The Effect of Habitat Fragmentation on Population Persistence in Spatially Heterogeneous Landscapes

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Chapter 1
Introduction

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Understanding how populations grow, decline, and persist is a central topic in theoretical and conservation ecology. The first attempts at using population dynamic models to answer these questions avoided complications of spatial configuration by assuming that all individuals are homogeneously distributed throughout the landscape. In reality, many populations are heterogeneously distributed in space, often as clusters of individuals linked by dispersal. Consequently, the connections between these segregated subpopulations can influence population growth. Experimental studies have shown spatial processes can be essential for understanding many species' population dynamics (Hanski 1999, Medina-Vogel et al. 2008). In addition there is an increasing urgency for understanding the effect of a population's spatial structure on its survival because human activities continually fragment natural habitats, potentially causing population extinctions. Therefore, in this thesis I will explore the effect of spatial heterogeneity and habitat fragmentation on the ability for populations to persist in patchy environments.

Models of population dynamics that incorporate space present a mathematical challenge in that individuals are no longer assumed to be well mixed. In this case, organisms do not interact with each other at a local level in the same way they interact with distant neighbors. Hence the assumptions of "mass action" are violated, and the population dynamics are not explicitly dependant on global population size. Therefore, descriptions of population density can no longer be encapsulated by a simple ordinary differential or difference equation.

Early attempts at describing population growth through space used partial differential equations. Skellam (1951) was one of the first to apply spatially explicit population modeling to ecology by reinterpreting Fisher's reaction-diffusion equation, which originally described the propagation of an advantageous gene. In Skellam's model, the reaction term corresponds to density dependant growth at the given location, while the diffusion term corresponds to random dispersal. Assuming the population exists in an interval on the real line with boundary conditions of zero density at the end points, he develops the first expression for the minimum habitat size needed for population persistence. This condition, known as critical patch size, is especially important for questions regarding habitat loss and fragmentation, because it gives a bare minimum size that must be preserved to save a population from going extinct.

While I will develop expressions in the same spirit as those first calculated using partial differential equations, the rest of this thesis will focus on metapopulation and integrodifference models. A metapopulation is a group of subpopulations of the same species, existing in patches, which interact through dispersal (Levins 1969). Levins developed the simplest model for a metapopulation by using a single ordinary differential equation to describe the proportion of occupied and unoccupied patches. Discrete time versions of this equation have also been studied. In these models persistence corresponds to a long term positive proportion of occupied to suitable patches. While the model was developed with spatial structure in mind, the model itself is not spatially explicit. Dynamics are described by the average patch extinction and colonization rate in the system; the size and spacing of the patches is ignored. Hanski modified this model to include the effects of distance between patches and patch size by creating a system of coupled differential equations (Hanski 1997b), with each equation corresponding to the probability of a

particular patch being occupied. The colonization rate of each patch is then a function of the distance between the centers of the patches, and the extinction term is a function of patch area. In chapter (2) I will develop a discrete time model similar to the Hanski's, but will reinterpret the state variable in terms of subpopulation abundance, as apposed to patch occupancy. Since the populations within vernal pools do not undergo frequent stochastic extinctions, the extinction term of the classic Hanski model will be deleted. I will use two methods to model dispersal, both involving a continuous dispersal kernel laid over a two dimensional landscape consisting of unsuitable habitat and discrete occupied pools.

Discrete time metapopulation models are actually a simplification of integrodifference equations. Integrodifference equations are similar to metapopulation equations except, like PDEs, they are continuous in space. Therefore instead of population growth being a function of density within a particular patch, growth is a function of the density at a particular point in space. Dispersal then occurs from all other points. However, if we imagine a metapopulation defined on a lattice, in which local population dynamics are determined by the density of individuals occupying each cell, as the grid becomes infinitely refined the metapopulation model converges to an integrodifference equation. Integrodifference equations were first introduced to ecology by Kot and Schaffer (1986) to explain the population dynamics of species with non-overlapping generations. Similar to the techniques used by Skellam (1951), Kot and Schaffer were able to formulate an expression for the minimum habitat size needed for a population to persist, assuming the population disperses its propagules according to a Laplacian distribution. Here they linearized their equation around the zero equilibrium corresponding to population extinction, and converted the integral equation into a second order ODE boundary value problem. From this they were able to derive an expression for when the transcritical bifurcation, where the stability of the zero and non-zero equilibrium exchanges, occurs. Unfortunately, this can only be done for a limited number of dispersal kernels. For even relatively simple kernels, such as a Gaussian distribution, the critical habitat size can only be approximated numerically (Latore et al. 1998).

While Kot and Schaffer developed a variety of techniques to determine the critical patch size for populations in homogeneous landscapes, they did not consider fragmented landscapes or landscapes characterized by spatial heterogeneity in habitat quality. However, Van Kirk and Lewis extended this analysis to habitats that vary in quality based on location (1997). They specifically looked at populations in which growth could be modeled as a periodic function in space, where good quality habitat corresponded to an intrinsic growth rate parameter greater than one and poor quality habitat corresponded to an intrinsic growth rate parameter less than one. The analysis showed that critical habitat size depended on a combination of dispersal distance and landscape heterogeneity. Yet, the analysis used did not extend to random landscapes. In chapter (3) I prove that the integrodifference equation governing the population dynamics in a random patchy landscape converges to the standard deterministic integrodifference equation multiplied by the proportion of suitable habitat, in the limiting case where the landscape is infinitely fragmented. Hence determining the critical habitat size is reduced to a problem which can be solved using the techniques provide by Kot and Schaffer (1986).

Chapter 2

The Population Dynamics of a Vernal Pool Plant: the effects of habitat fragmentation, conservation, and restoration on population persistence and abundance

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keywords: habitat fragmentation, restoration, metapopulation, vernal pools, *Lasthenia*

Introduction:

One of the greatest challenges in conservation biology is assessing the impacts of habitat loss and fragmentation on population viability and abundance (Brigham, & Schwartz 2003). Loss of suitable habitat not only reduces the population's available resources, but also can increase habitat fragmentation. It is conceivable that some species well adapted to fragmented landscapes may not be affected by further fragmentation. However, greater fragmentation may impede dispersal among subpopulations, which can be an essential for population persistence. While it is possible to test empirically the effect of fragmentation on the dispersal and population viability of some species (Peacock & Smith 1997; Trenham & Schaffer 2005), for others, this is logistically unfeasible. In such cases, mathematical models can help to understand the effect of habitat fragmentation on population viability and to guide conservation, restoration and development of such habitat (Ellner & Guckenheimer 2006).

Levins' metapopulation theory (1969) provides one approach to this problem. In the most general sense, a metapopulation is a group of subpopulations that exists in patches connected by dispersal (Hanski & Gilpin 1997). The Levins model assumes there are an infinite number of identical patches, in which the population is described by the presence or absence of the species in each patch. Extinctions and colonizations of the subpopulations in these patches define population growth and decline. However, most natural populations do not live in an infinite landscape of homogeneously distributed patches. Therefore, some theoretical ecologists have developed alternative approaches to model metapopulations. For example Huxel and Hastings (1999) used lattice models to analyze the effects of fragmentation on population growth. Similarly, one could use the integrodifference methods described by Kot and Schaffer (1986). Unfortunately, these models are computationally expensive for sites in which patches occupy a small portion of the landscape's total area (Hanski 1999). On the other hand, Hanski developed a more economical adaptation of the lattice model to study spatially fragmented populations (Hanski & Gyllenberg 1997; Hanski 2000; Ovaskainen & Hanski 2001). Instead of modeling the proportion of sites occupied, Hanski and Gyllenberg (1997) track the probability that each patch will be occupied through time, with a patch's extinction rate as a function of area, and its colonization rate decreasing exponentially as distance between patches increase. This model is advantageous because it explicitly accounts for the landscape's spatial distribution, and thus can be used to test the effect of habitat fragmentation on population dynamics. While this method may appear inappropriate for populations in which information on extinction and colonization is lacking, or populations that rarely go extinct (Hastings 2006), the model can be reinterpreted in terms of population density rather than the probability of a patch being occupied. Since this

interpretation no longer requires extinctions and recolonizations, the Hanski and Gyllenberg approach can be modified to understand the effects of habitat fragmentation on the population dynamics of species in many patchy systems.

One of these systems, California vernal pools, constitutes a habitat type of particular interest to conservation biologists because it is home to many endemic species. Vernal pools are ephemeral wetlands that fill with winter rains and desiccate during hot, dry, summer months (Zedler 1987; Keelely & Zedler 1998). Although they once occupied a large portion of the California landscape, increasing development has caused habitat loss and fragmentation (Wier & Bauder 1990). Pools separated by distances on the scale of meters form complexes at a local level; complexes are separated from one another by larger distances (tens to hundreds of kilometers). Pools at the local level are affected by similar rain patterns and are highly synchronous within a complex; therefore, the subpopulation within each pool likely experience correlated dynamics with the subpopulations in neighboring pools.

Vernal pool plants have annual life cycles with one generation per year. During winter rains, pools fill and seeds germinate. As the pools begin to dry, the plants flower, disperse seeds, and die (Bliss & Zedler 1997). Thus, unlike the continuous time model described by Hanski & Gyllenberg (1997), vernal pool plant populations should be modeled with discrete time equations. In addition, many vernal pool plants disperse dormant seeds that may remain in a seed bank for numerous years. In this case, it is important to model population density rather than extinction and colonization because extinctions are unlikely or difficult to detect since seeds may continue to germinate from the seed bank after several unfavorable years (Zedler 1987). This is a key feature of vernal pool plants, which is not accounted for in the traditional Hanski and Gyllenberg (1997) model.

