SPATIAL ECOLOGY

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Preface

Mathematical models and concepts have been important in ecology since its inception as a discipline. However, symbiosis between the disciplines of mathematics and ecology on any appreciable scale is a far more recent phenomenon. Fortunately, in the last few decades, there has been a growing recognition among many theoretical and empirical ecologists and mathematical scientists that they can and should work together to the benefit of both disciplines, science more broadly, and society at large. Promoting this kind of interaction and integration was the theme of a conference we helped organize here at the University of Miami in January 2005, along with colleagues from the Department of Biology and the Rosenstiel School of Marine and Atmospheric Sciences. The title of the meeting was "Workshop in Spatial Ecology." The choice of topic was deliberate and two-fold. First of all, space and spatial features are now solidly established as essential considerations in ecology, both in terms of theory and practice. Second, the mathematical challenges in advancing understanding of the role of space in ecology are substantial and mathematically seductive. We believed that the benefits of bringing together a select group of top-flight ecologists and mathematicians, many of whom would not have heretofore met each other, would be enormous, and if the atmosphere at the meeting is any indication, we were correct. Not long into our interactions, the suggestion arose for some kind of a follow-up volume to the workshop; not a conference proceedings per se, but something more substantial, more thoughtful, that would promote the kind of interplay between mathematics and ecology, and between theory and data, that we so enjoyed during the workshop. We immediately thought of two volumes of essays on ecological theory that have greatly influenced our development as mathematical scientists interested in serious ecological questions: *Perspectives in Ecological Theory*, edited by J. Roughgarden, R. M. May, and S. A. Levin, Princeton University Press, 1989; and *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, edited by D. Tilman and P. Kareiva, Princeton University Press, 1997. We thought that a volume along those lines that considered emerging challenges in spatial ecology could be highly valuable to a new generation of mathematical scientists and ecologists, especially if the choice of contributors to the volume reflected the current trend toward increased interaction of mathematical and ecological scientists and the resulting trend toward integration of the two disciplines. It was in that spirit that we arrived at the current volume.

We have identified emergent challenges in spatial ecology: understanding the impact of space on community structure, incorporating the scale and structure of landscapes

into mathematical models, and developing the connections between spatial ecology and the three other disciplines of evolutionary theory, epidemiology, and economics. This volume is divided into sections focused on those topics. Many of the authors of essays in this volume spoke at the Workshop in Spatial Ecology, but quite a number did not attend. Nevertheless, all of them share a commitment to the advancement of ecology as a truly quantitative science, particularly as it touches upon the role of space.

One of the fundamental problems in spatial ecology is to understand how spatial effects influence the dynamics of populations and the structure of communities. There has been significant progress in recent years on developing and analyzing spatial models for a single population in a temporally constant environment, and at least some on models for two competitors or a predator and its prey, but there has been much less work on models for spatial effects in communities involving several species or trophic levels or environmental variability in both space and time. On the mathematical side, much of the progress on understanding spatial models has been related to the development of a theory that can give criteria for unconditional persistence or extinction, that is, determining when a model has some sort of globally attracting set with certain species present and others absent. There has been some progress, but not as much, on methods for treating models that have multiple attracting sets so that their predictions are conditional on factors such as the initial state of the system. The chapter by DeAngelis et al. describes how models and simulations can provide insight into community and food chain structure in assemblages of fish species in wetland environments where the area of fish habitat is seasonally fluctuating. The chapter by Amarasekare presents results from models that illuminate how dispersal and spatial heterogeneity influence the mechanisms and patterns of species coexistence in multi-trophic communities with intraguild predation or predator-mediated coexistence. The chapter by Jiang and Shi describes recent progress on the mathematical theory for treating models where Allee effects, strong competition, or other mechanisms give rise to "bistability," that is, to multiple stable equilibria.

Classical modeling approaches in spatial ecology typically treat space as homogeneous and isotropic. For example, most spatially explicit models based on partial differential equations envision that organisms disperse through a uniform environment via simple diffusion. However, many ecological processes occur in spatial structures that display various sorts of heterogeneity and/or directionality at various scales, and the nature of the spatial structure of populations themselves is not always obvious. Organisms may disperse via nonrandom mechanisms that arise directly from the physical environment, for example by advection, and may decide whether or how to move in nonrandom ways based on environmental cues. The idea of connecting spatial scale and structure and dispersal behavior to phenomena in population dynamics, evolution, epidemiology, and economics is a recurring theme that is present in many of the chapters in this collection, and it is the specific focus of several of them. The chapter by Ovaskainen and Crone discusses how diffusion models can be extended and refined to describe dispersal in heterogeneous landscapes consisting of

patches and corridors of various types, and to account for dispersal behavior that may involve effects such as habitat preferences. The next three chapters are motivated or partly motivated by the problem of understanding ecological processes in river systems. Those systems present a branching spatial structure that is different from that of typical terrestrial environments, and dispersal in them is influenced by physical advection. The chapter by Fagan et al. addresses the issue of formulating metapopulation models for river networks and examines the effects of the "branchiness" of the network on metapopulations inhabiting it. The chapter by Hadeler et al. treats a variety of effects related to models for populations with quiescent phases. One particular problem that is discussed in that chapter is the "drift paradox," that is, the problem of understanding how populations in streams can resist being washed out by advection. Shifting into a quiescent phase is one possible mechanism by which a population can resist washout. The chapter by Nisbet et al. treats population dynamics in advective media, reviews the drift paradox, and identifies characteristic length scales related to population dynamics in such media. The final chapter in this section, by Hinrichsen and Holmes, addresses the problem of determining the spatial structure (or absence thereof) of a population from measurements at different sites. Specifically, it treats the application of state-space models to the problem of determining whether multi-site data correspond to independent populations with independent environmental drivers, independent populations with a shared environmental driver, a collection of populations with the same growth rate but independent environmental drivers, or a single population. Each of those cases would call for a distinct modeling approach, so determining which one represents the actual situation is important for connecting models with data.

