vacant at rate 1.

The above models are related in ways that are now well understood and that have been made mathematically rigorous both for the contact process and for many other models (Durrett and Neuhauser, 1994; for other examples see Durrett, 1995). For example, the reaction-diffusion equation follows from the contact process by scaling space and introducing fast stirring in the following way. The integer lattice is replaced by a lattice with sites distance ϵ apart, and neighboring sites exchange their contents at rate $\epsilon^{-2}/2$. One can show that in the limit as $\epsilon \rightarrow 0$, the probability that a site is occupied converges to a function satisfying the reaction-diffusion equation with $D = 1/2$.

An integro-differential equation can be obtained from the contact process through a similar rescaling procedure. Namely, replace the integer lattice by a lattice with sites distance ϵ apart and discretize the dispersal kernel so that as ϵ tends to 0, dispersing offspring have access to an ever-growing number of sites. For example, assume

in a one-dimensional model that offspring are dispersed uniformly over the interval $[-1, 1]$. When $\epsilon = 1$, the neighborhood consists of the two nearest sites, and when $\epsilon = 1/2$, the neighborhood consists of the nearest and the next nearest sites. As ϵ decreases further, more sites are included in the neighborhood, each site being equally accessible. Convergence to the above integro-differential equation can be shown under mild assumptions on the dispersal kernel.

The conceptual difference between the reaction-diffusion equation and the integro-differential equation is that in the former, individuals take many small steps in a random-walk-like fashion between reproductive events, like zooplankton in a water column, whereas in the latter individuals take only one big step right after they are born, like plant seeds. Both the partial differential equation and the integro-differential equation reduce to the Levins model when the initial distribution is constant in space.

In the following I will describe the framework of interacting particle systems in more detail. I will also mention two other frameworks that are popular in ecological modeling but less often used in mathematical studies.

Interacting Particle Systems

General Framework and Basic Techniques

Interacting particle systems are *continuous-time Markov processes* on $E^{\mathbf{Z}^d}$, where E is either a finite set or an infinite but countable set. (A Markov process is a stochastic process in which the future state depends only on the current state and the past becomes irrelevant.) The temporal evolution is given by rate functions that allow the process to evolve in continuous time. The contact process described above is just one of many examples studied over the last thirty years. See Liggett (1985) for the foundation of interacting particle systems, a description of analytical techniques, and some of the basic models and results, and Durrett (1988, 1995) for graphical methods and a summary of some more recent work.

Few analytical methods are available to analyze these models. The two most important techniques are *duality* and *coupling*, but whether these methods are available depends on the model. Duality can be loosely described as a technique that allows one to trace the history of a finite number of sites back to time 0, which then allows one to determine their state at the current time based on their history and the configuration at time 0. This is akin to identifying one's ancestors.

Coupling is a technique that allows comparison of two processes. For example, coupling can be used to show that if the contact process survives for some value of λ , then it will do so for all greater values. Namely, one can couple two contact processes with different birth rates in such a way

that whenever the process with the smaller birth rate has an occupied site, so has the process with the larger birth rate, provided both processes start with the same initial configuration.

Another powerful technique is *rescaling*. This method, developed by Bramson and Durrett (see Durrett, 1995), involves a comparison between the process of interest and *oriented site percolation*. Oriented site percolation with density p is a process on $\{(z, k) \in \mathbb{Z}^2 : z + k \text{ is even}\}$ in which every site, independently of all others, is open with probability p and closed with probability $(1 - p)$. If p is sufficiently large, there is a positive probability that there is an infinite *open path* starting at $(0, 0)$, and we say that the system *percolates*. (An open path from $(x, 0)$ to (y, k) is a sequence of points $z_0 = (x, 0), z_1, z_2, \dots, z_k = (y, k)$ such that for $0 \leq j \leq k - 1$, either $z_{j+1} = z_j + (-1, 1)$ or $z_{j+1} = z_j + (1, 1)$.) The basic idea of the rescaling argument is to show that for appropriate $p > 0$ the process under consideration, when viewed on suitable length and time scales, dominates an oriented site percolation model in which sites are open with probability p (Figure 1).

