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Succession, Invasion, & Coexistence: PDEs in Ecology

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Succession, Invasion, & Coexistence: PDEs in Ecology

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Abstract

We study the behavior of diffusive Lotka-Volterra systems in environments with spatially varying carrying capacities. In particular, we use numeric and analytic techniques to study two similar models for population growth, in order to determine their qualitative differences. Additionally, we investigate competition models in the presence of periodic disasters, in order to determine what factors affect competitive dominance. We found that under conditions of high spatial heterogeneity, the model for population growth was the main factor determining coexistence. Under low spatial heterogeneity, the effect of disturbance on the stronger competitor was the main factor determining coexistence.

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Chapter 1

Biological Significance

This thesis concerns the mathematical modeling of species interaction and succession. The first chapter is a short review of the biological processes that will be modeled throughout the remainder of the thesis, and is written so as to be accessible to any reader. The second chapter examines a variety of models that are used to model species interaction, succession, and the spread of invasive species. The third chapter considers two commonly used equations that model species interactions, and analyze the differences between them. The fourth chapter looks at a simulation for competing species in a temporally varying environment. The final chapter is a list of potential future research projects, growing out of this work.

1.1 Succession

Succession is the process of ecological community change. During succession, species are displaced by better competitors. These species are then either displaced by even stronger competitors, or grow to dominate a particular ecosystem. Succession is mainly studied in communities of sessile (non-mobile) organisms, namely plant communities and inter-tidal communities.

There are two basic types of succession: primary and secondary [Ricklefs and Miller, 2000]. During primary succession, all traces of previous life are lost, or were not there to begin with. The classic example of primary succession is life forming on volcanic pumice, as occurred on Mt. Saint Helens [del Moral and Jones, 2002]. Primary succession is often characterized as being more stochastic, as a result of species needing to migrate in from other areas. During secondary succession, traces of former life remain, such as in the seed bank. Classic examples of secondary succession include forest fires, clear-cutting, and other natural disasters [Ricklefs and Miller, 2000]. Any event which causes a local extinction is known

as a disturbance event.

There is a general pattern to the evolution of ecological communities during succession. Shortly after a disaster has occurred, the landscape is colonized by pioneer species [Ricklefs and Miller, 2000]. The classic example of a pioneer species in terrestrial habitats is grass. Pioneer species tend to thrive under high light conditions, and in heterogeneous landscapes. They spend most of their energy growing and reproducing rapidly (usually at least one reproductive bout per year), and as such spend very little energy on permanent structures. Because of this, they are eventually invaded and out-competed by species which do not reproduce or diffuse quickly, but put more energy into being better competitors. This process repeats itself until the landscape is in its climax state. A climax state is one which is approximately stable, as long as the environment is stable. Climax species tend to be those that are shade tolerant, live a long time, and do not reproduce until many years into their life. Because the best competitors are the slowest plants to enter a new area, it suggests that there is a trade-off between competitive ability and fast dispersal. This is likely due to the fact that forming permanent woody structures and growing to a great enough size to be a good light competitor takes time and energy, and could instead be used producing a huge number of seeds.

Currently there are three models for competitive interaction during succession [Ricklefs and Miller, 2000] [Sanchez-Velasquez, 2003]. The first is called the Facilitation Model. Under the Facilitation Model, organisms in each successional stage allow for the introduction of species in later stages. One example of this would be nitrogen-fixing plants, without whom trees would be unable to get their necessary amount of nutrients. The second model is known as the Inhibition Model. Under the inhibition model, when a species begins inhabiting an area, it prevents later species from invading, through methods such as allelopathy (the use of chemicals to alter soil, making it more difficult for other plants to grow there). A famous example of this was discovered by Sousa [Sousa, 1979], who studied succession on coastal boulders, and found that a particular algae, when it became attached to a boulder, was able to prevent any other algae from becoming attached. Often, it was not until the algae was damaged by predators that other species could grow on a boulder (for more details, see [Ricklefs and Miller, 2000]). The final model is known as the Tolerance Model. Under the Tolerance Model, timing of colonization does not affect an organism's ability to colonize (i.e., if species A colonizes an area before species B, it has the same end result as if species B colonizes an area before species A). Unless otherwise noted, species in my thesis will interact under the Tolerance Model. See Table 1.1 for a diagram of each model.

	Facilitation Model	**Inhibition Model**	**Tolerance Model**
Empty Habitat	Invasion Fails	Invasion Succeeds	Invasion Succeeds
Inhabited Habitat	Invasion Succeeds	Invasion Fails	Invasion Succeeds

Table 1.1: Three classic methods for succession. Under the Facilitation Model, early successional plants make it possible for later plants to colonize an area. Under the Inhibition Model, early successional plants prevent later plants from colonizing. Under the Tolerance Model, the timing of colonization does not affect the overall result.

1.2   Coexistence and Diversity

The process of competitive coexistence is important to the study of population interactions. According to the competitive exclusion principle, two species should not be able to coexist on shared resources. Instead, the tougher competitor should drive the other organism to extinction [Ricklefs and Miller, 2000]. However, this seems difficult to believe when one considers the vast number of plant and animal species in existence. There have been several mechanisms proposed to allow for coexistence. Perhaps the most famous mechanism is niche partitioning. Simply put, a niche is the ecological role that a species occupies [Ricklefs and Miller, 2000]. Therefore, two seemingly similar organisms can live in the same area if they are separated spatially, temporally, or if they eat different food sources.

Another theorized mechanism for coexistence is the Intermediate Disturbance Hypothesis. Originally introduced by Connell [Connel, 1978], the idea is that occasional disasters actually have the paradoxical result of increasing species diversity. Shortly after a disturbance event, an area will become dominated by pioneer species. As time goes on, more and more new species move into the disturbed area, and thus species richness increases. However, as an ecosystem approaches a climax state, weaker competitors are driven to extinction, and species richness declines. Because of this, the Intermediate Disturbance Hypothesis suggests that there exists a rate of disturbance under which species richness is maximized (see Figure 1.1). At this rate of disturbance, a large number of species will have immigrated into an area, but many will have not yet gone extinct.

There have been other proposed methods of coexistence. The Gradual Change
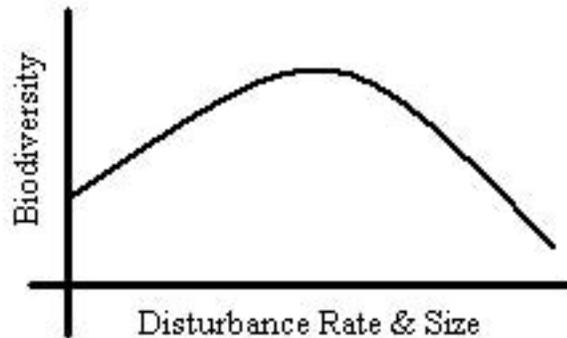
Figure 1.1: Under the Intermediate Disturbance Hypothesis, species richness is maximized when disturbance events occur at a moderate level.

hypothesis states that environments are constantly changing at a rate which is comparable to the time it would take for one species to drive the other to extinction. Under any given state, one or more species is competitively superior. However, no organism is optimal under all conditions, and as such no organism is capable of dominating [Connel, 1978]. This was originally theorized to explain why several species of plankton could coexist on the same resources in a what appeared to be a well-mixed environment [Hutchinson, 1961]. The Compensatory Mortality Hypothesis states that in certain situations, having a high population density causes an increased mortality [Connel, 1978]. This can occur if predators (or herbivores, frugivores, etc.) preferentially eat the more abundant species. This can also occur if seed mortality is the highest close to its parent, as would be the case for host-specific predators [Janzen, 1970].

1.3   Invasive Species

Invasive species are one of the most studied problems in ecology today, and for many good reasons. The invasion of exotic species has been linked to a whole host of environmental damage, including native species loss, chemical changes in the soil, and altering of geologic processes. Additionally, vast amounts of money are spent every year controlling invasive weeds [Sakai et al., 2001] [Myers and Bazely, 2003].

Currently the model for invasion involves three stages. For example, in the context of plants, the first stage is the plant's initial introduction. This happens in many ways, both accidentally or intentionally. During this first stage, the organ-

Figure 1.2: Kudzu is a well known and very problematic invasive species in the Southern United States. Image provided by Kerry Britton, USDA Forest Service, at Forestryimages.org (reprinted with permission).

ism must be able to survive and reproduce in a novel environment. The second stage is a lag period. During this stage, the population establishes itself. Some have claimed that the delay is only caused by the necessary time it takes for the population to grow, while others have claimed that it is a result of species needing to diversify genetically (often either through hybridization with native plants, or through repeated introduction). The final period of succession is the spread into neighboring communities. The methods of spreading and the ability to survive in novel environment are major factors influencing how rapidly spreading occurs. Similar dynamics have been shown for other organisms [Sakai et al., 2001].

What makes a plant capable of being invasive is currently much debated amongst biologists [Sakai et al., 2001]. Possible traits include the ability to reproduce asexually (or even both sexually and asexually), grow rapidly, mature early, and produce many seeds. Additionally, phenotypic plasticity (the ability to adapt to new environments), and high competitive ability are believed to be important. It is believed each stage of invasion selects for different traits. Traits such as these are often referred to as r-selected traits (see §2.3 for more details on r- and K-selection).