The remaining chapters in the collection treat topics related to space and ecology, but do so relative to the perspectives of evolutionary theory, epidemiology, or economics. These areas are related to ecology by both direct connections among the phenomena they examine and philosophical similarities in the issues they address. Ecology describes the framework in which the natural selection that drives evolution occurs. In a sense, epidemiology describes the population interactions between microbes and other organisms, and may involve other aspects of ecology in the contexts of vector-borne or zoonotic diseases. The economics of harvesting resources such as fish or forests are tied to the ecology of those resources. More broadly, all of these disciplines aim to describe the large-scale emergent behavior of systems consisting of many interacting independent agents that may cooperate, compete, or exploit each other. For that reason modeling ideas and approaches that have worked well in the context of one of them may be relevant to others. Finding unifying approaches to these disciplines may be one of the grand intellectual challenges of current scientific thought.

At our present level of understanding, the conclusions about spatial aspects of evolution that can be drawn from models seem to depend to a considerable extent on the detailed assumptions built into the models. The chapters on topics related to evolution in this volume provide a guided tour through a number of scenarios and modeling approaches that represent active areas of current research, and suggest some

paths toward conceptual unification. The chapter by Hanski discusses how realistic metapopulation models may provide a unifying approach to ecological and evolutionary theory in fragmented habitats. Those models account for the areas of patches and the connectivity among patches. Hanski discusses how metapopulation models can be used to study the evolution of migration rates in fragmented environments. The chapter by Holt and Barfield also connects metapopulation theory to evolution. It specifically addresses the problem of understanding how environmental heterogeneity influences the evolution of species' niches. The chapters by Cantrell et al. and Bolker, in contrast, treat problems related to the evolution of dispersal in continuous environments. Both of those chapters take the viewpoint of adaptive dynamics as a starting point. The key assumption behind adaptive dynamics is that the strategies which can be expected to be successful in an evolutionarily sense are those that allow populations using them to successfully invade resident populations using other strategies. Although Cantrell et al. and Bolker use similar philosophical approaches based on adaptive dynamics, they use different types of models to study different scenarios. Cantrell et al. use reaction-advection-diffusion models in spatially heterogeneous environments to examine the evolution of dispersal mechanisms arising from local movement behavior that may be responsive to environmental conditions. Bolker uses spatial moment equations to examine how the nature and scale of spatial autocorrelation in environmental suitability influence the evolution of the shape of nonlocal dispersal kernels. Taken together the chapters treating spatial aspects of evolutionary theory show how strongly assumptions about the nature of dispersal and the scale and structure of the environment influence the conclusions that can be drawn about the evolutionary causes and effects of dispersal.

Recent concerns about the emergence or resurgence and global spread of infectious diseases have motivated renewed interest in epidemiology. Many potentially dangerous pathogens are zoonotic or vector-borne and thus have aspects that are directly related to ecology. Some similar problems arise in both disciplines, and often these can be addressed by similar modeling approaches. That point is well illustrated by the chapters on epidemiology. The chapter by Lloyd and Sattenspiel uses a metapopulation approach to examine how nonlinear disease dynamics interact with seasonal forcing to determine spatiotemporal patterns in disease dynamics. The chapter by Potts and Kimbrell describes how simulation models can be used to compare different control strategies for vector-borne diseases. The chapter by Ruan and Wu reviews a selection of reaction-diffusion models for the spread of diseases with animal hosts. In each case the modeling approach is reminiscent of ideas that are widely used in ecology, but is modified by the specific features of the epidemiological system it describes.

As human populations increase they put increased pressure on natural resources, which makes it crucial that we learn how to use them in sustainable ways and if possible to optimize the benefits derived from them. To do that it is necessary to understand how economics interacts with ecology and then apply ideas from optimal control theory. The chapter by Sanchirico and Wilen addresses the problem of optimal fisheries management from the viewpoint of metapopulation modeling. The

chapter by Olson explores the general issue of constructing models that describe the dynamics of resources, human factors in harvesting them, and the flow of capital investment needed to support the harvesting. The chapter by Herrera and Lenhart reviews some results on optimal control in metapopulation models and shows how to extend the approach to reaction-diffusion models and related models based on partial differential equations.

Our friend and colleague Alan Lazer once remarked: "It is better to open up an area of research than to close one down." As the chapters in this volume show, there is a great deal more to be done before the discipline of spatial ecology is ready to be closed down. We hope that this volume will inspire readers to open up new areas of research in the mathematical theory of spatial ecology and its connections with evolutionary theory, epidemiology, and economics.

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CHAPTER 1

Competition dynamics in a seasonally varying wetland

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Abstract. We have used one- and two-dimensional, spatially explicit models to simulate fish communities in freshwater wetlands in which the seasonality of rainfall in these wetlands causes annual fluctuations in the amount of flooded area, or fish habitat. We have modeled the competition between small fish species that differ from each other in efficiency of resource utilization and dispersal ability. The simulations showed that these tradeoffs, along with the spatial and temporal variability of the environment, allow coexistence of several species competing exploitatively for a common resource type. This mechanism, while sharing some characteristics with other mechanisms proposed for coexistence of competing species, is novel in detail. Simulated fish densities resembled patterns observed in Everglades empirical data. We are also modeling trophic chains and how these chains respond to the annual fluctuations in available habitat. These studies are a step towards understanding the community and food chain structure of fishes in seasonally fluctuating environments. They raise many theoretical questions that we plan to discuss in our essay.