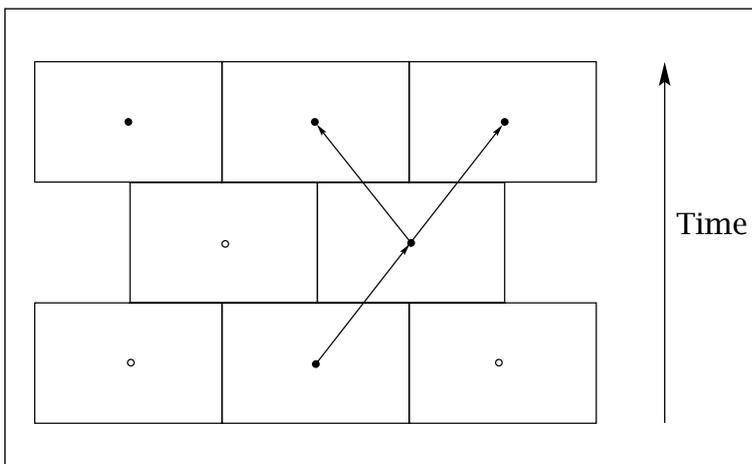


Figure 1. The rescaled lattice: Each box represents a space-time box. The dot in the center of each box represents a site in the associated oriented site percolation process; open sites are indicated by full circles, closed sites by open circles. Open paths are indicated by the arrows connecting open sites.

For instance, to show that the contact process survives (that is, there exists a nontrivial stationary distribution with a positive density of occupied sites), one needs to show that at any time the number of individuals in sufficiently large space-time boxes exceeds a certain threshold with probability close to 1. The space-time boxes are coupled to sites in an oriented site percolation process, so that whenever a site is open in the oriented site percolation process, the number of occupied sites in the contact process at any time in the corresponding space-time box exceeds a certain threshold. One can then show that the contact process

retains the desired properties for all times provided the sites in the oriented site percolation process do percolate.

The number of models that have been studied is quite large. In the following, I will focus on a class of single-species and multispecies demographic models that describe competitive interactions within and between species. The emphasis in single-species models is on whether a nontrivial stationary distribution exists in which the species has a positive density and what patterns result from local interactions. In multispecies models there is an additional aspect, namely, whether species can coexist and what the mechanisms of coexistence are.

Survival of a Single Species in Space

The simplest single-species population model is the contact process introduced above, which describes growth when the birth rate is density dependent but the death rate is density independent. The density dependence in the birth dynamics enters because only vacant sites can be colonized. After more than twenty-five years of study, the contact process is quite well understood. There exists a critical birth parameter, greater than 1 (recall that 1 is the critical value for the nonspatial model), which depends on both the spatial dimension and the type of neighborhood, such that if the birth rate exceeds this threshold, the process survives, and otherwise the process dies out. The density of occupied sites is a nondecreasing function of the birth parameter. The nontrivial stationary distribution (if it exists) has positive correlations. Though the correlations are weak, they can be seen in the nearest-neighbor case, where occupied sites appear clumped.

If deaths also depend on the density, the corresponding model is known as the *annihilating branching process*. Individuals die at a rate equal to the fraction of occupied neighbors, and the birth process is the same as in the contact process. Individuals give birth at rate λ , and their offspring disperse within a given neighborhood, establishing themselves only on vacant sites. If the dispersal neighborhood is the same as the neighborhood that determines mortality, then a nontrivial stationary equilibrium exists for all $\lambda > 0$. It is the product measure with density $\lambda/(1 + \lambda)$; that is, sites are independently occupied with probability $\lambda/(1 + \lambda)$. Despite local dispersal, no spatial correlations build up at equilibrium (for references, see Neuhauser, 1999).

Multispecies Models

Multispecies models can be built from single-species models by incorporating interactions between species. I will focus on competitive interactions and discuss different mechanisms for coexistence.