While the characteristics of vernal pool species do not fit completely within assumptions of the classic metapopulation approach, it is important to understand the effect of fragmentation on vernal pool species' population dynamics because the pools are continuously destroyed during agricultural and suburban development. Conservation efforts attempt to protect and to restore these habitats; however, there is no theoretical framework to guide such efforts.

In this paper we developed a general discrete time metapopulation model, with a seed bank, similar in structure to the continuous time model developed by Hanski & Gyllenberg (1997) and used analytic techniques along with deterministic simulations to examine the population dynamics of a vernal pool plant species. We first developed general persistence conditions at the level of pools and complexes and then used the simulations to explore the effect of pool spatial configuration on the plant species' persistence and abundance. We also used the simulation to understand the implications of adding and removing pools as a means of restoration and development.

The simulations were parameterized using two species in the genus *Lasthenia* (Family *Asteraceae*), commonly known as goldfields. The genus consists of 21 species and subspecies (Chan et al. 2001), many of which are endemic to California vernal pools. *Lasthenia* has a lifecycle typical of other vernal pool plants (fig. 2.1). *L. conjugens*, the Contra Costa goldfield, is currently federally listed as an endangered species with a distribution limited to the deltaic Sacramento Valley and a few other California counties (Hickman 1993). A closely related congener, *L. fremontii* (Chan et al. 2001), while also endemic to California vernal pools, has a broader geographic distribution, and can currently be found throughout the Sacramento and Central valleys ranging from Shasta to Santa Barbra (USDA 2008).

Methods:

Model Assumptions and Structure:

Our general model accounts for the effects of survival, germination, dispersal, and the size and spatial configuration of vernal pools, on the population dynamics of a typical vernal pool plant. We assume that the population consists of a series of subpopulations confined to individual vernal pools, with dynamics of the subpopulations interconnected by dispersal. Because vernal pool plants have an annual life cycle, we modeled the population using a system of discrete time equations, with each equation corresponding to the subpopulation size within a pool. These equations are essentially the MacDonald-Watkinson (1981) bottleneck model of annual plant population growth with a seed bank, modified to include dispersal within a patchy landscape.

In our model, between–pool interactions can only occur through dispersal during the adult stage. Therefore, we assumed that seeds in the seed bank are immobile and cannot directly contribute to the population in other pools. This assumption could be violated if animals disperse seeds. While laboratory experiments show that vernal pool plants can germinate from rabbit pellets (Zedler & Black 1992), S. Collinge showed no evidence for rabbit dispersal of *Lasthenia conjugens* in the field (personal communication). This assumption could also be violated if seeds can float into neighboring pools that connect during years with high rainfall. While some vernal pool plant seeds develop structures that allow them to float, this is not true for *Lasthenia*.

Rather than modeling plants and seeds as separate stage classes, we used the number of seeds in pool *i* at time *t* as a state variable. Biologically, this implies censusing the population after dispersal, when all individuals are seeds. This allowed us to capture the same processes as a model with separate seed and adult stage classes with half the number of equations.

We computed the number of seeds in pool *i* in year *t+1* as the sum of the number of seeds that stay in pool *i* or disperse into pool *i* from other pools in year *t*. Specifically, we have:

| Number of seeds in pool *i* at time *t+1* | = | seeds produced in pool *i* that stay in pool *i* at time *t* | + | seeds in pool *i* that do not germinate at time *t* | + | seeds produced in pool *j* that disperse into pool *i* at time *t*. |

The population growth of plants is affected by density dependence at various stages of the life cycle. Many plant populations experience negative density dependent survivorship (Silander & Pacala 1985; Heithaus 1982). After a plant survives to adulthood, positive density dependence may affect plant fecundity depending upon the plant's reproductive methods. Specifically, the mating systems of vernal pool plants range from obligate outcrossing, e.g. *L. conjugens* and *L. fremontii*, to obligate selfing, e.g. *L. glaberrima* (Ornduff 1963, 1966). If a species reproduces via obligate selfing, the reproduction of these plants will not be affected by low density. Since some species of *Lasthenia* reproduce in this way and because there is no data on density dependent seed set in *L. conjugens* or *L. fremontii*, we did not include positive density dependent effects on fecundity.

There is no density dependent survival in the seed bank because dormant seeds do not compete for resources. For many plant species, a constant proportion of seeds in the seed bank

lose their ability to germinate each year (Cook 1980). To incorporate this type of survival in the seed bank, we assumed that a constant proportion of viable seeds, γ, germinate each year. The proportion of seeds which do not germinate, $1-\gamma$, survive in the seed bank with probability ε_d. Thus, there is a constant proportion, $1-\varepsilon_d$, of seeds in the seed bank that lose the capacity to germinate every year. This means that the survival fraction, ε_d, does not explicitly depend on the age or density of the viable seeds. In contrast to survival in the seed bank, seeds that germinate must not only survive through a dormant stage during the summer, but also a seedling stage after germination. Survivorship during the seedling stage may be especially difficult considering early showers can cause premature germination. We combine these survivorship probabilities as ε_g.

Therefore, in terms of state variables and parameters, the equations become:

$$N_i(t+1) \quad = \quad \varepsilon_g \gamma \omega p_{ii} f_i(N_i(t)) \quad + \quad \varepsilon_d(1-\gamma)N_i(t) \quad + \quad \sum_{j=1, j \neq i}^{n} \varepsilon_g \gamma \omega p_{ij} f_j(N_j(t)), \quad (2.1)$$

where the state variable $N_i(t)$ is the number of seeds in pool i at year t. A constant fraction γ of seeds germinate. The function, $f_i(N_i(t))$, describes the survival of germinating seeds in pool i, indicating a seed's successful maturation into a reproducing adult. Each adult produces ω new seeds. A seed produced in pool j disperses into pool i with a probability p_{ij}. The contribution of seeds to pool i from pool j is then summed over all n pools in the complex.

For the rest of this paper, we assume that the density dependent growth function, $f_i(N_i(t))$, in pool i is the product of $N_i(t)$ and the reciprocal yield function (Levin et al. 1984; Ellner 1985b; Nilson et al. 1994; Mathias & Kisdi 2002). The reciprocal yield function gives compensatory growth for germinating seeds (Van Kirk & Lewis 1997). Specifically, we described the density dependence in pool i by

$$f_i(N_i(t)) = \frac{cA_i N_i(t)}{\varepsilon_g \gamma N_i(t) + cA_i}, \qquad (2.2)$$

where A_i is the area of pool i, and c is the maximum number of germinating seeds that can survive per unit area. Hence, cA_i is the effective carrying capacity for the germinating seeds in pool i, making the carrying capacity of a pool directly proportional to its area. Although Harper (1977) points out that the reciprocal yield description may be more accurate for density dependent mechanisms that affect plasticity rather than mortality, Martin & Carnahan (1983) found that this function fits survival data for individuals in some plant species.

Analytical Methods

Using linear stability analysis near the zero equilibrium, we calculated a sufficient persistence condition for a plant species living in an n pool system. We further calculated the necessary persistence condition for a two patch system using a method described by Hastings (2006). In this paper, he uses Perron-Frobenius theory to show that the persistence of a fragmented population depends on a local subpopulation's self-replacement by dispersal to and from all subpopulations in the complex. Furthermore, we developed an expression for the critical pool size needed in order for the subpopulation in a given pool to survive in isolation.

Simulation Methods

We programmed in MATLAB to simulate the effect of dispersal on the persistence of a vernal pool plant species. Because there is a lack of data on the spatial pattern of seed dispersal for vernal pool plants, and accurately measuring seed dispersal is difficult (Bullock and Clarke 2000), we used an analytical dispersal kernel to describe p_{ij}. A dispersal kernel is a probability density function that gives the distribution of dispersed seeds in space as a function of the seeds' location. While general dispersal kernels have been studied theoretically, (i.e. Okubo & Levin 1989) little is known about the seed dispersal of vernal pool plants. Therefore, we assumed that each plant disperses its seeds according to the Laplacian distribution. Not only is this one of the simplest dispersal kernels for wind dispersing plants (Okubo & Levin 1989), it is also leptokurtic. Theoretical models of seed dispersal suggest that the majority of plants have leptokurtic, as opposed to Gaussian, dispersal kernels (Okubo 1980, Howe & Westley 1986). Thus, our dispersal kernel is

$$k(x, y) = \frac{\alpha^2}{2\pi} e^{-\alpha\sqrt{x^2+y^2}}. \qquad (2.3)$$

The function $k(x,y)$ gives the probability distribution of seeds dispersed from a plant centered at the origin, where x and y are the coordinates of the dispersed seeds. Because $1/\alpha$ is the mean dispersal distance, the plant disperses more seeds near itself as α increases.

Using this dispersal kernel, we took two approaches to calculating p_{ij}: one in which we assume plants disperse all seeds from the center of the source pool and one in which plants are uniformly distributed in the pool before they disperse their seeds. The first method is the conventional one used in most metapopulation models (ie. Hanski & Gyllenberg 1997). However, assuming seeds are dispersed from the center of the pool overestimates the number of seeds dispersed back into the source pool and underestimates the number of seeds dispersed out into other pools. On the other hand, assuming the population is uniformly distributed, before dispersal, pushes more of the population out near the edge of the pool. Hence, this method underestimates the seeds that stay, and overestimates the seeds dispersed into other pools. The most accurate approach would be using a lattice or integrodifference model, which is too computationally expensive to run simulations for large landscapes. However, our two methods will provide a lower and upper bound for survival at low densities, equilibrium population abundance, and critical pool size.