1.1 Introduction

Models used in applied aspects of ecology, such as dealing with specific questions of conservation, assessment, and restoration, are usually far different from models used to elucidate theoretical issues. The former tend to include details that may be important to the particular applied question, while the latter are kept as simple as possible to reveal theoretical insights. However, theory should and can play a more prominent role in influencing the way that ecosystems are managed. The concept of trophic cascades from food web theory and metapopulation theory from spatial ecology are examples where theoretical models are beginning to make inputs to management plans.

1

As ecological theory is extended to more and more complex phenomena in which spatial heterogeneity and temporal fluctuations play a role, its potential application to real ecosystems and to specific applied issues is increasing. Practical models, even though necessarily more detailed and specific than those of theoretical ecology, may contain kernels of simpler theoretical concepts and models. Here we consider such a case of application of theory to a key component of the Everglades ecosystem.

The Everglades is a large freshwater marsh, characterized by the strong seasonal rainfall pattern of the region, which creates a cycle of wet and dry seasons. Water depths vary seasonally, but are seldom greater than one meter in this hydroscape of thousands of square kilometers. Because of the flat landscape, relatively small differences in mean water level amplify into large differences in the amount of wetted area and flooding duration, which affect the plant and animal communities. A community of small-bodied fishes, along with macroinvertebrates like crayfish, is a crucial component of the Everglades ecosystem (Kushlan 1990), as it is in many other seasonal wetlands, such as the Pantanal (Heckman 1998). These fishes are important connections that link both the small herbivorous fauna that feed on periphyton and the detritivores with the higher trophic level species, such as wading birds.

A question of great practical importance is how water levels in the Everglades should be regulated to maintain a system that is as close as possible to the natural ecosystem. The wetland small-fish community is strongly influenced by seasonal hydrologic fluctuations (Loftus and Kushlan 1987, Trexler et al. 2002). Human-induced changes in hydrology over the last several decades have altered hydroperiods in most wetland areas, thereby diminishing this fish forage-base or changing the pattern of its availability. Lack of sufficient biomass and availability of prey is hypothesized to have been a major factor in the decline of wading bird nesting at traditional Everglades' rookeries (Ogden 1994).

The species richness of the fish community is deemed to be important, both for its intrinsic value and for the contribution of species richness to biomass productivity of the community. The coexistence of many fish species of similar small body size and resource use also poses interesting questions for ecological theory. Numerous hypothesized mechanisms have been proposed for the maintenance of species richness in communities and the maintenance of the diverse Everglades freshwater fish community may be related to some current ecological theory on nonequilibrium communities. Environmental fluctuations are often proposed as means for maintaining richness in a dynamic community by preventing competitively dominant species from eliminating others. Chesson (2000) reviewed mathematical models showing that environmental fluctuations could promote diversity in nonequilibrium communities, when the fluctuations effectively provide distinct niches for the competing species. These circumstances may occur when the competing species have tradeoffs in key physiological and/or behavioral traits that allow the relative advantages to alternate among species in a fluctuating environment.

It is possible that some of the tradeoffs involve differences in the ability to move quickly into newly flooded areas and in the competitive ability in the permanently

flooded areas. As vast areas of wetland are re-flooded each year, opportunistic fish species can disperse into and exploit those areas first; while other species appear better at dominating more permanently inundated areas of marsh. Species better at exploiting more stable areas should have higher reproductive and/or survival rates in long-hydroperiod areas, and they should be slower to disperse.

This idea is related to some current theoretical ideas developed for other communities. For example, Litchman and Klausmeier (2001) developed a model based on tradeoffs in coexisting species, phytoplankton species in their case, competing under seasonally periodic light availability. One species ('opportunist') was able to grow faster under initially high levels of light, but, when phytoplankton biomass increased to the point that self-shading occurred, the advantage shifted to the other ('gleaner') species. Both species declined during the period of the year when external solar radiation was low. For certain ratios of light to dark period, coexistence was possible.

The model of Litchman and Klausmeier (2001) relies on periodic temporal variations for coexistence. Other theoretical ideas emphasize spatial movement, as in "successional mosaic" models (Armstrong 1976, Tilman 1994, Holmes and Wilson 1998). In that hypothesis, disturbances occur asynchronously across the landscape, creating new habitats ready to be recolonized. If some members of the regional species pool have traits that allow invasion of newly available gaps where they increase rapidly, while others invade slowly but are better competitors and eventually displace the pioneers, species diversity can be maintained. Areas within this dynamic landscape offer a range of successional stages at a given time, allowing niches for many different life-history traits. Other models of this class assume that all patches are continuously occupied by all the species, but differences in dispersal rates, along with differences in resource growth rates on different patches, can maintain more than one species on a given resource (Abrams and Wilson 2004, Namba and Hashimoto 2004).

Our conceptual model, which attempts to account for at least some aspects of coexistence within the South Florida wetland fish community, contains elements of the above nonequilibrium hypotheses. However, the mechanism we propose differs slightly from each of those. As in the "successional mosaic" hypothesis, fish species populations move at different rates into newly opened (flooded) habitat, with the more competitive species moving more slowly than the more opportunistic ones. But this re-colonization process does not occur in randomly and asynchronously opened habitat patches, as in gap creation in forest systems. As in the Litchman and Klausmeier (2001) model, rather than random disturbances, deterministic periodic temporal variation is assumed, here as large annual pulses during the seasonal flooding period. In addition, during the dry season, the recession of water forces all populations together into permanent or semi-permanent waterbodies, so that all species may be squeezed together for part of an annual cycle. The gradual opening of new habitat by the rising water gives the more effectively dispersing fish species a temporary advantage, during which they can build in numbers before being subjected to competition by the other invaders. When the waters recede, the opportunistic fish are subjected again to heavy competition, but if they have built up high enough numbers, the species may persist.