Lotka-Volterra type competition. The classical, nonspatial, two-species *Lotka-Volterra competition model* is given by

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - \alpha_{12} \frac{N_2}{K_1} \right), \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - \alpha_{21} \frac{N_1}{K_2} \right),\end{aligned}$$

where $N_i(t)$ is the abundance of species i at time t . The positive parameters r_i and K_i denote the intrinsic rates of growth and the carrying capacities, respectively, just as in the logistic model. The interaction between the two species is given by the nonnegative parameters α_{ij} , which describe the effect of species j on species i . The minus sign in front of the α_{ij} 's indicates that the interaction is *competitive*: the presence of either species reduces the density of the other. Besides Gause's experiment mentioned earlier, there have been many experiments that measure the strength of interspecific competition, such as the study by Rees et al. of a four-species community of annual plants that grow in a sand dune habitat in Norfolk, UK, and a study by Freckleton et al. of a community of rangeland annuals in Australia.

Analysis of the model (see Figure 2) reveals that if $\alpha_{12} < K_1/K_2$ and $\alpha_{21} < K_2/K_1$, then *coexistence* between the two species is possible; that is, there exists a locally stable equilibrium in which both species have positive densities. The mechanism for coexistence here is that each species impedes itself more than it is impeded by the other species. If $\alpha_{12} > K_1/K_2$ and $\alpha_{21} < K_2/K_1$, then species 2 *excludes* species 1: if species 2 has a positive density initially, then the system will converge to an equilibrium state in which species 1 is absent and species 2 is at its single-species equilibrium. (Similarly, if $\alpha_{12} < K_1/K_2$ and $\alpha_{21} > K_2/K_1$, species 1 excludes species 2.) If both $\alpha_{12} > K_1/K_2$ and $\alpha_{21} > K_2/K_1$, then eventually one species will exclude the other, but the winner depends on the initial densities of the two species; this phenomenon is called *founder control*.

Neuhauser and Pacala (1999) formulated this model as a spatial model on the d -dimensional integer lattice in which all sites are always occupied. Individuals die at a rate that depends on the densities of both species in the neighborhood (an individual of species 1 at $x \in \mathbf{Z}^d$ at time t dies at rate $u_1(x, t) + \alpha_{12}u_2(x, t)$, and an individual of species 2 dies at rate $u_2(x, t) + \alpha_{21}u_1(x, t)$, where $u_1(x, t)$ and $u_2(x, t)$ are the local relative frequencies at x at time t of species 1 and 2, respectively). If a site becomes vacant due to death, it gets filled immediately by an offspring from one of its neighbors, chosen at random. Using duality and rescaling, we showed that if the interspecific competition parameters are sufficiently close to 0, then coexistence occurs as in the nonspatial model. (Coexistence in the spatial

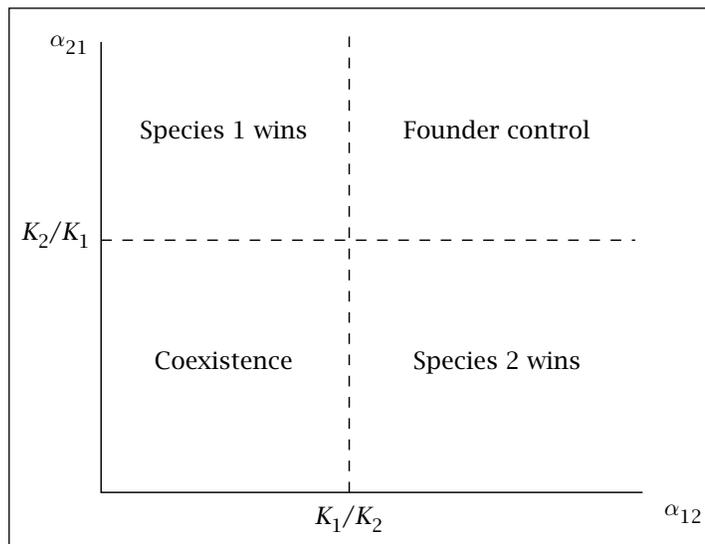


Figure 2. The phase diagram in the $\alpha_{12} - \alpha_{21}$ plane for the nonspatial Lotka-Volterra model with interspecific competition. The horizontal and vertical dashed lines represent the boundaries of regions where the behavior differs: coexistence, species 1 wins, species 2 wins, and founder control.