To calculate p_{ij} we assumed that a vernal pool complex is made up of n circular pools of the same depth. Using the pool-centered approach to calculate p_{ij} we numerically integrated the Laplacian distribution, centered at the center of the source pool, over each of the n target pools. Using the uniformly distributed plant method, we generated a sample of uniformly distributed seeds in the source pool and numerically integrated each seed's dispersal kernel over all the target pools. We summed the results for all the seeds in the source pool and divided by the number of seeds in the pool to obtain the desired probability.

In the simulation, we varied the area of the individual pools and the distance between pools to see the effect on the population dynamics of a vernal pool plant. Specifically, we used data from *L. conjugens* and *L. fremontii* to define a biologically realistic range of parameters for the germination fraction γ, maximum density c, and fecundity of the plant ω. Distance is measured in meters, thus, c, α, and A_i are scaled accordingly. A summary of the values used for the simulation are listed in the table of parameters (Table 2). We also simulated the effects of

pool removal and addition within a complex on plant population persistence to evaluate the effects of habitat destruction and restoration.

In addition, we calculated the eigenvalue as a measure of population persistence and tested how the eigenvalue and the population abundance responded to habitat fragmentation, assuming the total area of pool coverage is fixed. First we generated a landscape of non-overlapping pools of equal radius. We started by picking a location at random, putting a pool in that location, and checking to make sure the pool did not overlap any other pools in the complex. If the pool overlapped another pool, we discarded it and randomly selected a new location. We repeated this until we reached the desired number of pools for the complex. After generating the complex, we calculated the dominant eigenvalue and equilibrium population density. We then decreased the number of pools while simultaneously increasing the radii of the remaining pools so that the total area of pool coverage remained fixed. This process was repeated until we reach a single pool complex. The purpose of this method is to compare the population growth at low densities and the equilibrium population size when the complex is made of many small pools, fewer pools of intermediate size, and just a few large pools.

Results:

The model has an equilibrium at zero. We focused our analysis on this equilibrium because of our interest in population persistence. We define persistence of the population to mean that at least one of the subpopulations in the complex persists. After linearizing Equation (2.1) around the zero equilibrium, we calculated the dominant eigenvalue to determine persistence conditions for the population. If the eigenvalue is greater than one, the zero equilibrium is unstable. This means that when the population is small, it always grows and persists. If it is less than one, the equilibrium is stable and the population decreases and goes extinct. From this, the population persists if for any pool i, the following condition is satisfied:

$$\varepsilon_g \gamma p_{ii} \omega + \varepsilon_d (1-\gamma) > 1. \qquad (2.4)$$

This means a seed in pool i is replaced either by a dormant seed from pool i's seed bank or by a seed dispersed by a plant in pool i back into pool i. Condition (2.4) guarantees that the species persists in pool i without dispersal from other pools. Thus, if the subpopulation in at least one of the pools can survive on its own, the population in the complex persists. However, persistence can still occur if equation (2.4) is not satisfied, as long as dispersal from other pools allows for the replacement of individuals. The actual analytical expression for the eigenvalue gives a necessary persistence condition, but it is not biologically interpretable. Note that since we linearized our model, density dependence does not affect the persistence conditions.

Hastings (2006) outlines a more interpretable condition using results from *M*-matrices. Assuming equation (2.4) is not satisfied for any pool, Hasting's condition is equivalent to the eigenvalue condition. Using his method for our model with two pools, we get the necessary condition

$$(\varepsilon_g \gamma \omega p_{12})(\varepsilon_g \gamma \omega p_{21}) > \left| \left(\varepsilon_g \gamma \omega p_{11} + \varepsilon_d (1-\gamma) - 1\right)\left(\varepsilon_g \gamma \omega p_{22} + \varepsilon_d (1-\gamma) - 1\right) \right|. \qquad (2.5)$$

The expression on the left hand side represents the seeds that disperse between pool one and pool two. The right hand side is the product of how much condition (2.4) is not satisfied for each pool.

Thus, condition (2.5) means that a pool must disperse enough successful seeds to other pools that will return home, making up for the lack of successful seeds it gets from within patch dispersal. If this condition is satisfied, the number of seeds in a given pool will be greater than the number of seeds in the pool during the previous year. In this case, seeds in a particular pool replace themselves by a combination of within patch dispersal, seed bank germination, and dispersal of propagules to another pool that will return to the original site in a later generation (Hastings 2006).

The Hastings condition becomes difficult to calculate for a large number of pools (Hastings 2006). Additionally, since the Hastings condition only holds for subpopulations that do not persist in isolation, it is more appropriate to use the eigenvalue condition for our simulations. We cataloged these values to determine the persistence of the populations for *n* number of pools with various spatial configurations.

We found that species with a short mean dispersal distance automatically persist, regardless of pool configuration, because equation (2.4) is always satisfied. Specifically, with germination and fecundity parameters fixed to match *Lasthenia*, a pool has a critical size in relation to the mean dispersal distance of the plant that guarantees subpopulation persistence. For the pool centered dispersal kernel method of calculating p_{ij}, if the pool's radius is greater than *m* times the mean dispersal distance, then the subpopulation in that pool persists, where *m* is given by the equation

$$1 - m e^{-m} - e^{-m} = \frac{1 - \varepsilon_d (1 - \gamma)}{\varepsilon_g \gamma \omega}. \qquad (2.6)$$

If the radius is shorter than *m* times the mean dispersal distance, isolated subpopulations go extinct. For example, if $\gamma = 0.7$, $\varepsilon_g = 0.1$, $\varepsilon_d = 0.3$, and $\omega = 100$, *m* is approximately 0.6245, and therefore a pool must have a radius of at least 0.6245 times the mean dispersal distance in order for the subpopulation to persist without dispersal from other pools. This is a worst case scenario; persistence can occur when this threshold size is not met if there is enough dispersal between pools. However, using a pool-centered dispersal kernel to calculate p_{ij} underestimates the number of seeds dispersed out of the pool, and overestimates the number of seeds that remain in the pool. Therefore, the *m* value given by equation (2.6) underestimates the true critical pool size.

Using the method of calculating p_{ij}, where we assume seeds are uniformly distributed in the pool before they disperse, we can also calculate the relationship between mean dispersal distance and critical radius size. Using this approach there is no analytic expression for *m*, because calculating p_{ij} involves randomly sampling seeds from a uniform distribution. However, we can calculate p_{ij} numerically for an array of mean dispersal distances and pool radii, substitute this into equation (2.4), and plot the relationship between mean dispersal distance and pool radius, where *m* is now the slope of a line fitted to this graph (fig. 2.1). For the parameter values in the above example, the corresponding *m* for the uniform method is 0.6814. This value is likely an overestimate because assuming plants are uniformly distributed before they disperse their seeds pushes more plants closer to the edge than would likely be expected. Hence, the *m* value corresponding to the uniform method provides an upper bound for the critical pool radius, but the *m* given by equation (2.6) can be calculated as a quick estimate.

While a mean dispersal distance less than *r/m*, where *r* is pool radius, causes subpopulations to persist in isolation, pool radius and mean dispersal distance also affect the eigenvalue for populations that do not initially persist in isolation. We found that decreasing the

distance between two pools led to an exponential increase in the eigenvalue and eventually led to species persistence. Also, starting with two pools that are not persisting, increasing the radius of one pool led to persistence in that pool and eventually persistence in both pools. This occurs because as the area of a pool increases, the probability that pool retains seeds increases. Furthermore, increasing the area of a pool decreases the distance between pools, hence p_{ij} is larger for all j in conditions (2.4) and (2.5).

Increasing the area of a pool increases the likelihood of persistence, since this effectively increases the area of suitable habitat. However, there is a stronger relationship between increasing pool size and population persistence than just the effect of increasing viable habitat coverage. As we decreased the number of pools while simultaneously increasing pool area to keep the total area of pool coverage constant, the eigenvalue tended to increase (fig 2.2, fig. 2.4). This suggests that fewer large pools may be better for total population persistence than many small pools. This trend is strongest for larger mean dispersal distances, but still holds for mean dispersal distances small enough to guarantee persistence of all pools in isolation. However, when the mean dispersal distance is more than one order of magnitude less than the smallest pool's radius, pool size and the number of pools become less important for population persistence. This is because p_{ii} is approximately one and p_{ij} is approximately zero for all $j \neq i$. In this case the system has reached its maximum limiting eigenvalue, which is the left hand side of (2.4) with $p_{ii} = 1$ and $p_{ij} = 0$, basically meaning that the spatial configuration of vernal pools has no affect on the population dynamics at low densities. It is important to note that this is a scaling issue. For very small mean dispersal distances the eigenvalue is at its maximum even for very fragmented landscapes. However, if we were to decrease pool area and increase the number of pools to an unrealistic level, the eigenvalue would eventually start to decrease. Yet, because vernal pools are not the size of a coffee mug, we can only conclude that the fragmentation of a vernal pool landscape decreases the likelihood of persistence for plant's with a mean dispersal distance greater than an order of magnitude smaller than the smallest pool's radius. The trend does hold true for smaller mean dispersal distances, but the decrease in the eigenvalue only occurs in the one hundreths place or further. Applying the same methods only for population abundance rather than the eigenvalue led to the same general trend; increasing the number of pools while decreasing pool size causes a decrease in population abundance (fig 2.3). Like the eigenvalue condition, this trend held true for the same mean dispersal distances.