1.2 Model

The mechanism for small fish coexistence described above was incorporated into a detailed spatial simulation model of competing fish species described by DeAngelis et al. (2005). However, the mechanism can be transparently illustrated by a more abstract model. We first describe it conceptually and then show that it is plausible by showing model output for a particular parameterization.

Table 1.1. X_1, X_2, and X_3 represent the three species. ↑ represents increasing population size, ↓ represents decreasing population size, → represents emigration from a region, ← represent immigration to a region, and c stands for constant. There are 6 time periods denoted in the table, and 6 transitions between time periods, which may be very short.

						Period of Time During the Year						
Region	I	I→II	II	II→III	III	III→IV	IV	IV→V	V	V→VI	VI	VI→I
A	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 X_3 →	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 → X_3	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 X_3	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 X_3	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 ← X_3	X_1 c X_2 ↓ X_3 ↓	X_1 c X_2 X_3 ←
B		X_3 ←	X_2 ← X_3 ↑	X_2 ↑ X_3	X_2 X_3 ↓	X_2 ↑ X_3 →	X_2 X_3 ↓	X_2 ↑ X_3 ←	X_2 → X_3 ↓	X_3	X_3 ↑	X_3 →
C						X_3 ←	X_3 ↑	X_3 →				

The conceptual model considers three fish populations, each of which has a tradeoff in its competitive ability and ability to disperse into newly flooded areas. Instead of considering a smooth elevation gradient, we assume a step-wise gradient of three elevations. The first region, Region A, is low elevation and permanently flooded. Region B is flooded for a fraction of the year and Region C is flooded for a smaller fraction of the year. Fish Species 1 can only survive in Region A; the water is too shallow for it in Regions B and C. Both Species 2 and 3 can invade Regions B when it floods, but Species 3 can invade sooner and stay longer. When Region C, the highest elevation region is flooded, only Species 3 can invade.

The competitive dynamics are simplified in a crucial way by making competition asymmetrical. Species 1 has a negative effect on Species 2 and 3, and Species 2 has a negative effect on Species 3, but the reverse does not occur. We assume further that each population grows logistically in the absence of competition, but when in the presence of a competitively superior species, a population (e.g., Species i) is affected via Lotka-Volterra competition (i.e., $-c_{ij}X_iX_j$) by the competitively superior species j. Because the population of Species 1 does not move out of Region A and because it is assumed to suffer no negative effects of competition, it remains constant at its carrying capacity.

Imagine a yearly cycle in which water level rises and falls in a smooth, relatively deterministic manner. The dynamics of the community can be described by considering

the year divided into 12 intervals, as shown in Table 1.1. The simplifications made above allow the model to be solved analytically. The equations and parameters for a particular quantitative realization of this conceptual model are shown in the Appendix. Conceptually, the temporal sequence of dynamics through a year should be as follows.

Time period I. The water level is low, so all three fish species are confined to Region A. Species 1 is the best competitor. It is assumed to remain constant during this and all other period. The other two species are declining.

Time period I→II. This is an interval during which the water depth in Region B reaches a level that some part of the population of Species 3 can invade. (This, and all other transition intervals, is considered to be very brief in the model.)

Time period II. The population of Species 3 increases in density in Region B, following logistic growth. Both Species 2 and 3 continue to decline in Region A.

Time period II→III. With rising water level, during this brief interval part of the population of Species 2 invades Region B. The remaining populations of both Species 2 and 3 in Region A continue to decline.

Time period III. The population of Species 2 increases in Region B, and Species 3 may either grow, or decline, depending on the balance between its own growth rate and the Lotka-Volterra competition from Species 2.

Time period III→IV. Water level continues to increase, such that part of the population of Species 3 invades Region C.

Time period IV. The population of Species 3 increases in Region C according to logistic growth. The dynamics in the other regions remain the same.

Time period IV→V. The water level is now falling and is shallow enough in Region C that some of Species 3 migrates back to Region B, though some fraction of the population is stranded in Region C and dies.

Time period V. The dynamics in Regions A and B continue as before.

Time period V→VI. The water level is now falling and is shallow enough in Region B that some of Species 2 migrates back to Region A, though some fraction of the population is stranded in Region B and dies.

Time period VI. The population of Species 3 is able to increase again in Region B without competition from Species 2.

Time period VI→I. The water level is now falling and is shallow enough in Region B that some of Species 3 migrates back to Region A, though some fraction of the population is stranded in Region B and dies. The cycle now repeats.

1.3 Results

A quantitative evaluation of the model can be made using a hypothetical set of parameter values. At the beginning of the year, water level is assumed to be low and all populations are squeezed together in Region A. Populations of Species 2 and 3 decline at first in Region A (Figure 1.1a), a decline that is sharpened by a migration of parts of these populations (Species 3 first, and then Species 2) to Region B as water levels rise (Figure 1.1b). In Region B, Species 3 is first able to increase, but after Species 2 invades and starts to increase, the population of Species 3 declines. Species 3 is then able to invade Region C with further increase in water levels, where it grows logistically until falling water level causes that region to dry out (Figure 1.1c). Part of the population of Species 3 is able to migrate back to Region B, where competition with Species 2 continues. Finally, falling water levels compress both Species 2 and 3 back into Region A and the cycle begins again. This yearly cycle is stable and the system will return to it if perturbed.