In addition to what life history traits make a species invasive, what ecological traits make an ecosystem invasible has also been studied. Many biologists have theorized that a major reason invasive species are able to do so well in novel environments is because they are freed from the specialist predators and parasitoids, and as such can put less energy into defense mechanisms. However, this claim is still debated amongst ecologists [Myers and Bazely, 2003]. The abundance of generalist predators has been shown to hinder invasion. Additionally, it has been shown that environments with an abundance of resources are often much more invasible, since there are many unused niches that an invading organism can take advantage of. Because of this, disturbance events are a major gateway for invasion [Sakai et al., 2001] [Myers and Bazely, 2003].

Chapter 2

Ecological Modeling

In any field of science, predictive models are not merely important, but vital. Indeed, physics would have progressed at a snail's pace if every physicist needed to record the way their own special stone rolled down a hill. And yet, all too often this mistake is being made by ecologists [Belovsky et al., 2004]. In particular, partial differential equations remain unknown to most experimental biologists [Holmes et al., 1994]. In this chapter we present a short survey of mathematical tools that theoretical ecologists use to model the biological events described in Chapter 1.

2.1   Gap Models

Gap models are a way of modeling species interactions using computer simulations. Among other things, they have the advantage being relatively straightforward and easy to use. In a gap model, the forest is broken into a discrete set of "gaps," each of which is filled with individual trees. Time is broken into a series of steps. Each gap is environmentally homogeneous. During each step, reproduction, growth, and death are calculated probabilistically. For the most part, Gap models neglect plant interactions between gaps [Porte and Bartelink, 2002].

The first, and likely the most famous gap model was the JABOWA model [Botkin et al., 1972]. In this model, each gap was 10x10 meters, the plot considered was 208 gaps, and each time step represented a year. Growth was logistic, and related to the amount of light available, the average annual temperature, and competition for soil nutrients. Growth was measured in dbh (diameter at breast height, a common unit of measurement for tree size), and height and leaf area were calculated from these. Trees were grouped into two categories, shade tolerant and shade intolerant, with tolerant trees being more able to grow under poor light conditions. The appearance of saplings did not depend on the current or previous

makeup of the gap. At the beginning of each year, a species was selected at random for each gap, and 0-2 saplings were generated. If total leaf area over the entire forest was below a certain level, then 60-75 cherry saplings were added. Additionally, if total leaf area was above the cutoff level for adding cherry trees, but below another cutoff, then 0-13 birch saplings were added (locations chosen randomly, though sunnier gaps were preferred). There were two functions for mortality. The first function applied to all trees, and caused them to suffer an annual death rate of $p = 1 - (1 - \epsilon)^n$, where ϵ is 4 divided by the maximal age of a tree, and n is the current age of the tree. With this, only 2% of trees would survive to adulthood. The second function applied only to trees which grew less than 0.01 dbh cm per year, and gave them a 36% chance of dying each year. The results were consistent with those for a 200 year old growth forest, and helped explain how short lived trees could survive in climax forests (e.g., by moving in to places where large trees had died).

2.2   Markov Models

Markov models are another useful tool for studying competition, succession, and ecological community makeup, especially in plant communities. In a Markov model, one calculates the likelihood that each species will be replaced by an individual of any other species. These parameters are arranged in a matrix, known as a transition matrix, which can be used to determine a) the makeup of an environment N years from now, given its current makeup, and b) the steady state population. Often, this is done in forest communities by determining what saplings are growing beneath each tree [Ricklefs and Miller, 2000].

One famous use of Markov models was done by McAuliffe (1988, cited in [Ricklefs and Miller, 2000]). In his study, McAuliffe considered a desert population of *Ambrosia dumosa* and *Larrea tridentata*. Using data on a variety of factors, and assuming a facilitation model of competition, McAuliffe estimated how often each plant would replace the other, and how often each plant would die and not be replaced (thus, leaving open space). He found the steady-state vector predicted for the transition matrix was very similar to the actual population distribution.

2.3   Ordinary Differential Equations

Perhaps the most famous model for population interaction are the Lotka-Volterra equations. Under this model, population growth for each species is modeled logistically, using the equation

$$u' = ru(1 - u/K) \tag{2.1}$$

where $u = u(t)$ is the population density of the species, r is the intrinsic growth rate (or, how fast the species can reproduce in the absence of resource limitations), and K is the carrying capacity of species (or the maximum population density an environment will allow). By studying the life history of an organism, one can estimate r, and by observing an approximately steady state population, or by experimentally determining the population growth rates under various population levels, one can estimate K (see e.g., [Neubert and Caswell, 2000], [Okubo et al., 1989], and [van der Bosch et al., 1990]). Under this model, the population grows exponentially at low values of u, and saturates as it reaches the asymptotic value of $u = K$.

Ecologists classify organisms into r-selected and K-selected organisms. An r-selected organism is one which has traits that allow it to be a better competitor at low population densities (i.e., an organism with a large value of r). Such traits include small body size, short generation time, and a high number of offspring. Invasive species are often r-selected. A K-selected organism is one which is a better competitor at high population densities. Such traits include having larger, fewer, and more competitive offspring.

The accuracy of this model has at times been questioned. Whether or not the idea of a carrying capacity is actually realized in natural settings was hotly debated by ecologists. Currently, the most common view is that carrying capacity exists, though it often varies from year to year as a result of changing factors, such as annual rainfall [Ricklefs and Miller, 2000]. Additionally, some organisms are more strongly affected by density dependance than others. Because of this, some have claimed that Lotka-Volterra models with stable carrying capacities are bad models for r-selected organisms [Pianka, 1988]. Also, many authors (see e.g., [Ei and Yanagida, 1994], [Hutson et al., 2002], [Kan-on, 1997], [Shigesada et al., 1984], [Shigesada et al., 1986], and [Sneyd and Sherratt, 1997]) have adopted the convention of substituting rK for r, yielding the equation

$$u' = ru(K - u). \tag{2.2}$$

Equations (2.1) and (2.2) are equivalent if the product rK is constant. Later, with environmental heterogeneity in mind, we will consider spatially varying coefficients $r(x)$ and $K(x)$, in which case both models are quite different. This will be expanded upon further in Chapter 3. Also, the Lotka-Volterra equations assume that the moment an organism is born, it begins breeding. This is often not the case, especially for K-selected species [Pianka, 1988]. Because of this, some have begun using age-stuctured models, which take an organism's various life-history stages into account. The final problem with this equation is that it ignores spatial dynamics, and assumes a constant carrying capacity [Pianka, 1988].

In equation (2.1), the term $(1 - u/K)$ represents the amount of resources being

used. Thus one can represent competition between two species as

$$u' = r_u u \left(1 - \frac{u + \alpha_v v}{K_u}\right) \tag{2.3}$$

$$v' = r_v v \left(1 - \frac{v + \alpha_u u}{K_v}\right) \tag{2.4}$$

where α_u and α_v represents the competition coefficient (i.e., if you introduce one organism of species u into an environment, then to species v, it is equivalent to introducing α_u organisms of species v into the environment). Since α represents the amount of shared resources an organism uses, a low value of α corresponds to a high niche separation.

There are four possible equilibrium for System (2.4), depending on the parameter values (see Figure 2.1) [Ricklefs and Miller, 2000]. If $K_v/\alpha_u < K_u$ (i.e., intraspecific competition is stronger than interspecific competition for species u) and, $K_u/\alpha_v > K_v$ (i.e., interspecific, or within-species, competition is stronger than intraspecific, or between-species, competition for species v) then the species will go to the equilibrium $(u, v) = (K_u, 0)$ so long as $u_0 > 0$ (where u_0 is the initial population density of species u). Similarly, if $K_u/\alpha_v < K_v$ and $K_v/\alpha_u > K_u$, then the populations will reach equilibrium at $(u, v) = (0, K_v)$ if $v_0 > 0$. If $K_u/\alpha_v < K_v$ and $K_v/\alpha_u < K_u$ (i.e., interspecific competition is stronger than intraspecific competition for both species), then there are two stable equilibria, $(K_u, 0)$ and $(0, K_v)$. Which species dominates depends on how strong each competitor is, and on which species has a higher initial population density. This could be used to model inhibition competition (see §1.1). Finally, if $K_u/\alpha_v > K_v$ and $K_v/\alpha_u > K_u$,(i.e., intraspecific competition is stronger than interspecific competition for both species) both species coexist at $(u, v) = (\frac{K_u}{\alpha_u \alpha_v + 1}, \frac{K_v}{\alpha_u \alpha_v + 1})$. This could indicate niche separation.

It is also of interest to consider systems of more than two competing species. For example, Shigesada et al. [Shigesada et al., 1984] modeled a system of N competing species

$$u'_i = u_i \left(\epsilon_i - \sigma_i \alpha_i u_i - \sum_{j=1 \neq i}^{N} \sigma_i \beta_j u_j\right) \tag{2.5}$$

for $i = 1...N$. Under this system, ϵ represents the intrinsic growth rate, α represents the within-species competition, β represents between-species competition, and σ represents the species resilience (or the degree to which they are capable of resisting competition). They found that this system, for a certain range of parameters, has at most two stable equilibria, and described how each could be determined. This model was used by Ohsawa et al. [Ohsawa et al., 2002] to model succession in an ecosystem with 10 species, and periodic disturbance events.
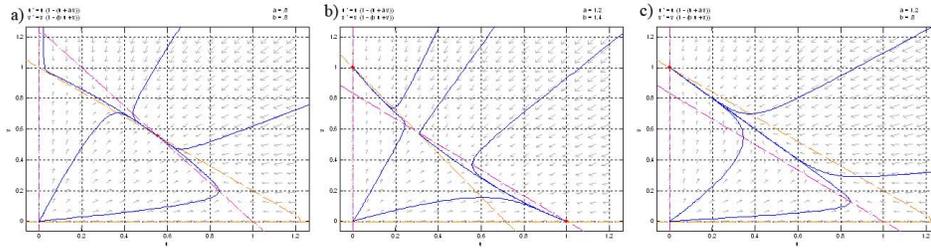
Figure 2.1: Three possible sets of equilibria are possible for the Lotka-Volterra competition model. Either species coexist (a), one species drives to the other to extinction, though which one goes extinct depends upon initial conditions (b), or one species inevitably drives the other to extinction (c).