Assuming an infinite landscape, where the effects of dispersing seeds outside of the complex can be ignored, as the landscape becomes increasingly fragmented, the limiting persistence condition is

$$\varepsilon_g \gamma l \omega + \varepsilon_d (1 - \gamma) > 1, \qquad (2.7)$$

where l is the proportion of the landscape covered by vernal pools. The left hand side of (2.7) is the limiting eigenvalue because as the landscape becomes more fragmented, the probability of dispersing a seed into any pool approaches the proportion of the landscape occupied by vernal pools. The idea that as fragmentation increases the eigenvalue decreases towards this limiting eigenvalue is supported numerically by (fig. 2.4).

While increasing habitat fragmentation led to a decrease in the dominant eigenvalue, this does not mean that populations will go extinct when pools are removed. This is because the pools are still larger than the critical pool size provided by condition (2.6). However, eventhough the population persists, fragmentation and pool removal always decreased the equilibrium

population abundance.

On the other hand, when generating a complex of many pools that cannot persist in isolation, destroying just a small number of pools can lead to population extinction. Similarly, adding pools to a declining population can lead to population persistence. Yet, these results depend on the pools' inability to survive in isolation. In contrast, we have shown that species with short mean dispersal distances persist regardless of the pools' spatial configuration, when Equation (2.4) is satisfied. Hence, it is more likely that short dispersing subpopulations persist independently of one another. However if some vernal pool plants disperse even intermediate distances fragmentation leads to a decrease in the eigenvalue, which corresponds to a greater likelihood of extinction when facing different kinds of disturbance. In other words, just because the eigenvalue is always greater than one, regardless of the spatial configuration, a bigger eigenvalue is always better. Hence removing pools is still a bad idea, even if it does not lead to population extinction in the deterministic model, because it decreases the dominant eigenvalue.

Discussion:

Our simulations show that fragmenting a vernal pool landscape by breaking up subpopulations into multiple smaller subpopulations never is beneficial for population persistence, even if the area of lost habitat is preserved by adding smaller pools to the complex. Fragmenting the landscape, while keeping the total area of suitable habitat constant, always substantially decreased equilibrium population abundance and survival at low densities for intermediate to long mean dispersal distances. For mean dispersal distances less than 0.2 meters this trend also existed but was of inconsequential magnitude.

Because we only considered one species in pools that do not vary in shape and depth, the results are most applicable to mitigation projects that attempt to establish or increase the population size of a single target species. In this case, the model suggests that if artificial pool complexes are built, the pools should be as large as possible in order to increase population abundance and the likelihood of persistence at low densities. Using the uniformly distributed method, we provided a conservative condition for the minimum pool radius needed for population persistence in an isolated pool, while equation (2.6) gives an underestimate which can be quickly calculated. In addition, the minimum l that guarantees condition (2.7) is satisfied can be used as a guideline for the minimum proportion of the landscape that must be covered by vernal pools as long as the land set aside for the complex is large enough that dispersal of seeds outside the complex's boarders is insignificant. A land manager could potentially use this l value along with the value for critical pool size to guarantee population persistence at the complex level.

While fragmentation of the landscape decreased the eigenvalue and population abundance, the population did not go extinct, as long as all the pools satisfied the critical radius size in condition (2.6). In these cases, plants disperse the majority of their seeds within their own pool so that the subpopulations persist in isolation. However, if the plants disperse their seeds long distances, our analytical results show that dispersal between the subpopulations can lead to total population persistence, even if the populations are not able to survive in isolation.

Although there is some evidence for short distance dispersal in vernal pool plants, frequent long distance dispersal events have not been ruled out. Seeds of vernal pool plants tend to be small and free of hairs or hooks, suggesting no visible adaptations for long distance dispersal (Baker 1972). Furthermore, Scheidlinger (1981) inferred that populations of *Pogogyne abramsii* may be to some extent dispersal-limited when measuring population density in Kearny

Mesa vernal pools located in San Diego country. While she expected population density would be higher in particular locations if long distance dispersal were occurring, she did not provide any direct evidence against long distance dispersal. Short distance dispersal may be favored by natural selection due to the large amount of unsuitable habitat surrounding the pools. However, classical models, such as those developed by Hamilton and May (1977), show that dispersal can be advantageous even when dispersed propagules have an extremely high rate of mortality. Although seed morphology suggests short distance dispersal, no studies have verified this dispersal pattern for vernal pool plants. Detailed data on dispersal is essential to understand how dispersal can affect persistence (Howe 1982). Specifically, our simulations show that mean dispersal distance greatly affects subpopulation persistence.

Since there is virtually no data on the dispersal of vernal pool plants, we used a simple Laplacian distribution to describe seed dispersal. The simplest theoretical models based on wind dispersal mechanisms can generate similar distributions (Okubo & Levin 1989). However, this kernel may not accurately describe the dispersal pattern of vernal pool plants. At Travis Air Force base, Collinge found that restored pools were colonized by seeds from surrounding pools, even after the restored pool's seed bank was destroyed (personal communication). This suggests that long distance dispersal may occur more frequently than one would predict by looking at seed morphology. Transportation by animals may be a viable explanation for such events. Though many vernal pool seeds do not exhibit features useful in long distance dispersal, they may be able to survive in the digestive tract of animals. Zedler (1992) found that rabbit pellets collected from vernal pools contained plant seeds that could germinate under lab conditions. However, Collinge found no evidence of seed germination from rabbit pellets in the field (personal communication). Rare yet strong winds can also be a potential cause of colonizations in many plants (Okubo 1989). Plants may disperse their seeds according to a unimodal distribution the majority of the time, but on rare occasions, strong winds and excessive rains can cause seeds to disperse further away than predicted (Nathan 2000). Thus, more studies tracking seed dispersal are needed to better understand its importance on vernal pool plant persistence.

While our model shows that dispersal can play a large factor in determining plant population persistence, dormancy may have a greater influence on persistence in stochastic environments. In the deterministic model, dormancy does not prevent extinction. However, we have started stochastic simulations, which do show dormancy can be beneficial for population persistence if weather patterns very randomly. Unfortunately, there are no studies that show how germination, fecundity, survival rates and dispersal depend on whether. Collecting such data is important because it can be incorporated with long term weather data to generate a more realistic model that can test the effect of dormancy on population persistence and abundance. For a rigorous treatment of ESS strategies of dormancy versus dispersal see Ellner (1985).

Our model can be used as a theoretical guideline for developers and environmental agencies aiming to restore or conserve vernal pools. The results from removing and adding pools as well as the simulation, where we increased habitat fragmentation while keeping the area constant, both suggest that building a large self-sustaining pool may be more effective for preserving single species populations as compared to building small pools close together. However, because it may not be immediately clear whether pools are self sustaining, population size should be monitored for long periods of time. If pools are only monitored for a few years, one may conclude that the population within the pool is self sustaining, when in fact the adult plants are the result of seeds from the seed bank originally planted by the land manager, rather than seeds produced by subsequent generations. This form of long term monitoring has shown to

be effective in determining general trends in highly stochastic environments (Lovett et al. 2007)

While developing large pools may seem optimal in conserving a particular endemic plant species or increasing the species' population abundance, it is important to note that a variety of pool sizes may be more efficient in maintaining biodiversity at the complex level. Specifically, trade offs between competitive ability, dormancy, and dispersal may influence species coexistence (Kneitel & Chase 2004). Hence, it is important to develop multi-species models to determine the effect of vernal pool size and spacing on biodiversity within a vernal pool community. Our model shows that long distance dispersers can go extinct due to increased fragmentation because their seeds do not land in suitable habitat the majority of the time. Additionally, when considering two species in competition, a short distance disperser may have a competitive advantage, and thus further add to the extinction of the long distance disperser.

This model is applicable to more than just vernal pool plants. The modification of classical metapopulation theory to annual plants with a dormant stage provides a starting point for studying the population dynamics of other annual plant species that exists in a patchy environment. Because plant populations rarely exhibit clear extinctions and recolonizations, many biologists have been hesitant to use classic metapopulation theory (Freckleton & Watkinson 2002). However, we have shown that the traditional metapopulation models developed by Hanski and Gyllenberg (1997) can be adapted to these systems. This is important because modeling can be used as a tool for guiding conservation decisions and can point out key features of the system that must be studied experimentally. Our model showed that habitat fragmentation decreases abundance and the dominant eigenvalue corresponding to population persistence, but that it does not likely cause population extinction if the majority of seeds are dispersed close to their parent plant. If the plants disperse their seeds long distances, habitat fragmentation can cause extinction. Therefore, the results suggest that vernal pool plant dispersal must be studied experimentally in order to make good conservation decisions when managing vernal pool systems.