This simple model illustrates the role that periodic fluctuations in the environment, in this case in water level, can play in biodiversity. Species 3 cannot exist if the amplitude of the regular flooding is decreased. If this amplitude is decreased such that the period of time that Region C is flooded decreases sufficiently from the 110 day period shown in Figure 1.1, Species 3 will disappear from the system (Figure 1.2).

1.4 Discussion

The model displays a highly simplified version of the actual dynamics of fish species along an elevation gradient subject to temporal fluctuations in water level. However, this is a first building block onto which more complexities can be added. The ability of this mechanism to operate in more realistic models has been demonstrated in a multi-species simulation model in which as many as five fish species with different competitive and dispersal abilities were able to coexist along an elevation gradient (DeAngelis et al. 2005). A surprising outcome of that model was that a species that was both a poorer competitor and had less dispersal ability than at least one other species in the model was still able to coexist. That result illustrates the emergent complexities that multiple competing species in a spatially and temporally varying environment can create. The simple model here, with highly asymmetric competition, cannot produce such complex phenomena as that. However, even the simple model of this paper demonstrates the importance of amplitude of annual fluctuations in water level. A decrease in amplitude may lead to the loss of a population that requires sufficient time in an area without competition to maintain population size.

The real Everglades ecosystem contains further complexities that must be encompassed by any model that aims at realism. One such complexity is the existence of microscale elevation heterogeneity, which leads to the existence of small permanent and temporary ponds in areas that have otherwise dried out. These can serve as
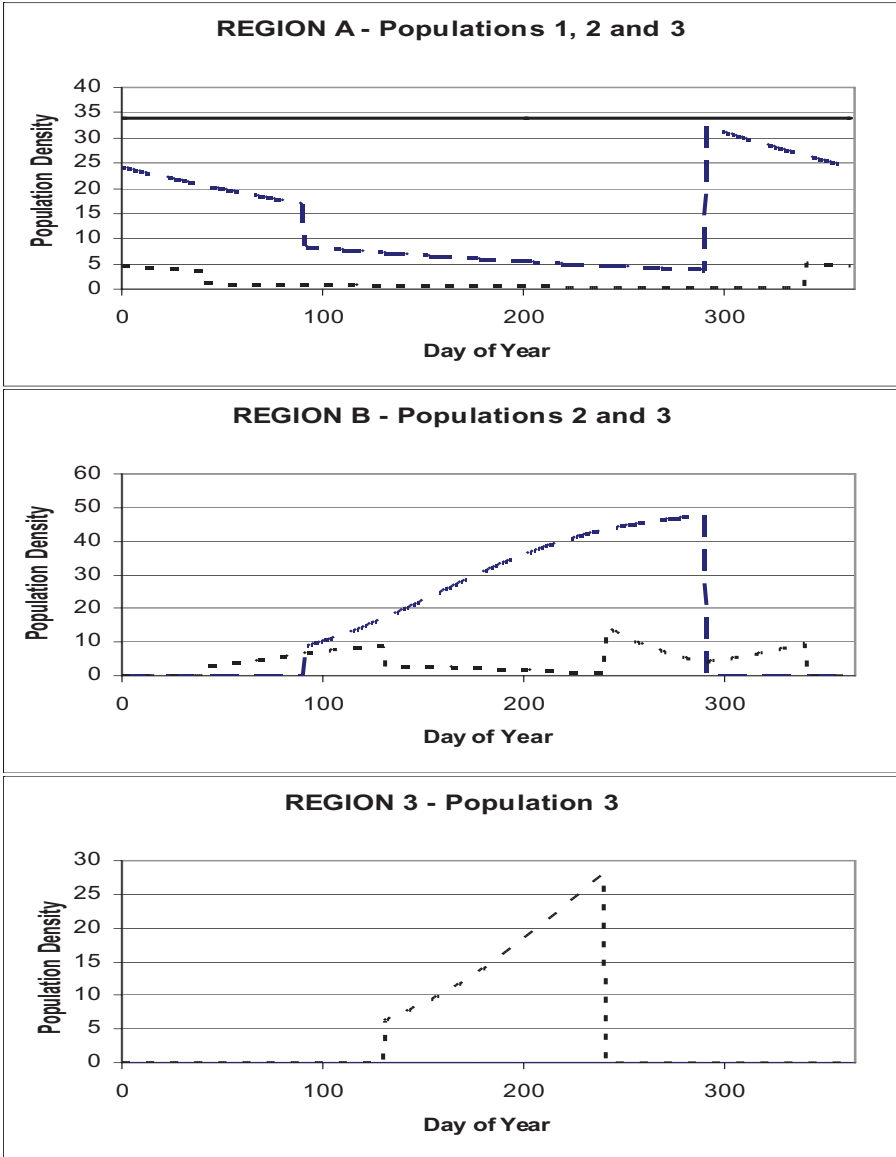
Figure 1.1 This shows the dynamics of three populations in three discrete regions of increasing elevation in a wetland, subject to regular seasonal fluctuations in water level that result in Regions B and C being flooded only part of the year. (a) Species 1 (solid line) exists on in Region A, and has a negative effect on the two other species. (b) Species 2 (dashed line) and 3 (dotted line) can migrate instantaneously to Region B when water becomes sufficiently deep. (c) Species 3 can briefly occupy the highest elevation area, Region C. The parameter values used are as follows. $T_1 = 40.$, $T_2 = 90.$, $T_3 = 130.$, $T_4 = 240.$, $T_5 = 290.$, $T_6 = 340.$, $r_2 = 0.012$, $r_3 = 0.02$, $k_2 = 50.$, $k_3 = 50.$, $c_{12} = 0.004$, $c_{13} = 0.005$, $c_{23} = 0.0002$, $f_{2wet} = 0.5$, $f_{2dry} = 0.6$, $f_{3wet} = 0.7$, $f_{3dry} = 0.5$.
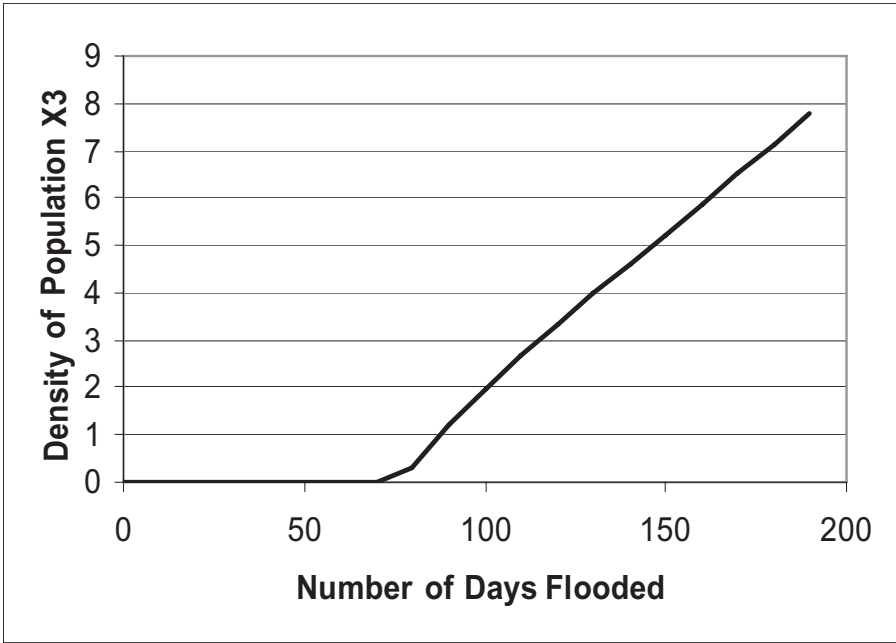
Figure 1.2 Size of the population of Species 3 in Region A at the end of the year, as a function of the length of the period that Region C is flooded.