2.4   Partial Differential Equations

Ordinary differential equations are a good first approximation for modeling species interactions. However, such a simplification ignores spatial effects, and simply averages the population densities across space. Such effects become important when an organism cannot use all of the resources in its environment, especially if there is an uneven distribution of organisms, as would be the case in succession. In order to take space into account, we must get into the realm of partial differential equations (PDEs). The most commonly used method of modeling species interaction in space are reaction-diffusion equations, such as

$$\frac{\partial u}{\partial t} = d_u \Delta u + r_v u \left(1 - \frac{u + \alpha_v v}{K_u} \right) \tag{2.6}$$

$$\frac{\partial v}{\partial t} = d_v \Delta v + r_v v \left(1 - \frac{v + \alpha_u u}{K_v} \right) \tag{2.7}$$

where d_u and d_v are the dispersion coefficients of organism u and v, respectively (e.g., how rapidly and how far each plant spreads its seeds), and Δ is the Laplace operator $\sum_{i=1}^{n} \frac{\partial^2}{\partial x_i^2}$, where the x_i represents each spatial direction in $\mathbb{R}^n$. The Laplacian is used to model random diffusion. Its main effect is to cause organisms (or whatever is diffusing) to flow down a concentration gradient.

PDEs are necessary to model species interactions in a spatially heterogeneous environment. This can be advantageous, since real environments are not homoge-

neous. The most general way of modeling m competing species is

$$\frac{\partial u_i}{\partial t} = div(d(x)\nabla u_i)_x + r(x)u_i\left(1 - \frac{u_i}{K_i(x)} - \sum_{j=0\neq i}^{m} \frac{\alpha_{ji}u_j}{K_j(x)}\right) \qquad (2.8)$$

where α_{ji} is the competitive effect species j has on species i, and $K(x)$, $r(x)$, and $d(x)$ are now spatially dependent.

   It is interesting to note that, if $K_u(x) = K_v(x)$ and $r_u(x) = r_v(x)$, then $d_u > d_v$ implies that species u will go extinct [Hastings, 1983] [Hutson et al., 2002] [Hutson et al., 2003]. The reason this occurs is because u migrates out of the good habitats much more rapidly than species v. This leads to more of u leaving population sources for population sinks, and as such, species v eventually dominates. This is interesting to note, since it implies that a greater dispersal rate is counterproductive, and thus should be selected against. This is counter to what is suggested in §1.1, since species often trade direct competitive ability for greater dispersal ability. However, when an environment is both spatially and temporally heterogeneous, this conclusion no longer applies, and greater dispersal ability may become beneficial [Ohsawa et al., 2002]. This will be covered more in Chapter 4.

2.4.1   Maximum Principle

Exact analytical solutions to PDEs are often not possible, though it is sometimes possible to determine general patterns of behavior. One general behavior that is often established is the Maximum Principle, a correlation of which is the larger of two populations of the same species (i.e., same parameter values) will always be larger. The following Theorem is from [Cantrell and Cosner, 2003], and was based on a paper by Protter and Weinberger (1967) .

   The Maximum Principle

Theorem 1. *Consider the operator $L = a\Delta u + c(x)$, where $c \leq 0$. If $\Omega \subseteq \mathbb{R}^n$ is a bounded domain and the coefficients of L are uniformly bounded on Ω, it follows that:*
(i) if $u \in C^2(\Omega)$ and $Lu \geq 0$, and if u attains some maximum $M \geq 0$ at any point in the interior of Ω then $u(x) \equiv M$ in Ω.
(ii) if $u \in C^2(\Omega) \cap C(\bar{\Omega})$, if each point on $\delta\Omega$ lies on the boundary of some ball contained in Ω, and if $u(x) = M$ at some point $x_0 \in \delta\Omega$ for which $\partial u/\partial\vec{n}$ exists, then either $\partial u/\partial\vec{n} > 0$ at all x_0 or $u(x) \equiv M$ in Ω.

   One fundamental application of this model is preserving order. To this end, consider two populations, u_1 and u_2, and suppose that $u_1, u_2 \in C^2(\Omega) \cup C(\bar{\Omega})$ are solutions to $Lu = f(x)$ in $\Omega(x)$, and that $u_1 - u_2 > 0$. If L satisfies the conditions in Theorem 1, then $u_1 - u_2 \equiv M > 0$ on Ω, and thus $u_1 - u_2 \equiv M > 0$ on $\delta\Omega$.

2.5   Traveling Waves

A traveling wave is a function of the form $f(x - ct)$. R. A. Fisher first introduced the idea of a traveling wave to mathematics as a way of modeling the flow of advantageous genes across a one dimensional environment (such as along a shoreline) [Fisher, 1937]. Physically, a traveling wave solution is one which is temporally stable, and moves with constant velocity through space (see Figure 2.2). Traveling waves can be the solutions to PDEs, and are good models of invasion. Often, traveling wave solutions of PDEs are found by looking for solutions of the form

$$u(x, t) = v(x - ct) = v(\xi), \tag{2.9}$$

where $\xi = x - ct$, x is the spatial vector, t is time, c is the speed of the wave, and v is the wave profile. This idea has since been used to model a wide variety of phenomenon, including calcium waves [Sneyd and Sherratt, 1997], spreading disease [van der Bosch et al., 1990], and species invasion [van der Bosch et al., 1990] [Holmes et al., 1994] [Okubo et al., 1989] .
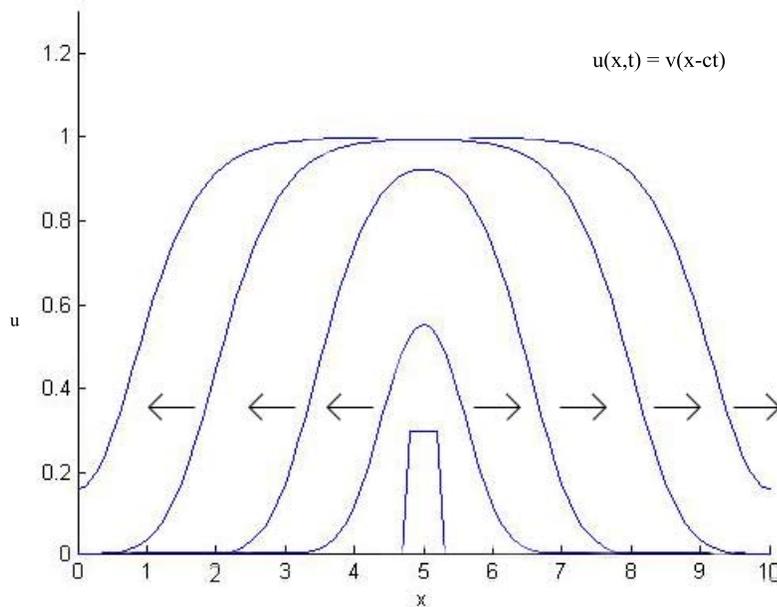

Figure 2.2: A traveling wave represents a fixed profile which moves linearly in time.

2.5.1   Logistic Traveling Waves

To demonstrate the idea of a traveling wave solution, we will begin with the Fisher Equation (which models logistic population growth in one dimension)

$$u_t = du_{xx} + ru(1 - u/K). \tag{2.10}$$

To find a traveling wave solution, we make the change of variables $u(x, t) = v(x - ct)$ to find v solves

$$-cv' = dv'' + rv(1 - v/K) \tag{2.11}$$

where $' = \frac{d}{d\xi}$. This nonlinear ODE defines the profile v and the possible speeds c. However, the value of c is not given, but rather must be determined. We do not have any initial conditions. To analyze this further we consider it as a system. If we let $a = v$ and $b = v'$, then we obtain

$$\begin{cases} a' = b \\ b' = -\frac{c}{d}b - \frac{r}{d}a(1 - a/K). \end{cases} \tag{2.12}$$

This system has two equilibrium points, $(a_1^*, b_1^*) = (0, 0)$ and $(a_2^*, b_2^*) = (0, K)$. Linearizing around each point, we find that the eigenvalues at (0,0) are $\frac{-c \pm \sqrt{c^2 - 4dr}}{2d}$, and the eigenvalues at $(0, K)$ are $\frac{-c \pm \sqrt{c^2 + 4dr}}{2d}$. To preserve nonnegativity of solutions, we require both equations to no have complex roots. Thus, $c^2 - 4dr > 0$ or $|c| > 2\sqrt{dr}$. It has been proven that a heteroclinic orbit (i. e., one which connects two disjoint equilibrium points with a single path, see Figure 2.3) must exist for systems of equations of this form [Hadeler and Rothe, 1975], and thus we know any solution beginning at one equilibrium will asymptotically reach the other. It can be shown for each c that this equation generates two waves, one when $c \geq 2\sqrt{dr}$, in which (0,0) is a stable and (0,K) is a saddle point, and another when $c \leq 2\sqrt{dr}$, in which case (0,0) is an unstable equilibrium and (0,K) is a saddle point. Thus, (2.10) exhibits traveling wave behavior.