Table 1: List of state variables and functions used in Equation 1

Functions and state variable	Description
$N_i(t)$	Number of seeds in pool i at time t
p_{ij}	Probability of dispersal from pool j to pool i
$f_i(N_i)$	Survival of germinating seeds in pool i
$k(x,y)$	Probability that a plant centered at the origin disperses a seed to the location (x,y)

Table 2: List of parameters, their biologically realistic data ranges, and the values used in the simulations

Parameter	Description	Data ranges for typical Vernal Pool Plants and Complexes	Values used in simulation
$1/\alpha$	Mean dispersal distance	Unknown	0.05 m - 15 m
γ	Germination fraction	0.7 - 0.8 for *L. conjugens*	0.7
ε_d	Seed bank survival fraction	Unknown	0.3
ε_g	Germinating seed survival fraction	Unknown	0.1
ω	Fecundity	0 - 200 for *L. fremontii*	100
N	Number of pools in system	1 - several hundred	1-75
A_i	Area of pool i	Less than 1m^2 – over 2 acres	3.14 m^2 – 3,125 m^2
c	Max number of germinating seeds that can survive per area	1000-1500 per m^2 from quadrats for *L. conjugens* at Travis air force base	1200

figure 2.1. Critical pool size for one pool in isolation. The green curve is using the uniformly distributed seed method with individual plant dispersal kernels. The blue curve corresponds to the pool centered laplacian dispersal distribution. The relationship between mean dispersal distance and pool size is given by the slope of the line, *m*. Both axes are in meters, and the parameters used were: $\gamma = 0.7$, $\varepsilon_g = 0.1$, $\varepsilon_d = 0.3$, $\omega = 100$.
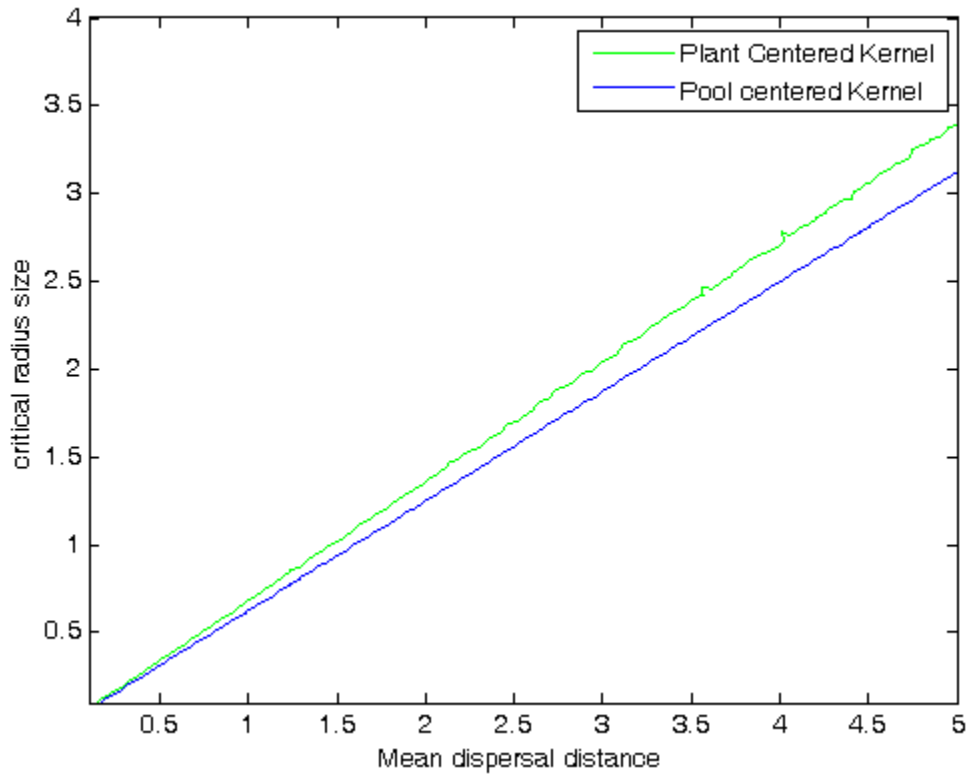
figure 2.2. Fixing the total area of coverage to five percent of a 250 meter by 250 meter landscape, as the number of pools increased, and their sizes decreased, the corresponding eigenvalue tends to decrease as well. Mean dispersal distance is 5 meters, $\gamma = 0.7$, $\varepsilon_g = 0.1$, $\varepsilon_d = 0.3$, $\omega = 100$.
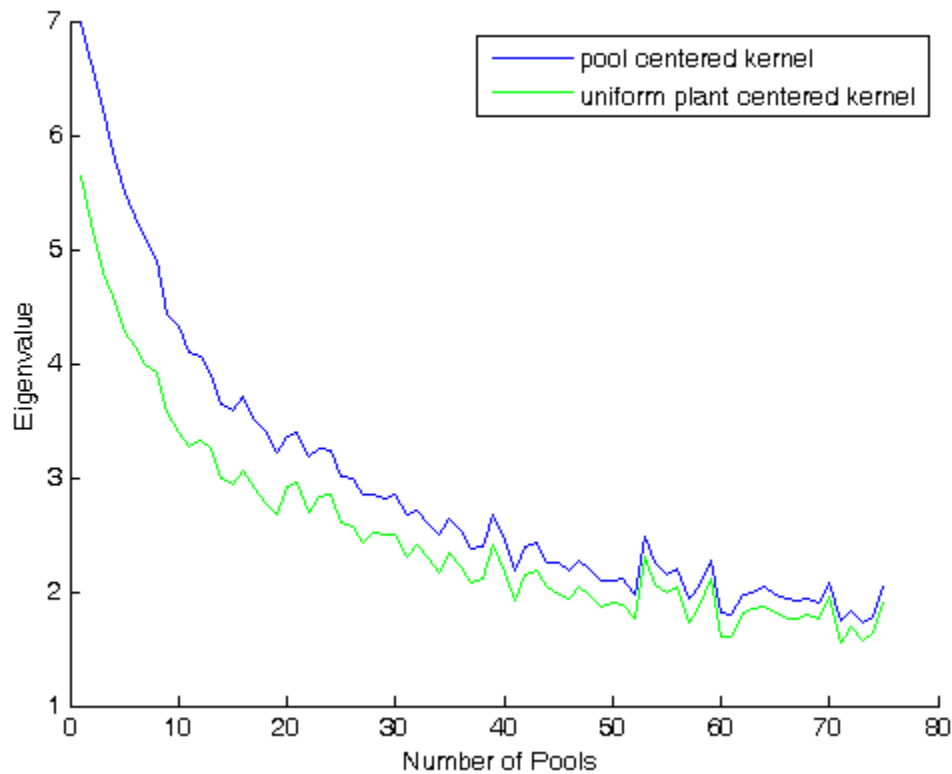
figure 2.3. Fixing the total area of coverage, as the number of pools increase, and their sizes decrease, the corresponding population abundance tends to decrease as well. Mean dispersal distance is 5 meters, $\gamma = 0.7$, $\varepsilon_g = 0.1$, $\varepsilon_d = 0.3$, $\omega = 100$.
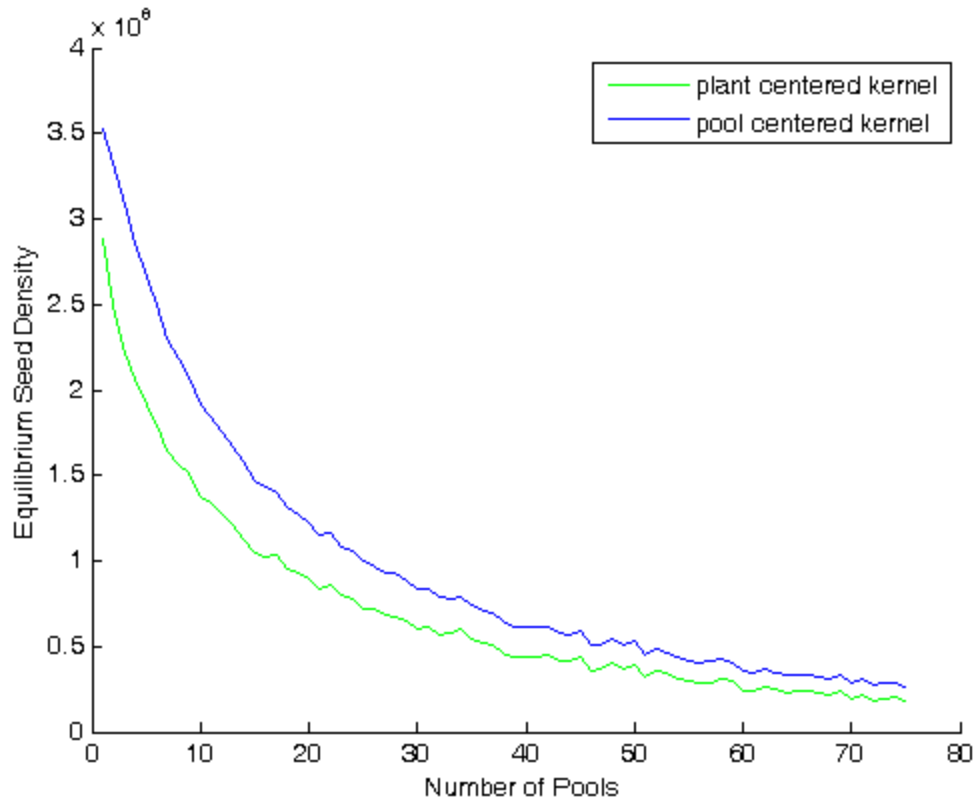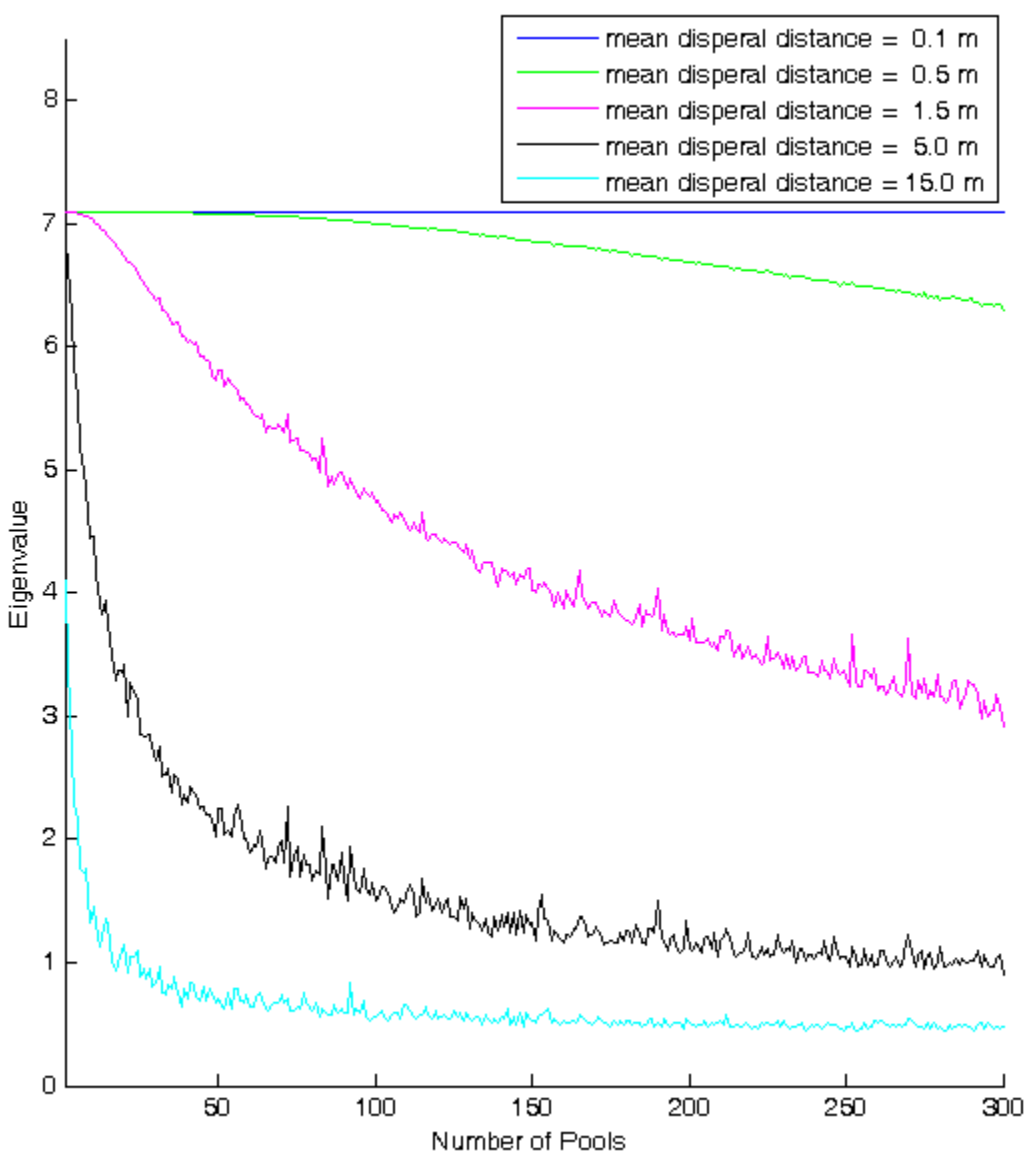
Figure 2.4. The effect of habitat fragmentation on a population with various mean dispersal distances. Note that for large enough mean dispersal distance (in this plot 15.0 m) the eigenvalue converges to 0.44 as expected. For all other mean dispersal distances it takes further fragmentation to achieve this convergence.