model means that for any $\epsilon > 0$, there exists a sufficiently large box such that with probability at least $(1 - \epsilon)$ both types will be in the box for sufficiently large times.) When the interspecific competition parameters are both equal to 1, the dynamics simplify and we recover a well-studied model, called the *voter model*: at rate 1 the state at each site is replaced by the state of one of its neighbors, chosen at random. One thinks of the “voter” at each site as adopting a neighbor’s opinion at rate 1. The voter model, which has been studied since the mid 1970s, shows spatial segregation in one and two spatial dimensions and coexistence in three and higher dimensions. Spatial segregation for the voter model means that the probability that any two sites are in different states tends to 0 as time tends to infinity.

The one- and two-dimensional spatial Lotka-Volterra models differ from the nonspatial model in several ways (Figure 3). (In the following discussion, I exclude the one-dimensional nearest-neighbor case, since it behaves atypically.) The most striking difference is that coexistence is harder to get than in the nonspatial model; this came somewhat as a surprise, since it was believed that space would act as an additional niche and thus facilitate coexistence. The reduction of the parameter space where coexistence occurs is due to a combination of two factors: local interactions and the discreteness of individuals. If one chooses competition parameters close to where the nonspatial model changes behavior from coexistence to exclusion but still within the coexistence region, then the nonspatial mean-field model predicts coexistence with one species at a very low density and the other species close to its single-species

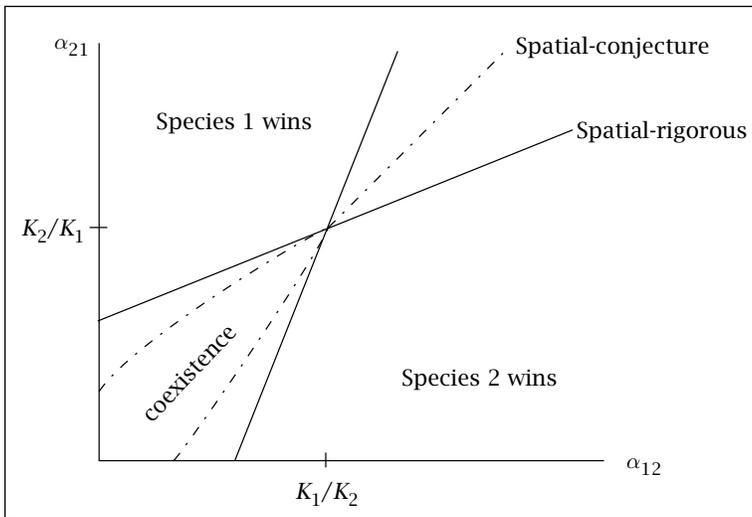


Figure 3. The phase diagram in the $\alpha_{12} - \alpha_{21}$ plane for the spatial Lotka-Volterra model with interspecific competition. Rigorous results for the spatially explicit model show that the coexistence and the founder control regions are smaller than in the nonspatial case (solid lines); we conjecture that the founder control region disappears in the spatial model (broken line).

equilibrium density. For the spatially explicit model with local interactions, it is impossible to maintain an arbitrarily small density of one species when the neighborhood size is kept fixed: a single individual of one type within a neighborhood of individuals of the other type has density equal to the reciprocal of the neighborhood size and thus cannot be made arbitrarily small. The smaller the neighborhood size, the more pronounced this effect is.

Furthermore, spatial segregation of species occurs as interspecific competition increases relative to intraspecific competition, resulting in cluster formation of like species. Using duality, we were able to give lower bounds on cluster sizes and conjectured that the clusters will not continue to grow forever if the α_{ij} 's are less than 1. This is different from the voter model ($\alpha_{ij} = 1$), where the clusters continue to grow. The spatial segregation of species for parameter values within the coexistence region of the nonspatial model again depends on neighborhood size. Namely, for equal competition parameters that are less than 1, we can choose a neighborhood size large enough so that coexistence is possible. But if the neighborhood size is fixed and the competition parameters approach 1 from below, then spatial segregation occurs.