refuges for fish, so that population recovery in a new flooded region does not have to depend on the arrival of immigrants from distant larger permanent waterbodies. Another complexity is that of the total food web. Predator-prey interactions generate oscillations, and the movement of pulses of migrating fish across the landscape creates spatially varying concentrations of periphyton, detritus, and nutrients. These dynamics are now being studied using a large, spatially explicit simulation model. This model, by using a 100×100 cell grid, also allows us to extend the analysis beyond the simple topography of the model described here, and also to more complex temporal changes in water levels, which may be highly irregular in the Everglades. These all may be expected to contribute to novel emergent qualities in the community dynamics. However, the new model still contains at its heart, though in far more elaborated form, the mechanism of species coexistence illustrated in the Appendix. As expected, it can produce results of coexistence that reflect those of the simpler model. Importantly, both the simple model and the more complex one demonstrate the importance of environmental fluctuations in maintaining species richness.

1.5 Appendix

A number of simplifying assumptions are made so that the mechanism behind coexistence of competing fish along an elevation gradient can be explained analytically. The equations for the three fish species, where the elevation gradient is divided into three regions of different elevation, are as follows.

Region A - Lowest elevation

This region is always flooded and always occupied by all three species. It is assumed that Species 1 is the dominant competitor, whose biomass density stays close to its carrying capacity, k_1. Species 2 and 3 always decline in this region due to asymmetric or one-sided competition, but are reinforced by immigration from the Region B when it dries, which prevents these populations from going to zero. The simplified equations for the three species are always

$$X_1^* = k_1$$

$$\frac{dX_2}{dt} = -c_{12}X_1^*X_2 \tag{1.1}$$

$$\frac{dX_3}{dt} = -c_{13}X_1^*X_3$$

Region B - Intermediate elevation

Both Species 2 and 3 can invade this region when it floods, though Species 3 invades first, at time T_1, and leaves at time T_6, while Species 2 invades at time T_2 and leaves at time T_5. Species 2 is competitively dominant and is always described by the equation

$$\frac{dX_2}{dt} = r_2\left(1 - \frac{X_2}{k_2}\right)X_2 \tag{1.2}$$

When Species 3 is alone, during the time intervals $T_1 < t < T_2$ and $T_5 < t < T_6$, it is described by

$$\frac{dX_3}{dt} = r_3\left(1 - \frac{X_3}{k_3}\right)X_3 \tag{1.3}$$

However, when both Species 2 and 3 are present, Species 3 is described as having the negative effect of one-sided competition from Species 2, as follows, where, for simplicity, we ignore the carrying capacity effect on Species 3:

$$
\begin{aligned}
\frac{dX_3}{dt} &= (r_3 - c_{23}X_2)X_3 \\
&= \left(r_3 - \frac{c_{23}f_{2wet}X_2^*(T_2)k_2e^{r_2(t-T_2)}}{f_{2wet}X_2^*(T_2)e^{r_2(t-T_2)} + (k_2 - f_{2wet}X_2^*(T_2))}\right)X_3 \quad (1.4)
\end{aligned}
$$

Here f_{2wet} is the fraction of population of Species 2 that migrates from Region A to Region B when it floods.