In fact, it has been proven that a traveling wave solution exists for a general growth equation $u_t = d\Delta u + f(u)$ [Hadeler and Rothe, 1975]. This equation makes several simple assumptions, which hold for most population growth equations not including the Allee effect, in which per capita growth is negative below a certain population density. Under these conditions, the minimum wave speed is $c = 2\sqrt{df'(0)}$.

2.5.2   Periodic Traveling Waves

The idea that an environment is completely homogeneous, while mathematically very nice, is not very realistic. In addition to roads and other human-caused heterogeneity, soil contents, light, and water vary across a landscape. However, we
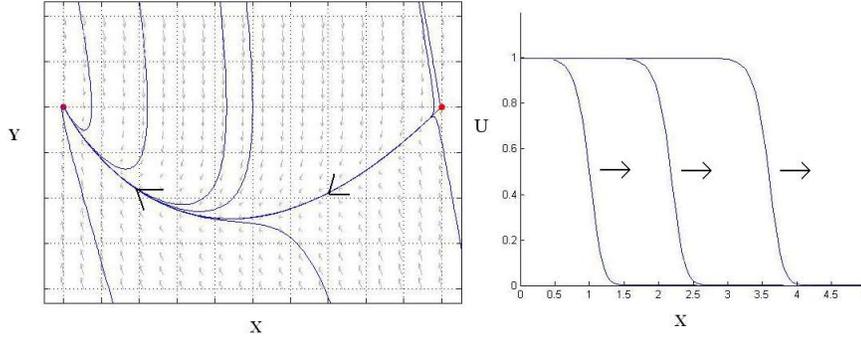
Figure 2.3: A heteroclinic orbit, such as the blue line pictured above, connects two equilibria. All other orbits asymptotically approach the hetorclinic orbit.

see that in Equation (2.12), $a(\xi) = K(x)$ can only occur when K is a constant function, and as such traveling waves of the classic form do not exist in heterogeneous environments. Because of this, it would be very useful to have a definition for a traveling wave which could exist in a heterogeneous environment. Shigesada et al. [Shigesada et al., 1986] defined the idea of a traveling periodic wave as a solution $u(x,t)$ for which there exists a length L^* and a time t^* such that

$$u(x,t) = u(x + L^*, t + t^*). \tag{2.13}$$

In their paper, the authors described a model for an invading species in a periodically constant environment. Population growth and movement are modeled as

$$u(x,t) = (d(x)u_x)_x + u(K(x) - u) \tag{2.14}$$

where

$$d(x) = \begin{cases} d_1 & x \bmod L^* < l \\ d_2 & x \bmod L^* > l \end{cases} \qquad K(x) = \begin{cases} K_1 & x \bmod L^* < l \\ K_2 & x \bmod L^* > l \end{cases} \tag{2.15}$$

for some distances l such that $0 < l \leq L^*$. A graphical representation of this environment is displayed in Figure 2.4. Note that when $l = L^*$, this equation reduces to (3.2). Shegisada et al. found that, under these conditions, a periodic traveling wave did in fact exist, and it moved at a speed

$$c = 2\sqrt{<d>_h <K>_a} \tag{2.16}$$

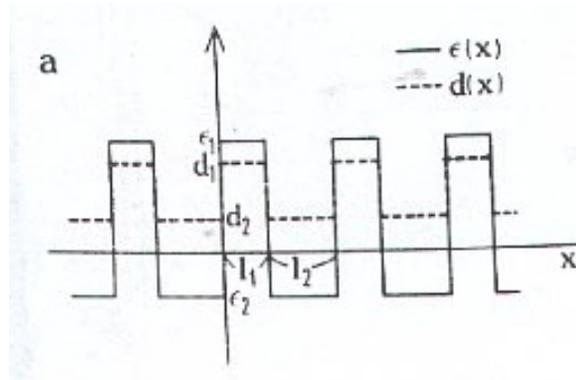where $<>_h$ is the harmonic mean and $<>_a$ is the arithmetic mean.

Figure 2.4: In order to model an organism invading a heterogeneous environment, [Shigesada et al., 1986] designed an environment in which the diffusion rate d and the growth and carrying capacity ϵ vary between two constant values. Reprinted from Theoretical Population Biology, 30, Nanako Shigesada, Kohkichi Kawasaki, and Ei Teramoto, Traveling periodic waves in heterogeneous environments, 97–113, 1984, with permission from Elsevier.

More generally, Berestycki et al. [Berestycki et al., 2005] considered equations of the form

$$u_t = div(d(x)\nabla u) + f(x, u) \qquad (2.17)$$

where $f_u(x, 0) = \mu(x) + Bv(x)$ and μ, v are periodic. They proved that a traveling wave exists as long as **(a)** $f_u(x, u)/u < 0$ (i.e., per capita growth is decreasing), **(b)** there exists K such that $u > K$ implies $f(x, u) < 0$ (i.e., a carrying capacity exists), and **(c)** either max $v > 0$ and B are large enough, or $\int \mu \geq 0$, $\int v \geq 0$ and max $v > 0$. Again, these assumptions do not consider the Allee effect. Additionally, in [Berestycki et al., 2005] they showed adding heterogeneity actually increased the speed of a traveling wave.

2.5.3   Competitive Traveling Waves

All of the models so far consider a species invading a new area, without interacting with local inhabitants. In reality, this is often not the case, and invasive species do have a major impact on native flora and fauna. This can then be described by the introduction of a small number of species v into an area in which species u is uniformly at carrying capacity. Many authors have considered this (see e.g., [Al-Omari and Gourley, 2003], [Ei and Yanagida, 1994], [Fei and Carr, 2003], [Kan-on, 1997], [Kan-on, 1998]). In such a model, the traveling wave moves with

both populations (u as it goes from K to either 0 or its new equilibrium, and v as it goes from 0 to its new equilibrium). Kan-on [Kan-on, 1998] proved that a traveling wave existed to any general competition equation, so long as a maximal carrying capacity exists, and the per-capita growth rate is decreasing. Fei and Carr [Fei and Carr, 2003] found that, under the system

$$u_t \;=\; u_{xx} + u(1 - u - \alpha_1 v) \tag{2.18}$$
$$v_t \;=\; v_{xx} + v(1 - \alpha_2 u - v) \tag{2.19}$$

the speed of a traveling wave was $c \geq 2\sqrt{r(\alpha_2 - 1)}$, as long as $1 - \alpha_1 \leq r(\alpha_2 - 1) < 1$ and $0 < \alpha_1 < 1 < \alpha_2$.

In the next chapter, we consider populations modeled in a one dimensional environment. We analyze the effect that environmental heterogeneity and the parameters r and d have on populations modeled with Equation (2.1) and (2.2).

Chapter 3

Single Species Growth Models

As discussed in §2.4, the equations

$$u_t = du_{xx} + ru(1 - u/K(x)) \tag{3.1}$$

and

$$u_t = du_{xx} + ru(K(x) - u) \tag{3.2}$$

are equivalent when carrying capacities are constant. However, if $K = K(x)$, with $K'(x) \not\equiv 0$, there is a difference. Because r is a constant, and $K(x)$ is not, we can no longer simply rescale r in terms of K. Under Equation (3.1), population growth is an intrinsic trait of a species, and thus for small u, $u_t \approx ru$, regardless of the carrying capacity of the environment. Under Equation (3.2), population growth is directly proportional to environmental quality, and thus for small u, $u_t \approx ruK$.

When a species is diffusing in a heterogeneous environment, the equations predict different asymptotic average population levels. In this section, we analyze the differences using numerical and analytic means, and discuss physical implications of these results.

3.1   Analytical Results

In this section we develop several results for (3.1) and (3.2). In what follows we consider populations on a habitat $[0, L] \subseteq \mathbb{R}$. Throughout this section we assume homogeneous Neumann boundary conditions $u_x(0) = u_x(L) = 0$. We assume that $u > 0$ and $K(x) > 0$ for all $x \in [0, L]$. Let $U^* = \lim\limits_{t \to \infty} \int_0^L u(x, t)dx$ denote the total asymptotic population. We are interested in the dynamics of U^* as r and d are varied.

Proposition 1. *Assume $u^* \in C^2[0, L]$ is a positive equilibrium solution of (3.1) or (3.2). We further assume that there exists an $\epsilon > 0$ such that $u^* > \epsilon$ for all $x \in [0, L]$, for all r and d sufficiently large. As the ratio $r/d \to \infty$, the total equilibrium population $U^* \to \int_0^L K(x)$ for both (3.1) and (3.2).*

Proof. We will first consider Equation (3.2). We want to show $\int_0^L u^*(x)dx \to \int_0^L K(x)dx$ as $r/d \to \infty$, where u^* is the equilibrium solution defined by

$$0 = du^*_{xx} + ru^*(K(x) - u^*). \tag{3.3}$$

Equivalently, u^* solves

$$u^*(K(x) - u^*) = \frac{d}{r}u^*_{xx} \tag{3.4}$$

for $x \in [0, L]$. Since $u^* \in C^2[0, L]$, there exists $M > 0$ such that $\|u^*_{xx}\| < M$, then $\|u^*_{xx}\|_\infty < M$, then

$$|u^*(K(x) - u^*)| = \frac{d}{r}|u^*_{xx}| \le \frac{d}{r}M \qquad \text{for all } x \in [0, L]. \tag{3.5}$$

Therefore, as $d/r \to 0$ (which corresponds to $r/d \to \infty$), it follows

$$|u^*(K(x) - u^*)| \to 0 \qquad \text{for all } x \in [0, L]. \tag{3.6}$$

Thus, either $u^* \to 0$, or $u^* \to K(x)$. Since $u^*(x) > \epsilon$ for all x, it follows that $u^*(x) \to K(x)$ for all $x \in [0, L]$. Therefore, $U^* = \int_0^L u^*(x)dx \to \int_0^L K(x)dx$. The proof that this proposition holds for Equation (3.1) is similar.