Finally, using coupling, we found an expansion of the parameter region where one species excludes the other, but the winner depends on the competition parameters rather than on initial densities. In other words, the founder control region shrinks; we conjecture that the founder control region disappears altogether. The loss of the founder control region appears to be a common phenomenon in

spatial models. The reason is that even though the mean-field model has two locally stable equilibria and the outcome of competition depends on initial densities, one of the two equilibria turns out to be stronger when using the partial differential equation or integro-differential equation approach. That is, as long as the stronger species occurs somewhere at a sufficiently high density over a sufficiently long interval, that species will expand its range via traveling waves and will eventually take over.

Competition-Colonization Trade-Off. The competition-colonization trade-off is another mechanism that is frequently invoked to explain coexistence, for instance in the Minnesota grasslands studied by Tilman's group. Some grass species allocate more biomass to their roots, which makes them better competitors for nitrogen, while others allocate more to seeds, which makes them better colonizers; and the different species coexist. The trade-off can be illustrated in a model in which species are hierarchically ordered. This model is known as the *grass-bushes-trees model* in mathematics (for references, see Durrett, 1995) and the *hierarchical model* in ecology (for references, see the article by Lehman and Tilman in Tilman and Kareiva, 1997). In the two-species mean-field version, the model is given by the following system of ordinary differential equations:

$$\begin{aligned} \frac{du_1}{dt} &= \lambda_1 u_1(1 - u_1) - u_1, \\ \frac{du_2}{dt} &= \lambda_2 u_2(1 - u_1 - u_2) - u_2 - \lambda_1 u_1 u_2, \end{aligned}$$

where $u_i(t)$ is the density of species i at time t . Species 1 behaves like a contact process, and therefore for species 1 to survive, λ_1 needs to exceed the critical value (which is 1 for the mean-field model). Species 2 behaves like a contact process in the absence of species 1 but is replaced by offspring of species 1 if they land on sites that are occupied by species 2. Offspring of species 2 can land only on vacant sites, whereas offspring of species 1 can land on vacant sites or on sites occupied by species 2. Species 1 is thus considered the superior competitor. The principal conclusion from this model is that the inferior competitor (species 2) can coexist with the superior competitor (species 1) only if its birth rate exceeds the square of the birth rate of species 1, which makes species 2 the superior colonizer. Rescaling shows that the spatial version of this model has the same qualitative properties.

Spatial Heterogeneity. If factors such as temperature, pH, light, and soil moisture vary over small enough scales, then species can coexist by specializing on particular conditions. Biologically this is a very important factor for coexistence. From a mathematical point of view, however, this type of coexistence is less interesting, since one essentially

deals with noninteracting communities, each specialized to its own habitat type, and coexistence is trivial provided dispersal allows exchange of migrants.

Spatial heterogeneity generated by species dynamics is mathematically more interesting and also biologically important. For instance, light gaps in forests are created through tree fall. These gaps represent small-scale spatial heterogeneity in light availability and can allow species that differ in their light requirements to coexist. A light-tolerant species that reproduces on a fast time-scale and disperses over short distances can coexist with a shade-tolerant species by temporarily exploiting the gaps before the shade-tolerant species dominates the location again. This mechanism is called *successional niche* (Pacala and Rees, 1998).

We saw in the spatial Lotka-Volterra competition model that competitive interactions between species can generate spatial segregation, a form of spatial heterogeneity. This can facilitate coexistence of a large number of species by allowing different communities to exist side by side in patches without ever competing with species that live in another type of patch.