Chapter 3

Critical Patch Size for fragmented Populations in a Random Landscape

Matthew Holden

Many plant and animal populations with non-overlapping generations live in landscapes fragmented by suburban sprawl. To reduce future impacts on these natural populations, it is critical to understand how this fragmentation affects population growth. In chapter (2), I showed that for annual plants in a two dimensional patchy landscape, population growth at low density decreases with increased habitat fragmentation. In addition, numerical simulations suggest that as the population becomes increasingly fragmented, the growth rate at low population densities approaches a limiting value. Since limiting values may be used to calculate the minimum proportion of landscape needed to be set aside for population persistence, it is important to have a solid theoretical foundation for calculating such values. Unfortunately, the limiting value for population growth at low densities, supported by numeric simulations in chapter (2), is difficult to prove analytically because pool locations were chosen at random and then discarded if they overlapped other pools. However, it is possible to derive an expression for the population growth at low densities for infinitely fragmented populations in simpler random landscapes.

In this chapter, I will look at a more realistic model of population dynamics, on a simple one-dimensional landscape, and prove a condition in the same spirit as condition (2.7) of chapter (2). Although it is generally thought that one dimensional landscapes are a major simplification of the two dimensional habitats that exist in nature, it should be noted that they can describe some species ranges fairly accurately (Hastings and Botsford 2006, Medina-Vogel et al.2008). In general, integrodifference models are more realistic in the sense that population growth at a particular location is defined by the population density at that location. In addition dispersal is no longer modeled as a probability of moving from one patch to another, but rather the probability of dispersing from one exact location in space to another exact location. For the model presented in chapter (2), either populations were assumed to disperse all their propagules from the center of the pool, or dispersal was determined by an averaged dispersal kernel, assuming uniformly distributed individuals within the pool. Neither of these accurately model dispersal because individuals that live on the edge of a pool will disperse more of their propagules outside the pool's boundaries than individuals located in the center. For this reason, it was hypothesized in chapter (2) that the uniform version of modeling dispersal gave a lower bound for population growth at low densities, and the pool centered method gave an upper bound. However, an intergrodifference model should produce a value closer to the actual population growth at low densities.

The Model:

Assume a population is contained in a one dimensional landscape, and let this landscape be the subset of the real line [0,1] divided into subintervals characterized as suitable or unsuitable habitat. There are many ways in which suitable habitat can be distributed through out a landscape. One could imagine an example where suitable habitat is densely packed in certain

parts of the interval but separated by large obstructions such as lakes or mountain ranges. Other potential habitat configurations may include patches evenly spread or patches randomly distributed throughout space. In all these cases the landscape can be represented by a general function $L(y)$, where if location y denotes suitable habitat $L(y)=1$, and if the habitat is unsuitable at location y, $L(y)=0$. Imagine a population of size N_t, in year t, that inhabits such a landscape and survives based on the local density at time t according to the function $g(N_t(x)):[0,\infty)\to[0,\infty)$, and disperses propagules from location y to location x according to a continuous dispersal kernel $k(x,y):[0,1]\times[0,1]\to[0,\infty)$. Hence, we can model the population as the integrodifference equation:

$$N_{t+1}(x) = \int_0^1 k(x,y)g(N_t(y))L(y)dy. \qquad (3.1)$$

For the rest of this paper I will consider L(y) to be a random function, in which η patches of length $1/\eta$ are randomly chosen as suitable or unsuitable habitat. Specifically, equation (3.1) now becomes:

$$N_{t+1}(x) = \int_0^1 k(x,y)g(N_t(y))L_\eta(y)dy \qquad (3.2)$$

Where L_η is the landscape function corresponding to a habitat with η patches, defined as:

$$L_\eta(x) = \sum_{i=1}^{\eta} Y_i f_i(\eta x), \qquad (3.3)$$

with Y_1, Y_2,…, Y_n as a sequence of independent Bernoulli random variables with $\Pr(Y_i=1)=\rho$ and $\Pr(Y_i=0)=1-\rho$. The function f_i is defined by $f_i(x)=1$ for $x\in\left[\dfrac{i-1}{\eta},\dfrac{i}{\eta}\right)$ and zero otherwise. This function essentially puts each Y_i value on the ith subinterval, and allows us to define a random landscape in which the ith subinterval is unsuitable if $Y_i=0$ and suitable if $Y_i=1$.

Anaysis:

Assume for a given x, that the functions k and g are continuous in y. Therefore combining k and g into a single function $h(y)$, we have the dynamics at a particular point in space, x, governed by

$$N_{t+1}(x) = \int_0^1 k(x,y)g(N_t(y))L_\eta(y)dy = \int_0^1 h(y)L_\eta(y)dy. \qquad (3.4)$$

Now to understand how the dynamics behave as the landscape becomes infinitely fragmented we have the following theorem.

Theorem 1: $\int_0^1 h(y)L_\eta(y)dy \longrightarrow \rho \int_0^1 h(y)dy$ as, $\eta \to \infty$, with probability one, for all $h(y)$ continuous on $[0,1]$.

In the proof of this theorem, I will use the following two lemmas:

Lemma 1: $\int_a^b L_\eta(y)dy \longrightarrow \rho(b-a)$ as $\eta \to \infty$ with probability one for all $[a,b] \subseteq [0,1]$.