Region C - Highest elevation

Only Species 3 can invade this region, during the interval $T_3 < t < T_4$. Its growth is described by

$$\frac{dX_3}{dt} = r_3 \left(1 - \frac{X_3}{k_3}\right) X_3 \tag{1.5}$$

When these equations are integrated over each of the time intervals, with appropriate initial conditions at the start of each interval, the following mathematical expressions are obtained in each time period and region (see Table 1.1):

Time Period I $(0 < t < T_1)$

Region A:

$$X_{2A}(t) = X_{2A}(0)e^{-c_{12}X_1^* t}$$
$$X_{3A}(t) = X_{3A}(0)e^{-c_{13}X_1^* t} \tag{1.6}$$

Time Period II $(T_1 < t < T_2)$

Region A: Here f_{3wet} is the fraction of population of Species 3 that migrates to Region B from Region A when it floods.

$$X_{2A}(t) = X_{2A}(T_1)e^{-c_{12}X_1^*(t-T_1)}$$
$$X_{3A}(t) = (1 - f_{3wet})X_{3A}(T_1)e^{-c_{13}X_1^*(t-T_1)} \tag{1.7}$$

Region B:

$$X_{3B}(t) = \frac{f_{3wet}X_{3A}(T_1)k_3 e^{r_3(t-T_1)}}{f_{3wet}X_{3A}(T_1)e^{r_3(t-T_1)} + (k_3 - f_{3wet}X_{3A}(T_1))} \tag{1.8}$$

Time Period III $(T_2 < t < T_3)$

Region A:

$$X_{2A}(t) = (1 - f_{2wet})X_{2A}(T_2)e^{-c_{12}X_1^*(t-T_2)}$$
$$X_{3A}(t) = X_{3A}(T_2)e^{-c_{13}X_1^*(t-T_2)} \tag{1.9}$$

Region B:

$$X_{2B}(t) = \frac{f_{2wet}X_{2A}(T_2)k_2e^{r_2(t-T_2)}}{f_{2wet}X_{2A}(T_2)e^{r_2(t-T_2)} + (k_2 - f_{2wet}X_{2A}(T_2))}$$

$$X_{3B}(t) = X_{3b}(T_2)e^{Q_{3B}}$$

$$Q_{3B} = r_3(t - T_2) + \frac{c_{23}k_2}{r_2}\ln(R(t)/k_2) \tag{1.10}$$

$$R(t) = f_{2wet}X_{2A}(T_2)e^{r_2(t-T_2)} + (k_2 - f_{2wet}X_{2A}(T_2))$$

Time Period IV ($T_3 < t < T_4$)

Region A:

$$X_{2A}(t) = X_{2A}(T_3)e^{-c_{12}X_1^*(t-T_3)}$$

$$X_{3A}(t) = X_{3A}(T_3)e^{-c_{13}X_1^*(t-T_3)} \tag{1.11}$$

Region B: Here f_{3wet} is the fraction of population of Species 3 that migrates from Region B to Region C when it floods

$$X_{2B}(t) = \frac{X_{2B}(T_3)k_2e^{r_2(t-T_3)}}{X_{2B}(T_3)e^{r_2(t-T_3)} + (k_2 - X_{2B}(T_3))}$$

$$X_{3B}(t) = (1 - f_{3wet})X_{3B}(T_3)e^{Q_{3B}}$$

$$Q_{3B} = r_3(t - T_3) + \frac{c_{23}k_2}{r_2}\ln(R(t)/k_2) \tag{1.12}$$

$$R(t) = X_{2A}(T_3)e^{r_2(t-T_3)} + (k_2 - X_{2A}(T_3))$$

Region C:

$$X_{3C}(t) = \frac{f_{3wet}X_{3B}(T_3)k_3e^{r_3(t-T_3)}}{f_{3wet}X_{3B}(T_3)e^{r_3(t-T_3)} + (k_3 - f_{3wet}X_{3B}(T_3))} \tag{1.13}$$

Time Period V ($T_4 < t < T_5$)

Region A:

$$X_{2A}(t) = X_{2A}(T_4)e^{-c_{12}X_1^*(t-T_4)}$$

$$X_{3A}(t) = X_{3A}(T_4)e^{-c_{13}X_1^*(t-T_4)} \tag{1.14}$$

Region B: Here f_{3dry} is the fraction of population of Species 3 that migrates from

Region C to Region B when the former is too shallow.

$$X_{2B}(t) = \frac{X_{2A}(T_4)k_2e^{r_2(t-T_4)}}{X_{2B}(T_4)e^{r_2(t-T_4)} + (k_2 - X_{2B}(T_4))}$$

$$X_{3B}(t) = (X_{3B}(T_4) + f_{3dry}X_{3C}(T_4))e^{Q_{3B}}$$

$$Q_{3B} = r_3(t - T_4) + \frac{c_{23}k_2}{r_2}\ln(R(t)/k_2)$$

$$R(t) = X_{2B}(T_4)e^{r_2(t-T_4)} + (k_2 - X_{2B}(T_4))$$

(1.15)

Time Period VI ($T_5 < t < T_6$)

Region A: Here f_{2dry} is the fraction of population of Species 2 that migrates from Region B to Region A when the former is too shallow.

$$X_{2A}(t) = (X_{2A}(T_5) + f_{2dry}X_{2B}(T_5))e^{-c_{12}X_1^*(t-T_5)}$$

$$X_{3A}(t) = X_{3A}(T_5)e^{-c_{13}X_1^*(t-T_5)}$$

(1.16)

Region B:

$$X_{3B}(t) = \frac{X_{3B}(T_5)k_3e^{r_3(t-T_3)}}{X_{3B}(T_5)e^{r_3(t-T_3)} + (k_3 - X_{3B}(T_5))}$$

(1.17)

Time Period VII ($T_6 < t < 365$)

Region A: Here f_{3wet} is the fraction of population of Species 3 that migrates from Region B to Region A when the former is too shallow.

$$X_{2A}(t) = (X_{2A}(T_5)e^{-c_{12}X_1^*(t-T_6)}$$

$$X_{3A}(t) = (X_{3A}(T_5) + f_{3dry}X_{3B}(T_6))e^{-c_{13}X_1^*(t-T_5)}$$

(1.18)

Then set

$$X_2(0) = X_2(365)$$

$$X_3(0) = X_3(365)$$

(1.19)

and begin a new annual cycle.