Spatial heterogeneity does not always facilitate coexistence. Indeed, habitat fragmentation, which results in a spatially heterogeneous landscape, is implicated as a major cause of species extinction. For instance, vast areas of Minnesota consisted of continuous prairie before European settlement. Now a large proportion of the original prairie has been converted either to urban areas or to farm land, resulting in a sparse patchwork of prairie fragments. Many of the fragments are so isolated that they have ceased to fulfill their ecological function. The effects of habitat fragmentation have been studied both theoretically and empirically. The hierarchical model has been explored quite extensively in the context of habitat fragmentation where a fixed proportion of habitat is assumed to be destroyed. The mean-field model exhibits somewhat surprising behavior: namely, the best competitor is affected most severely by habitat destruction and goes extinct first as the fraction of destroyed habitat increases (for references, see the article by Lehman and Tilman in Tilman and Kareiva, 1997). However, this effect depends crucially on the relative dispersal ranges of the competitors, and one can construct situations in a spatially explicit model that produce the opposite conclusion (Neuhauser, 1998).

The Point-Process Framework

Point processes are stochastic processes in which points are distributed in d -dimensional real space and the temporal dynamics are described by rate functions. Each point represents an individual, and the rate functions determine the demographic processes. Point processes differ from interacting

particle systems primarily by placing individuals on continuous space, such as the real plane, rather than restricting them to a regular lattice. To obtain biologically sensible results, one needs to introduce a local carrying capacity that limits the number of individuals locally. Questions of interest are similar to the ones I discussed above within the framework of interacting particle systems.

The point-process framework is particularly suitable for modeling plant populations. Several forest models employ this framework (for references, see the article by Pacala and Levin in Tilman and Kareiva, 1997). Point processes model dynamics at the level of an individual. Each individual is represented by a point with a unique location and any other attributes one wishes to track (species type, genotype, and so forth). The advantage of models based on individuals is that they allow calibration using field data. For example, Pacala and coworkers calibrated the forest model SORTIE by collecting field data for fecundity, survivorship, mortality, dispersal, and so on for every tree species in the simulation model. The simulation model was used, for instance, to predict biomass and species diversity under different disturbance regimes.

Spatial point distributions describe the spatial patterns of point processes. As in the case of interacting particle systems, local dispersal of individuals can result in spatial correlations. Since it is generally impossible to obtain the probability distribution that describes the spatial pattern in equilibrium, much more modest goals are pursued, like finding the average number of individuals per unit area or the covariance structure of the spatial pattern. But even this is difficult. Pacala and collaborators have developed a nonrigorous approximation method called the *moment closure method*. (This method had been used before in physics.) The method works only for a certain class of rate functions, and even then it does not always give the correct answer. It amounts to deriving equations for the mean vector of species densities and the associated covariance matrix. These equations contain higher-order moments and are therefore not closed. The equations can be closed and then solved numerically either by neglecting higher-order central moments or by approximating them by lower-order moments (the latter works, for instance, in the case where global dispersal results in a Poisson distribution). This method allows one to study spatially homogeneous models that are at the onset of exhibiting spatial correlations, such as when offspring are dispersed over intermediate distances. (Dispersal over very short distances has the potential to result in large spatial correlations, whereas dispersal over long distances can be well approximated by deterministic partial differential equations or integro-differential equations, similarly to the de-

terministic approximations for interacting particle systems, which do not exhibit spatial correlations.)

Interacting particle systems and point processes are not very different qualitatively. For instance, the same mechanisms mentioned above that allow for coexistence in interacting particle systems are present in the corresponding point-process model. This suggests at least some degree of robustness with respect to the modeling framework. However, point processes are much harder to analyze than interacting particle systems, which explains why studies of point processes rely primarily on simulations or approximation methods.

The Metapopulation Framework

Many populations live in patchy habitats due to habitat fragmentation or to naturally occurring spatial heterogeneities. The metapopulation framework, introduced into ecology by Levins in 1969, is ideally suited to deal with such situations. Subsequently this modeling framework has been greatly expanded, in particular due to Ilkka Hanski's empirical and theoretical work on butterfly populations in Finland (for a summary, see Hanski, 1999).

Metapopulations are spatially implicit or explicit patch models. Each patch is either occupied or vacant; occupied patches become extinct at a rate that may depend on population size or patch area, and vacant patches become colonized by migrants from other patches. The dynamics within a patch can be deterministic or stochastic. Frequently, instead of modeling individuals, one tracks the probability of patch occupancy, and one uses area as a proxy for population size to determine extinction and colonization rates of patches.