Proof: Let a', b' be such that $a < a' < b' < b$, where a' and b' lie exactly on one of the divisions of the $1/\eta$ subintervals, closest to a and b respectively. Therefore,

$$
\begin{aligned}
\left| \int_a^b L_\eta(y)dy - \rho(b-a) \right| &\leq \left| \int_a^b L_\eta(y)dy - \int_{a'}^{b'} L_\eta(y)dy \right| + \left| \int_{a'}^{b'} L_\eta(y)dy - \rho(b-a) \right| \\
&= \left| \int_a^{a'} L_\eta(y)dy + \int_{b'}^b L_\eta(y)dy \right| + \left| \int_{a'}^{b'} L_\eta(y)dy - \rho(b-a) \right| \\
&= \left| \sum_{i=1}^\eta Y_i \int_a^{a'} f_i(\eta x)dy + \sum_{i=1}^\eta Y_i \int_{b'}^b f_i(\eta x)dy \right| + \left| \sum_{i=1}^\eta Y_i \int_{a'}^{b'} f_i(\eta x)dy - \rho(b-a) \right| \\
&= |a' - a| + |b - b'| + \left| (b' - a')\sum_{i=1}^\eta \frac{Y_i}{\eta} - \rho(b-a) \right| \\
&\leq \frac{2}{\eta} + \left| (b' - a')\sum_{i=1}^\eta \frac{Y_i}{\eta} - \rho(b-a) \right|
\end{aligned}
$$

Since,

$$
\left| (b' - a')\sum_{i=1}^\eta \frac{Y_i}{\eta} - \rho(b-a) \right| \leq (b' - a')\left| \sum_{i=1}^\eta \frac{Y_i}{\eta} - \rho \right| + \rho|b' - b| + \rho|a' - a| \leq (b' - a')\left| \sum_{i=1}^\eta \frac{Y_i}{\eta} - \rho \right| + \frac{2\rho}{\eta}
$$

and the Strong Law of Large Numbers implies that $\sum_{i=1}^\eta \frac{Y_i}{\eta}$ converges with probability one to ρ, it follows that

$$
\limsup_{n \to \infty} \left| \int_a^b L_\eta(y)dy - \rho(b-a) \right| \leq \lim_{n \to \infty} \frac{2\rho + 2}{\eta} = 0,
$$

with probability one. Clearly, since the $\liminf_{n \to \infty} \left| \int_a^b L_\eta(y)dy - \rho(b-a) \right|$ is non-negative as well, we have:

$$\lim_{n\to\infty}\left|\int_a^b L_\eta(y)dy - \rho(b-a)\right| = 0 \text{ with probability one.}$$

Therefore,

$$\int_a^b L_\eta(y)dy \longrightarrow \rho(b-a), \text{ with probability one, as } \eta\to\infty \text{ for all } [a,b]\subseteq[0,1].$$

<div align="right">QED</div>

Lemma 2: There exists a dense countable subset of the set of all continuous functions from $[0,1]\to\mathbb{R}$.

Proof: To see this we construct one by defining H_n, for any $n\geq 1$, to be the piecewise continuous functions h given by $h(i/n)$ is rational for any $i = 0,\ldots, n$ and h is linear on the intervals $\left[\dfrac{i-1}{n},\dfrac{i}{n}\right]$ for $1\leq i\leq n$. For each n, H_n is countable, since the rationals are countable and there are finitely many intervals. Therefore, because a countable union of countable sets is countable, $H = \bigcup_{n=1}^{\infty} H_n$ is countable.

To prove that H is dense in the set of all continuous functions from $[0,1]\to\mathbb{R}$, we need to show that given an $\varepsilon > 0$, and a continuous $h:[0,1]\to\mathbb{R}$, there exists a $\tilde{h}\in H$ such that $\left|h(x)-\tilde{h}(x)\right| < \varepsilon$ for all $x\in[0,1]$.

Since h is continuous, choose n such that $|x-y| < \dfrac{1}{n}$ implies $\left|h(x)-h(y)\right| < \dfrac{\varepsilon}{5}$ for all $x,y\in\left[\dfrac{i-1}{n},\dfrac{i}{n}\right]$, where $1\leq i\leq n$. In addition, because the rationals are dense in the reals, there exists a $\tilde{h}\in H$ such that $\left|h(i/n)-\tilde{h}(i/n)\right| < \dfrac{\varepsilon}{5}$ for all i, $0\leq i\leq n$. Therefore, for $x\in\left[\dfrac{i-1}{n},\dfrac{i}{n}\right]$, we have

$$\left|h(x)-\tilde{h}(x)\right| \leq \left|h(x)-h(i/n)\right| + \left|h(i/n)-\tilde{h}(i/n)\right| + \left|\tilde{h}(i/n)-\tilde{h}(x)\right|$$
$$< \frac{2\varepsilon}{5} + \left|\tilde{h}(i/n)-\tilde{h}(x)\right|$$

Since $\tilde{h}$ is linear on $\left[\dfrac{i-1}{n},\dfrac{i}{n}\right]$, we know $\left|\tilde{h}\left(\dfrac{i}{n}\right)-\tilde{h}(x)\right| \leq \left|\tilde{h}\left(\dfrac{i}{n}\right)-\tilde{h}\left(\dfrac{i-1}{n}\right)\right|$ and consequently,

$$\left|h(x)-\tilde{h}(x)\right|<\frac{2\varepsilon}{5}+\left|\tilde{h}\left(\frac{i}{n}\right)-h\left(\frac{i}{n}\right)\right|+\left|h\left(\frac{i}{n}\right)-h\left(\frac{i-1}{n}\right)\right|+\left|h\left(\frac{i-1}{n}\right)-\tilde{h}\left(\frac{i-1}{n}\right)\right|\leq\varepsilon$$

Thus H is dense in the set of all continuous functions from $[0,1]\to\mathbb{R}$.

$$\text{QED}$$

Proof of Theorem: Let $\eta\in\mathbb{N}$ be the number of intervals on the landscape with size $1/\eta$. Since all continuous functions on a closed interval are uniformly continuous, $h(y)$ is uniformly continuous with respect to y. Therefore, given $\varepsilon>0$, there exists a $\delta>0$, such that for all $y, y_0\in[0,1]$, $\left|y-y_0\right|<\delta$, implies $\left|h(y)-h(y_0)\right|<\frac{\varepsilon}{6}$.

Choose $m\in\mathbb{N}$ such that $\frac{1}{m}<\delta$. By the triangle inequality we have,

$$\left|\int_0^1 h(y)L_\eta(y)dy-\rho\int_0^1 h(y)dy\right|\leq\left|\int_0^1 h(y)L_\eta(y)dy-\rho\sum_{j=1}^m\frac{h(y_j)}{m}\right|+\left|\rho\sum_{j=1}^m\frac{h(y_j)}{m}-\rho\int_0^1 h(y)dy\right| \quad (3.5)$$

The first term on the right hand side has the following upper bound:

$$\left|\int_0^1 h(y)L_\eta(y)dy-\rho\sum_{j=1}^m\frac{h(y_j)}{m}\right|\leq\sum_{j=1}^m\left|\int_{(j-1)/m}^{j/m}\left[h(y)-h(y_j)\right]L_\eta(y)dy\right|+\sum_{j=1}^m\left|\int_{(j-1)/m}^{j/m}h(y_j)L_\eta(y)dy-\rho\frac{h(y_j)}{m}\right|$$

$$<\frac{\varepsilon}{6}\sum_{j=1}^m\int_{(j-1)/m}^{j/m}L_\eta(y)dy+\sum_{j=1}^m\left|h(y_j)\int_{(j-1)/m}^{j/m}L_\eta(y)dy-\rho\frac{h(y_j)}{m}\right|$$

$$\leq\frac{\varepsilon}{6}+\sum_{j=1}^m\left|h(y_j)\right|\left|\int_{(j-1)/m}^{j/m}L_\eta(y)dy-\frac{\rho}{m}\right|$$

For the second term of the right hand side of the inequality (3.5), we have:

$$\left|\rho\sum_{j=1}^m\frac{h(y_j)}{m}-\rho\int_0^1 h(y)dy\right|=\left|\rho\sum_{j=1}^m\int_{(j-1)/m}^{j/m}\left[h(y_j)-h(y)\right]dy\right|<\frac{\varepsilon}{6}\rho.$$

Therefore, by **lemma 1** and the fact that $\rho\leq1$, for any $\varepsilon>0$,

$$\limsup_{\eta\to\infty}\left|\int_0^1 h(y)L_\eta(y)dy-\rho\int_0^1 h(y)dy\right|\leq\frac{\varepsilon}{3},$$

for a measureable set of $\{Y_i\}$ sequences, Ω_ε, such that $\Pr(\Omega_\varepsilon)=1$. Letting $\{\varepsilon_n\}=\frac{1}{n}$, we have

$\Pr\left(\bigcap_{n=1}^\infty\Omega_{\varepsilon_n}\right)=1$, since the intersection of countable sets with probability one also has probability

one.

Now we have a set of sequences that work for a given continuous $h(y)$ for all ε, call it

$\Omega_h = \bigcap\limits_{n=1}^{\infty} \Omega_{\varepsilon_n}$, i.e. $\lim\limits_{\eta\to\infty}\left|\int_0^1 h(y)L_\eta(y)dy - \rho\int_0^1 h(y)dy\right| = 0$ for all $\{Y_i\} \in \Omega_h$. However, we need a set

of sequences that will not only satisfy the limit for a particular $h(y)$, but for all continuous $h(y)$. By **lemma 2** we have a countable set of continuous functions, $\{h_i, i = 1,2,\dots\}$, that are dense in the set of all continuous functions. By the above result we have the inequality holding for a particular set of sequences for each h_i. To find a set of sequences h_i that work for all $h(y)$ we

take the intersection of the sequences $\{Y_i\}$ that work for each function h_i, i.e. $\tilde{\Omega} = \bigcap\limits_{n=1}^{\infty}\Omega_{h_n}$. The

claim is that this set of sequences will satisfy $\lim\limits_{\eta\to\infty}\left|\int_0^1 h(y)L_\eta(y)dy - \rho\int_0^1 h(y)dy\right| = 0$ for any

continuous h.