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Spatial dynamics of multitrophic communities

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Abstract. I discuss the influence of dispersal on two multitrophic communities: intraguild predation and keystone predation. The key finding is an asymmetry between species in their dispersal effects and responses. In both intraguild predation and keystone predation, dispersal of the predator-resistant inferior competitor has a large effect, but dispersal of the predator-susceptible superior competitor has little or no effect, on coexistence and species' distributions. In the case of keystone predation, the inferior competitor's dispersal also mediates the predator's dispersal effects: predator dispersal has no effect when the inferior competitor is immobile, and a large effect when it is mobile. The direct and indirect effects of the inferior competitor's dispersal changes species' distributions from inter-specific segregation in resource-poor and resource-rich habitats to inter-specific aggregation in resource-rich habitats. The important point is that the interaction between competition and predation creates asymmetries between species that lead to unexpected effects of dispersal. These asymmetries suggest the existence of keystone dispersers, species that, through their dispersal, have disproportionately large effects on species distributions and diversity in multitrophic communities.

2.1 Introduction

The interplay between species interactions and dispersal is the key determinant of diversity in spatially structured environments (Leibold et al. 2004, 2005). A great deal is known about this interplay in communities with one or two trophic levels (e.g., resource, consumer; Levin 1974; Holt 1985; Murdoch et al. 1992; Amarasekare and Nisbet 2001; Jansen 2001; Abrams and Wilson 2004) but relatively little is known about it in communities with multiple trophic levels (e.g., resource, consumer, natural enemy).

Most theory on spatial coexistence focuses on nontrophic or pairwise trophic interactions where species cannot coexist in the absence of dispersal (e.g., competitive dominance, predator overexploitation, Allee effects induced by the absence of a mutual-

istic partner). In such situations, dispersal can allow coexistence given spatial varia-
tion in species' traits (Levin 1974; Holt 1985, 1993; Amarasekare and Nisbet 2001;
Codeco and Grover 2001; Amarasekare 2004; Leibold et al. 2004). Two aspects of
multitrophic communities suggest the need for a different framework for understand-
ing the interplay between dispersal and species interactions. First, multitrophic com-
munities are characterized by two types of interactions (trophic and nontrophic in-
teractions) that are dynamically quite different. Second, in multitrophic communities
species occupying a particular trophic level can coexist in the absence of dispersal,
but the operation of such coexistence mechanisms is variable in space and time. Thus,
local and spatial coexistence mechanisms can operate simultaneously, and their inter-
action can lead to emergent properties (Amarasekare 2006, 2007). Dispersal effects
on multitrophic communities are therefore likely to be quite different from dispersal
effects on communities with only one type of species interaction.

Two examples of multitrophic community modules illustrate these differences. In-
traguild predation (IGP) occurs when species competing for a common resource also
prey on or parasitize one another (e.g., Polis et al. 1989; Arim and Marquet 2004);
keystone predation (KP) occurs when species competing for a common resource also
share a natural enemy (e.g., Sih et al. 1985; Navarette and Menge 1996). In both
cases the two consumer species can coexist via a trade-off that allows for local niche
partitioning. In intraguild predation local niche partitioning is possible because the
inferior resource competitor can prey on or parasitize its competitor; in keystone
predation it occurs because the inferior competitor gains more of the resource by
being less susceptible to the predator. A key feature of these trade-offs is that their
expression depends on traits of species occupying other trophic levels within the
community (Amarasekare 2007, 2008). In intraguild predation it is the common re-
source; in keystone predation it is the common resource and/or natural enemy. In the
absence of dispersal or other ameliorating factors, spatial variation in resource pro-
ductivity or predator mortality can shift the advantage to one consumer species and
cause the other's exclusion. For instance, when resource productivity is low (preda-
tor mortality is high), exploitative competition dominates and the inferior resource
competitor is excluded; when resource productivity is high (predator mortality is
low), predation dominates and the species more susceptible to predation is excluded
(Holt and Polis 1997; Diehl and Feissel 2000; Noonberg and Abrams 2005). Thus,
the trade-off between competition and predation allows coexistence only at interme-
diate productivity/mortality levels. This illustrates another feature that distinguishes
multitrophic interactions. In nontrophic or pairwise trophic interactions, spatial vari-
ation in species' traits typically facilitates coexistence (Leibold et al. 2004). In mul-
titrophic interactions, spatial variation in resource or predator traits can constrain the
coexistence of intermediate consumers. Thus, diversity maintenance in multitrophic
communities depends crucially on whether dispersal by intermediate consumers can
counteract the diversity reducing effects of spatial variation that act through a shared
resource or natural enemy (Amarasekare 2007).

Here I present some theoretical insights on the spatial dynamics of multitrophic com-
munities characterized by competition and predation. These insights are based on a