The metapopulation framework has the flexibility to accommodate any spatial arrangement and thus provides a more realistic framework than interacting particle systems. This is particularly important if one attempts to parameterize a real population, as Hanski and coworkers have done in their butterfly studies in the Åland islands in Finland. The butterflies are the Glanville fritillary, a species that occurs in dry meadows that contain the larval host plants. There are a large number of (mostly small) suitable patches, scattered throughout the landscape. Local butterfly populations are small, with a high turnover rate. For many years Hanski and coworkers have collected data, such as population sizes, extinction rates, and recolonization rates. Their study is unique in both spatial and temporal extent. By combining empirical and theoretical work, they demonstrated that demographic stochasticity and inbreeding cause frequent local extinctions but that the metapopulation as a whole persists because of recolonization and asynchrony in local dynamics. Their study also points to the importance of sufficiently large and closely connected networks of patches to

maintain the metapopulation: patches that are too isolated are never colonized.

Theoretical results on the persistence of such metapopulations are difficult to obtain due to the complex spatial arrangement of patches. Hanski and Ovaskainen (2000) have made some progress in the case of deterministic models. They defined a quantity, the metapopulation capacity, that depends solely on the spatial arrangement and the area of patches and that allows one to determine whether the population will persist. Theoretical results of persistence of stochastic metapopulations are lacking, though they are quite important, in particular when dealing with small populations where demographic stochasticity affects extinction of subpopulations.

Most metapopulation work deals with single populations. However, populations do not live in isolation. A habitat can contain tens to hundreds of species which interact in complex ways. Though it is not feasible to investigate models at this level of complexity by specifying all possible interactions between a large number of species, it would be worthwhile to study communities of a small number of species that live in a patchy environment. Different species have different life histories resulting in different dispersal strategies. How this affects persistence of the entire community is not well understood. Much work is needed to understand such metacommunities.

The Future of Spatial Ecology

I discussed spatial models that deal with a single species or with competition between species and for which various results have been proved mathematically rigorously. We have a good understanding of what types of spatial patterns emerge in single-species models and also what mechanisms produce coexistence or mutual exclusion of different species and which of these mechanisms require an explicitly spatial component. Even though little is known rigorously about how robust the results are with respect to specific dynamics, there is a general sense that the results are robust and that we have identified the basic mechanisms. Determining the relative importance of the different mechanisms in natural populations, however, remains a challenge.

In the following I wish to point to challenges in areas in ecology that I did not discuss above and to topics that would benefit from a mathematically rigorous investigation.

Other Areas

A large part of the theoretical ecology literature deals with predator-prey or host-pathogen interactions. Hassell, May, and collaborators (see the article by Hassell and Wilson in Tilman and Kareiva, 1997) have developed a sizable body of work on *coupled map lattices*, primarily in the context of host-parasitoid models. (Coupled map lattices are

spatially explicit, deterministic models with local dynamics.) In addition, some stochastic and spatially explicit versions of predator-prey and host-pathogen models have been analyzed mathematically rigorously (see Durrett, 1995). Most models involve just pairwise interactions. Less well understood are models that deal with multiple hosts, multiple predators/pathogens, and more complex interactions, such as a predator feeding on a prey species that in turn feeds on some other host.

Ecological models often neglect genetics. Starting with Wright's work, there is a large literature on genetics models that include space either implicitly or explicitly. The mating structure can create genetic variation due to reduced gene flow between locations, resulting in a patchy distribution of genotypes. In addition, different genotypes might be favored in different parts of the range. This variation can have important consequences, in particular when individuals are suddenly faced with new ecological and evolutionary conditions, such as rapid climate change or reduction in range due to habitat destruction.