$\square$

Lemma 1. *Under Neumann boundary conditions, $0 = \int_0^L f(u^*)dx$, where f is population growth term in Equation (3.1) or (3.2), and u^* is its equilibrium solution.*

Proof. Consider the equation

$$u_t = du_{xx} + f(u). \tag{3.7}$$

At equilibrium, the solution to this equation is

$$0 = du^*_{xx} + f(u^*). \tag{3.8}$$

By integrating, we find that

$$0 = d \int_0^L u_{xx}^* dx + \int_0^L f(u^*) dx. \tag{3.9}$$

However, because of Neumann boundary conditions, $u_x^*(0) = u_x^*(L) = 0$. Thus,

$$0 = \int_0^L f(u^*) dx. \tag{3.10}$$

$\square$

Proposition 2. *Assume that u^* and $K(x)$ are C^2 in $[0, L]$ for all $r, d > 0$. As $r/d \to 0$, $U^* \to \frac{1}{L} \int_0^L K(x) dx$, the average of $K(x)$.*

Proof. We want to show $\int_0^L u^*(x) dx \to \int_0^L K(x) dx$ as $r/d \to 0$, where u^* is the equilibrium solution defined by

$$0 = du_{xx}^* + ru^*(K(x) - u^*). \tag{3.11}$$

Equivalently, u^* solves

$$u^*(K(x) - u^*) = \frac{d}{r} u_{xx}^* \tag{3.12}$$

for $x \in [0, L]$. By the triangle inequality,

$$|u^*(K(x) - u^*)| = |u^*||K(x) - u^*| \le |u^*|(|K(x)| + |u^*|). \tag{3.13}$$

Because $u^*(x)$ and $K(x)$ are C^2, $\exists M$ such that $\|u^*(x)\|_\infty < M$ and $\|K(x)\|_\infty < M$. We see that

$$|u^*(K(x) - u^*)| \le \|u^*\|_\infty(\|K(x)\|_\infty + \|u^*\|_\infty) < 2M^2. \tag{3.14}$$

Therefore, as $r/d \to 0$, we find

$$|u_{xx}^*| < \frac{r}{d} 2M^2, \tag{3.15}$$

and thus $u_{xx}^* \to 0$ for all $x \in [0, L]$. This means that as $r/d \to 0$, $u^*(x) \to Ax + B$, for some $A, B \in \mathbb{R}$. However, by Neumann boundary conditions, $A = 0$. thus

$$u^*(x) \to B > 0 \qquad \text{for all } x \in [0, L]. \tag{3.16}$$

Hence, we see that

$$U^* = \int_0^L u^*(x) \to BL \qquad (3.17)$$

By Lemma 1,

$$0 = \int_0^L u^*(K(x) - u^*)dx. \qquad (3.18)$$

As $r/d \to 0$, this equation converges to

$$0 = \int_0^L u^*(K(x) - u^*)dx \to \int_0^L K(x)dx - \int_0^L Bdx. \qquad (3.19)$$

Therefore, $B = \frac{1}{L}\int_0^L K(x)dx$, and so $U^* \to \frac{1}{L}\int_0^L K(x)dx$.

$\square$

Proposition 3. *Assume that u^* and $K(x)$ are C^2 in $[0, L]$. As $r/d \to 0$, $U^* \to \frac{1}{L}\int_0^L K(x)dx$, the harmonic mean of $K(x)$.*

Proof. We want to show $\int_0^L u^*(x)dx \to \frac{1}{L}\left(\int_0^L K(x)^1 dx\right)^{-1}$ as $r/d \to 0$, where u^* is the equilibrium solution. By the triangle inequality,

$$|u^*(1 - \frac{u^*}{K(x)})| = |u^* - 1 - \frac{u^{*2}}{K(x)}| \le |u^*| + |\frac{u^{*2}}{K(x)}|. \qquad (3.20)$$

Because $u^*(x)$ and $K(x)$ are C^2, and $K(x) > 0$, $\exists M$ such that $\|u^*(x)\|_\infty < M$ and $\|1/K(x)\|_\infty < M$. We see that

$$|u^*(1 - \frac{u^*}{K(x)})| \le \|u^*\|_\infty + \frac{\|u^{*2}\|_\infty}{\|K(x)\|_\infty} \le M + M^3. \qquad (3.21)$$

Therefore, by similar

$$|u^*_{xx}| < \frac{r}{d}(M + M^3), \qquad (3.22)$$

and thus $u^*_{xx} \to 0$ for all $x \in [0, L]$. By an argument similar to the one in Proposition (2), for some $B \in \mathbb{R}$,

$$u^*(x) \to B > 0 \qquad \text{for all } x \in [0, L]. \qquad (3.23)$$

Hence, we see that

$$U^* = \int_0^L u^*(x) \to BL \qquad (3.24)$$

By Lemma 1,

$$0 = \int_0^L u^*(1 - \frac{u^*}{K(x)})dx. \qquad (3.25)$$

As $r/d \to 0$, this equation converges to

$$0 \to \int_0^L B(1 - \frac{B}{K(x)})dx. \qquad (3.26)$$

By simple algebra, this becomes

$$B \to \left(\int_0^L \frac{1}{K(x)} dx \right)^{-1}. \qquad (3.27)$$

And thus, $U^* \to L \int_0^L K(x)dx$.

$\square$

One other difference that is worth noting is the change in traveling wave behavior. As stated in §2.5.2, Shigesada et al. [Shigesada et al., 1986] found that in equation (3.2), periodic traveling waves move at a minimum speed of

$$c = 2 \sqrt{dr\frac{1}{L} \int_0^L K(x) \, dx} \qquad (3.28)$$

In Equation (3.1), we find that $f'(0) = r$. Therefore, by Hadeler and Rothe [Hadeler and Rothe, 1975], the minimum speed of a traveling wave for this equation is $c = 2\sqrt{rd}$. This is interesting, because it means that traveling waves will travel at a constant speed in Equation (3.1), regardless of environmental heterogeneity. However, the average traveling wave speed will be the same in both equations.

3.2 Numerical Results

To find the equilibrium solutions of Equation (3.1), we solved the equation using numerics. To find the equilibrium, we simulated two populations, one of which began at $0.75K(x)$, and the other of which began at $1.50K(x)$. By the Maximum Principle (see §2.4.1), the later population will always be greater than the former. Since one population begins below the carrying capacity, and the other begins above it, they should converge to u^*. When both populations were within 0.001 of each other, we averaged them, and used this to approximate U^*. The numerical simulator used a Crank-Nicholson scheme. Population growth was calculated both before and after diffusion, and the average population growth was added to post-diffusion population levels.

To measure the effect of changing environmental heterogeneity, we started with three carrying capacity functions $K(x)$, which are shown in Figure 3.1. Each was constrained so that $\int_0^1 K(x)\, dx = 1$. Additionally, each carrying capacity could have its heterogeneity level rescaled, as can be seen in Figure 3.2. The rescaling of $K(x)$ did not change the average carrying capacity.

After several simulations with many different parameters, we found that all simulations gave solutions essentially similar to those in Figure 3.3. As heterogeneity increased in Equation (3.1), U^* decreased. When environmental heterogeneity increased in (3.2), U^* increased. The results had the same shape for all carrying capacities, but were the most extreme in the step function carrying capacity (the top carrying capacity displayed in Figure 3.1). We believe this is because this function had the steepest changes in carrying capacity.