Since $\{h_i\}$ is dense in the set of all continuous functions, for all h, there exists a h_i such

that $\left|h_i(y) - h(y)\right| < \dfrac{\varepsilon}{3}$ for all $y \in [0,1]$. By the triangle inequality we have,

$$\left|\int_0^1 h(y)L_\eta(y)dy - \rho\int_0^1 h(y)dy\right| \le \left|\int_0^1 h(y)L_\eta(y)dy - \int_0^1 h_i(y)L_\eta(y)dy\right|$$
$$+ \left|\int_0^1 h_i(y)L_\eta(y)dy - \rho\int_0^1 h_i(y)dy\right|$$
$$+ \left|\rho\int_0^1 h_i(y)dy - \rho\int_0^1 h(y)dy\right|$$

Applying the density property of h_i, the right hand side becomes:

$$\le \frac{\varepsilon}{3} + \left|\int_0^1 h_i(y)L_\eta(y)dy - \rho\int_0^1 h_i(y)dy\right| + \frac{\varepsilon}{3}\rho$$

Taking the limit and by the definition of $\tilde{\Omega}$, we get

$$\limsup\limits_{\eta\to\infty}\left|\int_0^1 h_i(y)L_\eta(y)dy - \rho\int_0^1 h(y)dy\right| \le \varepsilon$$

for all $\{Y_i\} \in \tilde{\Omega}$. Since $\varepsilon > 0$ was arbitrary we get

$$\lim\limits_{\eta\to\infty}\int_0^1 h(y)L_\eta(y)dy = \rho\int_0^1 h(y)dy \text{ for all } \{Y_i\} \in \tilde{\Omega}.$$

QED

To determine whether the growth of the population is positive or negative at low densities, one cam find the eigenvalue of the linearized version of equation (3.1) around the zero

equilibrium. This leads to the general eigenvalue problem:

$$\lambda \mu(x) = \int_0^1 k(x, y) g'(0) L_\eta(y) \mu(y) dy . \qquad (3.6)$$

Kot and Schaffer (1986) are able to derive an expression for the eigenvalue for the simplest landscape function, $L(y) = 1$, and specific $k(x, y)$. However, the major difficulty in finding the eigenvalue given by (3.6) is that the expression on the right is the integral of a random function. Yet, we showed in our theorem that the dynamics given by (3.2) as the number of patches approaches infinity converges almost surely to a non-random integral for each x. From this new equation one can more easily calculate the eigenvalue using the methods outlined in (Kot and Schaffer 1986). Specifically, by our Theorem, as the landscape becomes infinitely fragmented, the population dynamics at a particular point in space, x, well approximated by

$$N_{t+1}(x) = \rho \int_0^1 k(y, x) g(N_t(y)) dy \qquad (3.8)$$

Thus, the general eigenvalue problem for this random landscape, given by (3.6), turns into

$$\lambda \mu(x) = \rho \int_0^1 h(y) \mu(y) dy . \qquad (3.9)$$

The proof of our theorem can be extended from [0, 1] to any interval [-S/2, S/2] where S is the length of the habitat. Hence, using the steps outlined in Kot and Schaffer, for a population with a Laplacian dispersal kernel, given by equation (2.3), with a mean dispersal distance of $1/\alpha$ and a Beverton-Holt growth function,

$$g(N(y)) = \frac{rN(y)}{aN(y) + b} \qquad (3.10)$$

analogous to the reciprocal yield law used in (2.2), where the parameters were $r = cA_i$, $a = \varepsilon_g \gamma$, and $b = cA_i$, the critical patch size becomes:

$$S^* = \frac{2}{\alpha \sqrt{\frac{\rho r}{b} + \rho - 1}} \tan^{-1} \left(\frac{1}{\sqrt{\frac{\rho r}{b} + \rho - 1}} \right) . \qquad (3.11)$$

Note that if $\rho < 1$ the critical habitat size must be larger than if the landscape is homogeneous. As the proportion of the landscape occupied by suitable habitat increases the critical habitat size decreases exponentially (fig. 3.1). Interestingly there is also a critical fraction of habitat that must be occupied no matter how large the habitat is, in order for the population to persist, defined by

$$\rho^* = \frac{b}{r + b} . \qquad (3.12)$$

The limit as $\lim\limits_{\rho \to \rho^{*+}} S = \infty$. If $\rho < \rho^*$ the critical patch size is a complex number with a negative real component, which obviously can not be satisfied in nature, meaning the population always goes extinct.

Discussion:

Although not analogous to finding the eigenvalue for the vernal pool plant metapopulation in chapter (2), the analysis from both models produce a similar result. In chapter (2) it was shown numerically that the limiting eigenvalue, as the population became infinitely fragmented, depended on the intrinsic growth of the population determined by the life history parameters of the plant, and the proportion of the landscape occupied by vernal pools. The integrodifference model shows that the limiting value also depends on the growth rate of the population $g'(0)$, but also ρ, the probability of a patch being occupied. **Lemma 1** showed that in the limiting case, where the number of patches approaches infinity, the proportion of landscape occupied by suitable habitat converges to ρ with probability one. However, the difference between these landscapes is great for a small number of patches. In the one patch case for the model in chapter (2) there is one vernal pool that occupies a specified proportion of the landscape. However, for the random landscape function L_1 there is either one pool that occupies the whole landscape with probability ρ or there is no suitable habitat at all with probability 1-ρ. Even for L_2, the landscape is either completely suitable, half suitable, or completely unsuitable. Therefore, in these cases the proportion of the landscape occupied is not analogous to ρ.

However, one can create one dimensional landscapes that more closely match the two dimensional configuration described in chapter (2). In this case we could let $\rho = p/q$ be a rational number equal to the proportion of the landscape occupied by inhabitable patches. Then divide the landscape into nq intervals and choose ρnq intervals without replacement to deem as suitable habitat. Unlike the last example, in this landscape there is the limitation that ρ is restricted to rational numbers. However, this would not create problems in a practical sense, because a land manager would only be using rational numbers for measurements in the field. This model has a more complicated probability space, and hence may be more difficult to prove a theorem similar to the one proved in this chapter. In the future I would like to be able to prove or disprove the convergence of the integral using this random landscape method. This will be a step closer to understanding why the eigenvalue in chapter (2) converges to a number proportional to the amount of habitat occupied by vernal pools as the population becomes infinitely fragmented.

Figure 3.1. The critical habitat size vs. habitat fragmentation with $r/b = \alpha = 1$. Note that $\rho^* = 0.5$, as the theory predicts.
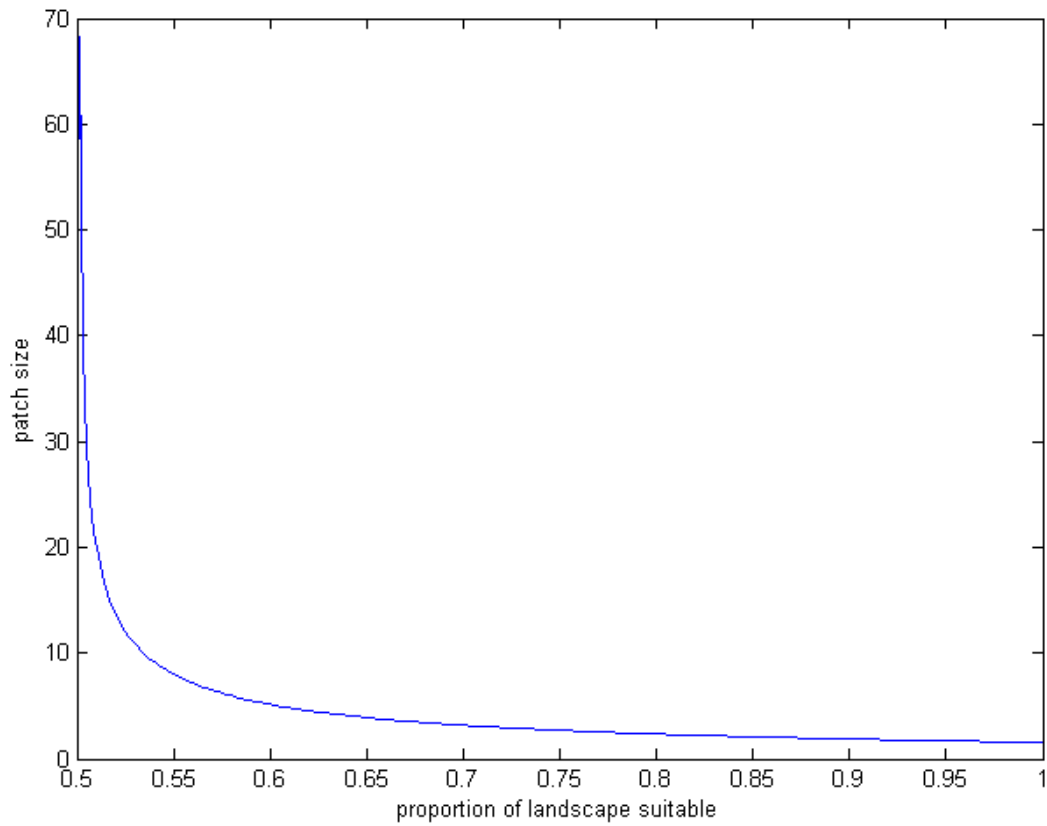
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