Robustness

Results from theoretical models are based on specific dynamics within a specific framework. This is particularly true for spatially explicit stochastic models; proofs break down when the dynamics change ever so slightly. For instance, the birth rate in the contact process is proportional to the number of occupied sites in the neighborhood. Many results for the contact process use duality, which crucially relies on this exact linearity of the rates. But many results, like the existence of a critical value and positive correlations, should hold for more general rate functions. Likewise, the dynamics are crucial in the proof of spatial segregation of the two competing species in the Lotka-Volterra model in one and two spatial dimensions when interspecific competition becomes more important relative to intraspecific competition, but the same phenomenon should occur for other rate functions as well. Understanding this type of robustness is essential if we want to make general statements.

Robustness is needed also with respect to the modeling framework. For instance, deterministic spatial models often exhibit complex patterns that are not robust with respect to stochastic perturbations. Though these patterns are intriguing, and their study has given rise to a whole field that studies emerging phenomena, it is doubtful whether patterns that rely on specific deterministic dynamics and that are not robust to stochastic perturbations are relevant to natural systems where environmental and demographic stochasticity are important factors.

Tools

The development of analytical tools that are accessible to biologists is of high importance. Such

tools are available for analyzing systems of differential or difference equations, but little is available for more complex models. One example of a tool that can be readily used for spatially explicit stochastic models is the moment closure method mentioned above. This approximation method has provided insight into the effects of local interactions in space, but has the drawback that it does not always yield correct answers. A better understanding of this method and the development of other methods are needed.

Computer simulations play an important role in spatial ecology. It is often easy to write the code for the spatial model, but the parameter space is frequently too large to do an exhaustive search to identify regions of qualitatively different behavior. In this case analytical approximations can prove very valuable. One way to proceed is to use the progression of models outlined above as a guide. Starting with a spatially explicit interacting particle system, one can first look at the corresponding reaction-diffusion or integro-differential equation that results from introducing either fast stirring or long-range dispersal. Since these models are more tractable, one can find regions in the parameter space where the behavior changes qualitatively. Often, the spatially explicit model has interesting behavior close to where the corresponding deterministic models have phase transitions; boundaries of those subspaces may be a good starting point for examining the interacting particle system (though by no means the only place where one should look for interesting behavior).

Empirical Studies

A frequent objective of empirical studies is to describe and explain spatial patterns and to determine the mechanisms that underlie the observed patterns. A mathematical model can help identify such mechanisms, but caution is in order since different mechanisms can result in similar patterns. Building models that distinguish between the different mechanisms is necessary to guide empirical studies to determine which mechanisms likely cause the observed patterns. This is a challenging task that requires both the creation and the analysis of new models. Only a thorough understanding of the theoretical properties of these models will inform empirical studies.

Currently, most spatial studies focus on just one species. In the future there will be an increased need for multispecies spatial models that can be parameterized by field data. It will thus be necessary to develop both robust models that can be parameterized and statistical methods that will allow the analysis of data from multispecies studies.

Finally, close collaboration between mathematicians and experimental biologists is needed for mathematical studies to have an impact on the understanding of how ecosystems function. This poses

a different kind of challenge: communication between the two groups. To effectively communicate, biologists and mathematicians need to speak a common language. This typically means that mathematicians need to make an effort to translate their results into plain English and to explain why they might be relevant to a biologist, and biologists need to make an effort to explain their terminology and to learn to identify situations in which mathematics can be useful.

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About the Cover

This month's cover is associated with the article in this issue by Claudia Neuhauser on spatial models. It is based on data calculated by Linda Buttel and Rick Durrett of Cornell University. Durrett, who has been a collaborator of Neuhauser, writes, "It shows the behaviour of a model of the spread of a disease like measles that you can only acquire once. Black sites are individuals susceptible to the disease, yellow sites are infected, and red sites are those who have had the disease and are now immune. This sequence of snapshots in time illustrates a result proved by Ted Cox and me in 1988—when the epidemic does not die out, it expands linearly and has an asymptotic shape, which is a convex set with the same point symmetries as the square lattice."

Other images like this one can be found in Durrett's article "Stochastic spatial models" in volume 41 of the *SIAM Review* (1999), pages 677–718.

One of the papers by Durrett and Neuhauser is "Epidemics with recovery in $D = 2$ ", *Ann. Appl. Probab.* **1** (1991), pages 189–206.

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