This makes sense mathematically because of the behavior of growth rates in environments with changing carrying capacities. Under each equation, populations grow at different rates above and below their carrying capacities. In Equation (3.1), when u is, say, ϵ less than K_1, the growth rate is $f'(x) = (\epsilon - \frac{\epsilon^2}{K_1})$. On the other hand, when u is ϵ greater than K_2, population growth rate $f'(x) = -(\epsilon + \frac{\epsilon^2}{K_2})$. Because of the nature of diffusion, organisms tend to be below carrying capacity in good environments, and above carrying capacity in bad environments. Therefore, because $K_1 > K_2$, the negative growth rate above a low carrying capacity will be greater than the positive growth rate below a high carrying capacity. On the other hand, in Equation (3.2), when u is ϵ below a high carrying capacity K_1, the growth rate is $f'(x) = (K_1\epsilon - \epsilon^2)$. When u is ϵ above a low carrying capacity K_2, the growth rate is $f'(x) = -(K_2\epsilon + \epsilon^2)$. Therefore, the positive growth rate below a high carrying capacity is more than enough to counterbalance the decline of a population near a low carrying capacity.
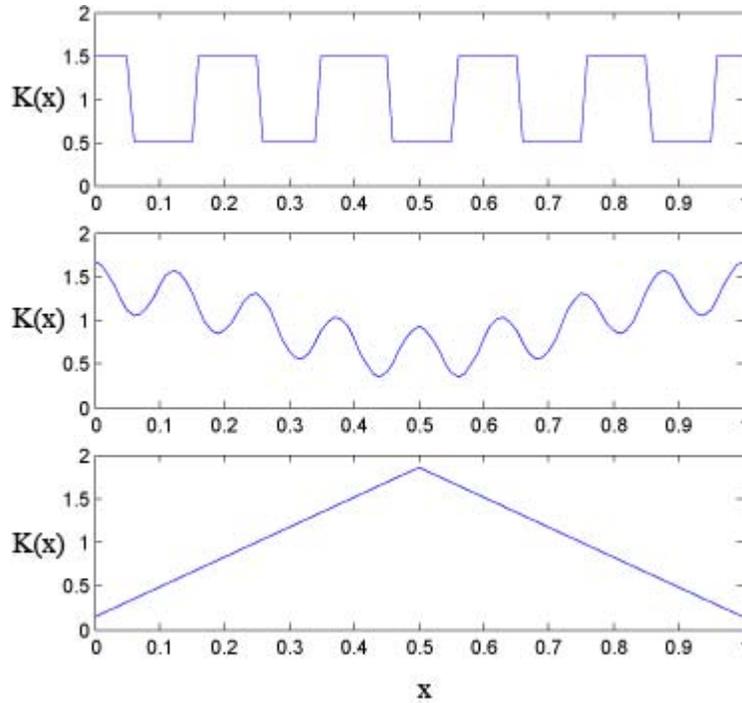
Figure 3.1: To test the effect of changing the environmental heterogeneity, we considered three different carrying capacities. For each model we maintain $\int_0^1 K(x)dx = 1$.

We ran simulations where we varied the parameter r/d, and found solutions similar to those in Figure 3.4. We found that only the ratio r/d mattered, instead of the actual values of r or d. The results are consistent to those proved in § 3.1. As $r/d \to \infty$, $U^* \to 1$ in either equation. As $r/d \to 0$, $U^* \to L\left(\int K(x)^{-1}\right)^{-1}$ when using (3.1), and $U^* \to 1$ when using (3.2). In equation (3.1), as r/d increases, U^* asymptotically grows towards 1. In (3.2), as r/d increases, U^* increases to a maximum, and then decreases toward $U^* = 1$. It would be interesting to determine what the maximal value of U^* is and where it occurs.
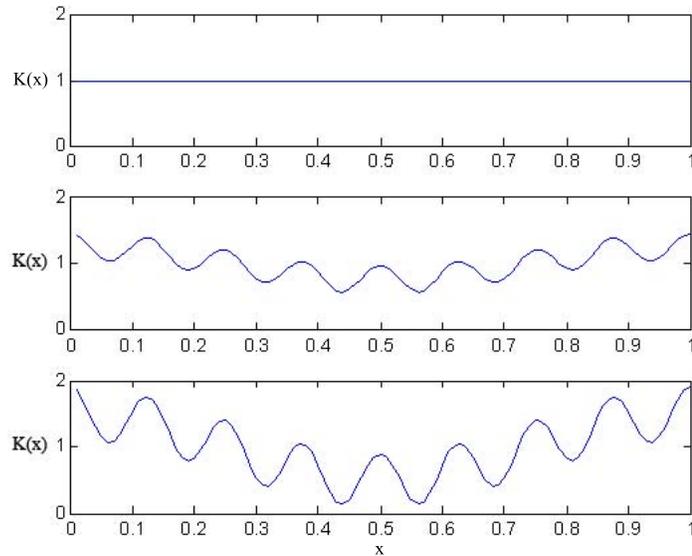
Figure 3.2: The heterogeneity level of each $K(x)$ could be altered, to represent the same environment becoming more heterogeneous. At minimal heterogeneity, $K(x) \equiv 1$. At maximal heterogeneity, $\max K(x) \approx 2, \min K(x) \approx 0$.

3.3   Implications

There are two major implications we can gain from the differences between these models. The first has to do with habitat protection and restoration. If we believe that Equation (3.1) more accurately predicts population growth, then our predictions suggest protection and restoration projects should focus on keeping a healthy environment everywhere. On the other hand, if we choose to work with the assumptions in Equation (3.2) , it predicts that it is better to spend our money to conserve the best habitats, even if this leads to a patchy environment. The other implication has to do with species invasion. If we use Equation (3.1), we would predict there is no way to indirectly slow an invading species. If we use Equation (3.2), our results would suggest an invader can be slowed by weakening the habitat around it.
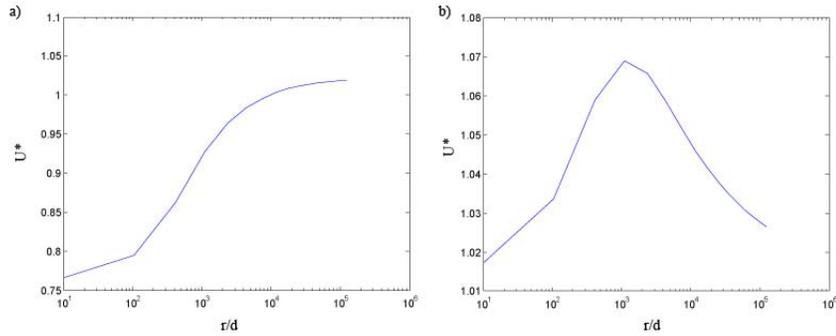
Figure 3.3: To test the effect population growth and diffusion rates had on U^*, we ran several simulations. All simulations gave similar results to those seen here. Part (a) represents populations governed by Equation (3.1), and (b) represents populations governed by (3.2).

Figure 3.4: To test the effect population growth and diffusion rates had on U^*, we ran several simulations. All simulations gave similar results to those seen here. Part (a) represents populations governed by Equation (3.1), and (b) represents populations governed by (3.2).
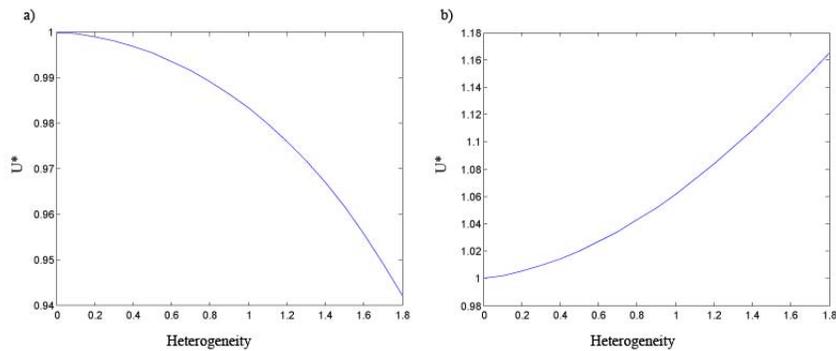
Chapter 4

The Successional Competition Model

In §2.3, we saw that generation time has no effect on competitive ability, and in §2.4, we saw that all things being equal, if an environment is spatially variant but temporally stable, the faster diffusing species goes extinct. These claims are rather disturbing, because they are not what is seen in nature. Indeed, if taken to their logical conclusions, it would indicate that grass should be long extinct. Because this is not the case, it indicates that temporal interactions must have an effect on population dynamics. A full exploration of every factor that could affect population levels was far beyond the scope of this paper, so instead we chose to consider disturbances. In [Ohsawa et al., 2002], they built a 10 species diffusive competition model, and showed that the existence of periodic disturbances could affect which species coexist. However, this model mainly addressed the question of who would coexist, and not how species parameters or environmental heterogeneity affected coexistence. Here we consider a one-dimensional model of species coexistence, in a spatially heterogeneous environment with periodic disturbance events.

4.1   Model Design

To gain a better qualitative understanding of how competition models operate in a changing environment, we designed a simulation which tracked the population levels of two competing species in an environment peppered by disturbance events. To simulate a disturbance event, the environment was broken into 10 sections of equal length. Periodically, a set number of sections were randomly selected, and population levels within that section were reduced to 0. After a set period of time, population levels were analyzed to determine which species was dominant, or if both

species had coexisted. Because of the random nature of the disturbance events, all trials were run 5 times. We ran each simulation under a wide range of disturbance sizes, in order to determine what disturbance regimes allowed for coexistence.

4.1.1   Competition Equation

We consider a successional model for both Equations (3.1) and (3.2). Until we have a better understanding of which model better represents reality, we should analyze both. This has the benefit that any qualitative differences can be compared, to determine which is most like reality. We assume a tolerance model of competition under most situations.

4.1.2   Species Viability and Coexistence

Population levels $U^* = \frac{1}{L} \int_0^L u(x,t)\, dx$ were assessed before disturbance events occurred. If $U^* < 0.01$ during five consecutive samplings, the simulation was halted, and that population was considered non-viable. If this did not occur, values of U^* were averaged over the latter half of data points. If this average was less than 0.025, the population was considered non-viable. If the average was above 0.025, but less than 0.1, then the population was considered possibly non-viable. Finally, it was possible that a population was in decline, and eventually would go extinct, but would show that $U^* > 0.025$. For example, it has been analytically proven when $\alpha_u = \alpha_v = 1$, $d_u > d_v$, and there are no disturbances, u will go extinct [Hastings, 1983], [Hutson et al., 2002], [Hutson et al., 2003]. However, in some cases this happens so slowly that $U^* > 0.3$ during the entire simulation, as can be seen in Figure 4.1. To account for this, we attempted to determine if the population was monotonically (or almost monotonically) in decline. Simply, if we define $U^*(t)$ as the value of U^* at time step t, then we say that u was in decline if $U^*(t) + 0.05 > U^*(t+1)$ for all $t \geq 0$. The 0.05 was used, because several populations, such as the one pictured in Figure 4.2 were not declining monotonically, but were clearly in decline. However, this is not enough, since it predicts that v will go extinct in Figure 4.1. Therefore, we also ran a simple regression, to make sure that a population was actually declining. This definition was also slightly problematic, since in some situations a population would be almost level, but still register as decreasing, such as was the case in Figure 4.3. To correct this problem, we stated that a population could only be monotonically decreasing if $U^* \leq 0.4$ at the end of the simulation.

After each simulation, the population was assigned a viability score S. If a population was completely viable, we assume $S = 1$. If it was non-viable, we
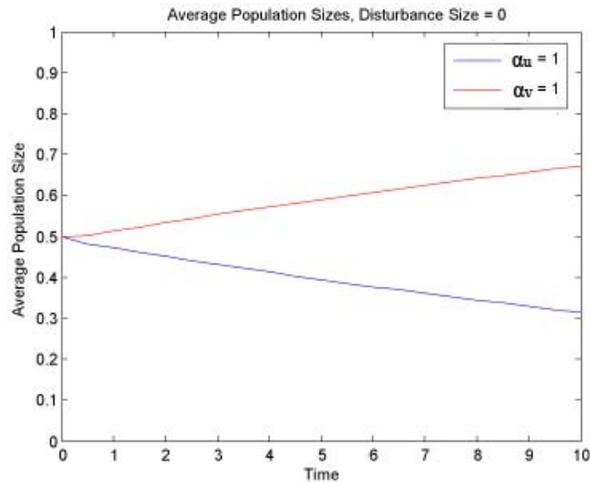
Figure 4.1: The graph above shows the average population levels over time of two competing species. In this simulation, $\alpha_u = \alpha_v = 1$, $d_u > d_v$, and there are no environmental disturbances. This will eventually lead to species u being wiped out.

assigned $S = 0$. If it was possibly non-viable, we assigned it $S = 0.5$. These values were averaged over the 5 trials, and at the end we determined the likely viability of the species by looking at this average. For example, if a population was non-viable in 2 trials, possibly non-viable in 2 trials, and viable in 1 trial, it would receive an average score of $S = 0.4$.

Coexistence was defined as mutual survival (see §4.1.2 for details on quantifying survival). We determined the exact coexistence value by multiplying the viability scores of both species together.

4.1.3   Parameter Values

In each simulation, $\alpha_u + \alpha_v = 2$ [Okubo et al., 1989]. To study how differences in diffusion rate affected competitive edge, we ran simulations in which $r_u = r_v = 10$, and $K(x) = 1 + 0.25\cos(2\pi x) + 0.2\cos(16\pi x)$ (the middle carrying capacity function in Figure 3.1). We also considered how population growth rate affected competitive edge. To examine this, we ran simulations in which $d_u = d_v = 0.05$ or $d_u = d_v = 0.005$, and used the same carrying capacity stated above. We also ran several simulations in which $r_u = r_v = 10$, $d_1 = 0.1, d_2 = 0.01$, and K varied. We ran simulations under each form of carrying capacity, in Figure 3.1, and at varying
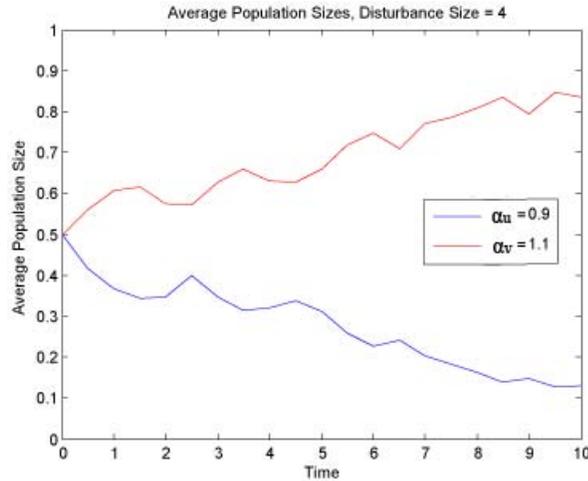
Figure 4.2: The graph above shows the average population levels over time of two competing species. In this simulation, $\alpha_u = 0.9, \alpha_v = 1.1, 10d_u = d_v$, and there is a moderate disturbance rate. We have shown that this will eventually lead to species u being wiped out.

degrees of heterogeneity, including no heterogeneity.

4.1.4   Numerical Scheme

We used a Crank-Nicholson finite-differences scheme to model diffusion. To model species growth, we calculated the amount our species would grow both before and after diffusing, and averaged that. This sum was added to our population after it diffused. We used values $dx = 0.01$ and $dt = 0.001$.

4.1.5   Time Saving Algorithm

Due to time constraints, we did not run every simulation on most trials, but rather ran a more efficient algorithm. If we denote $S_i(a, d)$ the viability of species i with $a = \alpha_i$ and $D = $ disturbance rate, we assumed

a) $S_u(\alpha, D_x) = 0$ and $D_y < D_x$, imply $S_u(\alpha, D_y) = 0$, and

b) $S_v(\alpha, D_x) = 0$ and $D_y > D_x$, imply $S_v(\alpha, D_y) = 0$.

These statements were consistently satisfied in numerical tests, in which all points were examined. They also make intuitive sense. If a certain level of disturbance is so extreme that it causes a species to be wiped out, one would not expect them to
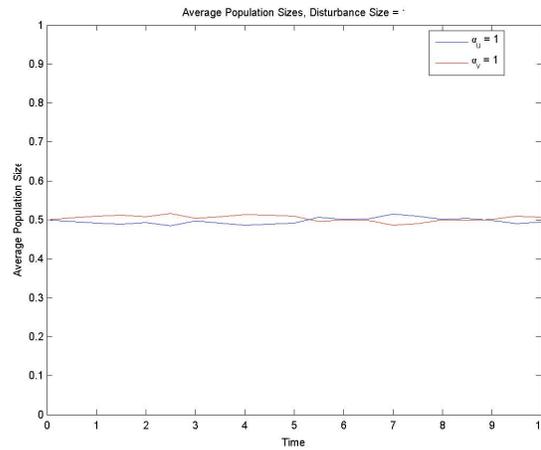
Figure 4.3: The graph above shows the average population levels over time of two competing species. In this simulation, $\alpha_u = \alpha_v = 1$, $d_u > d_v$, and environmental disturbances are small. A regression fit of u gives a negative slope. For this reason, we further insist the average population must be below 0.4 by the end of the simulation.

survive at a more extreme level of disturbances.

We took advantage of this fact to produce an algorithm which attempted to only check values where $S_u S_v > 0$. Simply, a particular disturbance level D was chosen. Tests were run on every level of disturbance below D until $S_u = 0$. Then, tests were run on every level of disturbance above D until $S_v = 0$ was found. In early trials, this method reduced the number of calculations by an average of 40%.

4.2 Results

To determine which environments allowed for coexistence, we multiplied $C = S_u S_v$ for every simulation with the same parameters. If $C = 0$, then coexistence did not occur in any trial. If $C = 1$, then coexistence occurred in every trial. If $0 < C < 1$, coexistence occurred in some trials. We graphed C as values of α and D changed, to determine how easily coexistence could occur in that environment (see graphs below for an example). If a particular α and D gave $C = 1$, this point was marked with either a blue dot. If those values gave $0 < C < 1$, we marked that point with a red dot. If $C = 0$, we marked that point with a black x.

In most cases, we found that it made very little difference whether we used
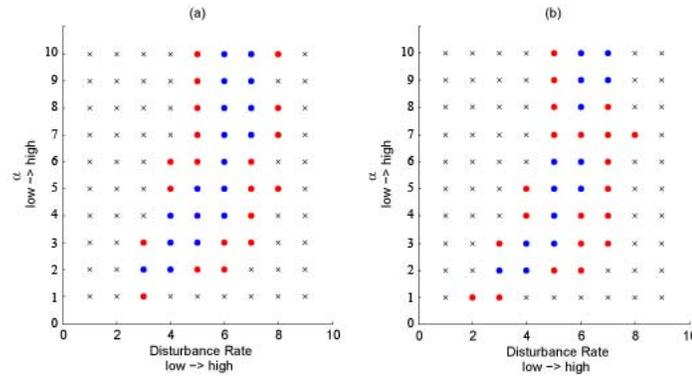
Figure 4.4: Tests seemed to show little to no overall difference between Equations (3.1) and (3.2) in a temporally varying environment when heterogeneity was low.

Equation (3.1) or Equation (3.2). See Figure 4.4 for a comparison. However, when environmental heterogeneity was high, or when a step function carrying capacity was used (the top function pictured in Figure 3.1), there were major differences, as can be seen in Figure 4.5. When either of these two things occurred, Equation (3.1) allowed almost no coexistence under most circumstances. The one exception to this statement we found was when diffusion rates were low. Populations modeled with Equation (3.2), on the other hand, seemed unaffected by changes in carrying capacity and environmental heterogeneity. In fact, it may be the case that major increases in heterogeneity slightly increase the ability of the two species to coexist.

We tested how changing d affected coexistence, using $d_i = 0.1, 0.01$, and 0.001. Typical results can be seen in Figure 4.6. We found when $d_u = 0.1, d_v = 0.01$, very high disturbances were generally necessary for coexistence to occur, unless competition was minimal. On the other hand, when $d_u = 0.1, d_v = 0.01$ or $d_u = 0.01, d_v = 0.001$, a moderate disturbance size was enough for coexistence to occur under nearly competition levels. Behavior was similar under both equations and all environments, except when Equation (3.1) was used in highly heterogeneous environments.

We also analyzed how changing r affected coexistence, using $r_i = 1, 5$, and 25. Typical results can be seen in Figure 4.7. When running a test where $r_u = 25, r_v = 5$, we saw that coexistence could occur when the degree of competition grew linearly with the degree of disturbance. This was fairly stable, so little changes in α or D would not affect coexistence. When $r_u = 5, r_v = 1$ or $r_u = 25, r_v = 1$, however, coexistence almost never occurs.
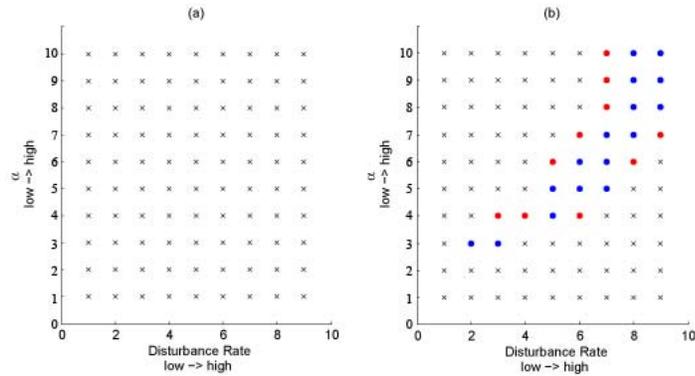
Figure 4.5: Tests showed major differences between Equations (3.1) and (3.2) in a temporally varying environment when environmental heterogeneity was high.

4.3   Discussion

Our results suggest that in a Lotka-Volterra competition model with no spatial or temporal heterogeneity, coexistence is entirely determined by the relative values of α_u and α_v (the "competition coefficients"). Because of this, it is not inaccurate to summarize competitive ability as a single number. However, in spatially or temporally varying carrying capacities, d and r can affect whether a species survives. Two conclusions can be drawn from this. First, that in a temporally and spatially varying environment, organisms can compete by using various strategies. Second, when coexistence occurs, these strategies appear to be equivalent. This should be studied more thoroughly, to see what effect combining strategies have, or whether this type of equivalence is transitive.

In highly varying environments, it seemed that the most important factor affecting coexistence was which equation was used. If we modeled species using Equation (3.1), environmental heterogeneity and fragmentation could effectively stop any chances two species have of coexisting. On the other hand, when Equation (3.2) is used, environmental heterogeneity made little to no difference. This is likely to be simply a factor of maximum population levels. When population levels are already quite low, it takes longer for the population to spread out and recolonize after a disaster. As we saw in Chapter 3, an increase in spatial heterogeneity causes the maximum sustainable population level U^* to decrease when modeling a species with Equation (3.1). When using Equation (3.2), there appears to be no difference. It appears that this may be what is occurring here.

In environments with low spatial variability, the exact parameters seemed to be
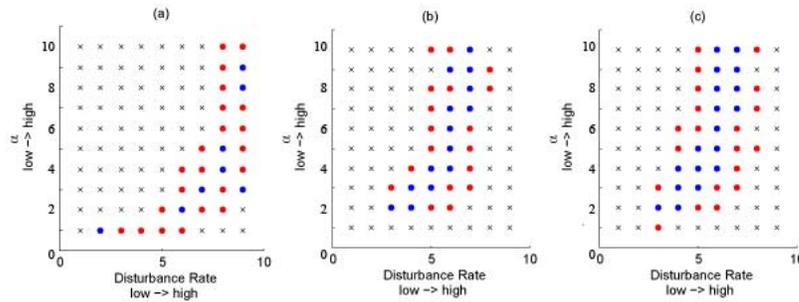
Figure 4.6: We ran several simulations on the effect of dispersion coefficients on coexistence. In the left panel, $d_u = 0.1, d_v = 0.01$. In the middle panel, $d_u = 0.01, d_v = 0.001$. On the right panel, $d_u = 0.1, d_v = 0.001$.
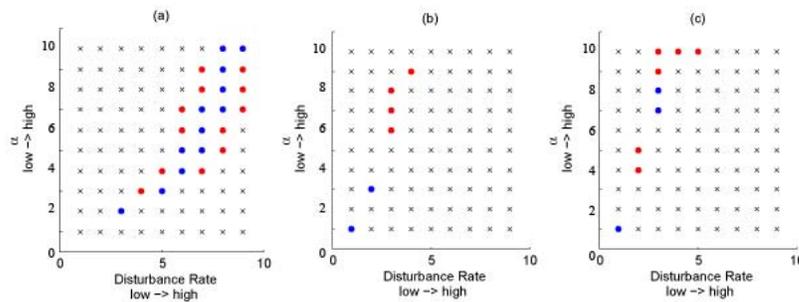

Figure 4.7: We ran several simulations on the effect of population growth rates on coexistence. In the left panel, $r_u = 25, r_v = 5$. In the middle panel, $r_u = 5, r_v = 1$. On the right panel, $r_u = 25, r_v = 1$.

the best judge of whether coexistence was possible. It seems that the actual values of parameters is more important than their specific ratios. This could a factor of how long it takes for a stronger competitor to establish itself in a new environment. In other words, no matter how strong a competitor is, it cannot move into a new environment any faster than c (the rate of a traveling wave), and it cannot increase in population levels any faster than r. It seems likely that in situations where $r_v = 1$ or $d_v = 0.001$, that the population v simply cannot survive conditions of high environmental disturbance. Indeed, numerical tests seem to verify that under such conditions species cannot survive, even in the absence of competition. This claim seemed to hold up to numerical tests, as can be seen in Figure 4.8.
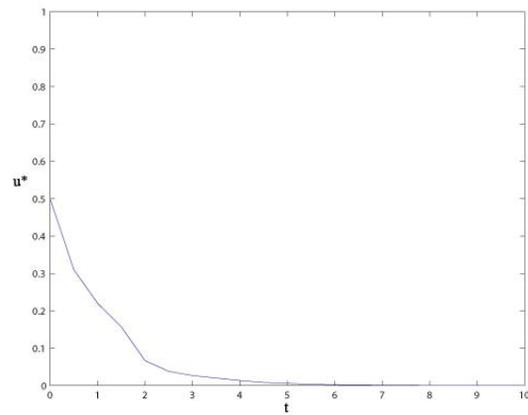
Figure 4.8: In the above simulation, $r = 1$. This occurrence may explain why coexistence did not happen under certain circumstances.

Chapter 5

Conclusions and Future Work

In this work, we hope to have proven the importance of including the effects of spatial and temporal heterogeneity when modeling competing species. When modeling species in a spatially heterogeneous environment, the degree of habitat fragmentation can have a large effect on expected population sizes, depending upon which variables one has chosen to use. When modeling species in a temporally heterogeneous environment, species can compete either directly, or through advancing more quickly.

We have shown that in fragmented environments, the equations one uses to model species growth has a major impact on the expected outcomes. When working within one framework, we expect fragmentation to increase population numbers and species diversity. When working in the other, we expect just the opposite results.

Finally, our results so far have seemed to indicate that the main mechanism which affects the possibility of coexistence is the agility of the strong competitor. This is surprising, but makes sense when one considers that all a fast competitor needs to do to avoid extinction is survive to each successive disturbance, after which they are free to grow and expand once more. It may be that too narrow of a range of parameters was chosen, and it may be that this occurrence is unique to two species environments. More simulations should be run to determine the generalizability of these results.

There are several spin-off projects that could come from this research:

1. Though there has been much work done on competitive traveling waves, and traveling waves in a heterogeneous environment, there appears to be no work that contains both conditions simultaneously. This would be an interesting problem to consider analytically or numerically.

2. More work is necessary to determine for which habitats and which organisms

Equation (3.1) or (3.2) is more valid.

3. One could analyze species competition under a multiple competing species environment. This could be very interesting, since two species is a good first approximation, but often not the case in real environments. One could also analyze the theoretical effects invasive organisms could have on a changing environment this way.

4. One could consider the effects a stage-structured model of population growth could have. Under such a model, species are assumed to have a juvenile stage and an adult stage, and they do not reproduce until their adult stage, however all stages consume resources. Additionally, one could create a model with three stages: seed, juvenile, and adult. In this model, only the seeds would diffuse, and only the adult trees could create seeds.

5. Extensions of this work to a two- (or possibly even three-) dimensional model may model reality more realistically.

6. In my model, disturbance events happened completely at random, and did not change the environment. It may be the case that disturbances effect some species more than others, happen in a more deterministic (or at least stochastic) fashion, and/or change the carrying capacity of an environment, whether permanently, temporarily, or until repaired by particular species. Additionally, the effects of facilitation or inhibition were not considered (although, considering the former would likely require a 3+ species environment).

7. The model proposed only considers major disturbance events, when in fact there are many factors that could cause a fluctuation in carrying capacity, such as rainfall. It would be interesting to study what effects more minor environmental changes have on species coexistence.

8. It would be extremely interesting if real data were available to determine the validity of there simulations.

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