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THE EFFECTS OF HABITAT CORRIDORS AND EDGES

ON SOURCE OF SEED MORTALITY:

IMPLICATIONS FOR RESTORING A THREATENED LEGUME

by

Melissa Joy Simon

A thesis presented to the
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ABSTRACT OF THE THESIS

The Effects of Habitat Corridors and Edges on Sources of Seed Mortality:

Implications for Restoring a Threatened Legume

By

Melissa Joy Simon

Master of Arts in Evolution, Ecology & Population Biology

Washington University in St. Louis, 2010

Professor Ellen Damschen, Chairperson

The unprecedented rate of global biodiversity decline can be attributed to anthropogenic influences, primarily habitat loss or the change in land use. Habitat loss creates isolated habitat fragments, reduces the area of previously contiguous habitat, and increases the amount of edge relative to area. Additionally, these factors with induced edge effects, influence the survival and abundance of species, and ultimately increase the likelihood of local extinction.

Corridors are conservation tools used by land managers to mitigate the negative effects of fragmentation. While several studies have shown that corridors can be beneficial for species and their interactions, few have examined how corridors can influence species mortality. Such studies, especially for species of conservation concern are essential for informing restoration and conservation planning.

Using a replicated, large-scale experimental landscape, I examined how corridors and edge effects influence interactions that may be detrimental to plant population dynamics: seed predation by small mammals and invertebrates, and seed mortality induced by pathogenic fungi. Because corridors connect two otherwise isolated patches and inherently add habitat area and change habitat edge-to-area ratios, such "connectivity", "area" and "patch shape" effects were controlled for in the design of the study. A threatened legume, *Baptisia lanceolata* (Fabaceae) was the study's focal species. Because of its restoration concern, my results yield information directly applicable to its conservation.

I found that corridors do not facilitate seed predation of *B. lanceolata* by small mammals or arthropods. However, I provide evidence that *B. lanceolata* suffers more from the small mammals than arthropods in patch centers and when ground cover by plants is high. These results imply that small mammals use the ground vegetation as refuges, allowing them to increase foraging rates while decreasing exposure and thus risk from edge-dwelling predators.

My results also indicate that corridors do not increase the seed mortality caused by pathogenic fungi. I found no significant difference in the viability of fungicide treated and untreated seeds, implying that *B. lanceolata* is able to withstand the potential soil

microorganism changes induced by landscape alteration and edges. In addition, seed germination showed a response to patches with high amounts of edge and soil moisture holding capacities. This trend suggests that corridor or winged patches may provide conditions favorable for seed to break dormancy.

It is possible that *Baptisia lanceolata* will benefit from its net interactions influenced by corridors. However, more research will be required to determine how corridors and edges affect the other transitions and stages in the rare plant's life history.

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Dedication

To my parents, Larry and Ana Simon, thank you for always believing in me

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Chapter 1

The effects of corridors and edges on the seed predation of a threatened legume:

Implications for restoring *Baptisia lanceolata*

Abstract

Studies on habitat corridors have increased over the past decade, providing evidence that corridors are mostly beneficial for species. As tools used by land mangers to maintain biodiversity, corridors may facilitate the beneficial or antagonistic interactions for species of conservation concern. Seed predation can be influenced by corridors and can be detrimental to plant populations. However, evidence of this antagonistic interaction has focused on common plants, and not on species of conservation of concern. In this study I use large-scale replicated experimental landscapes to examine how corridors affect the seed predation of a rare legume, *Baptisia lanceolata* by small mammals and arthropods. I examined this interaction among three different habitat patch types to test the connectivity, area, and "drift fence" effects of corridors. Because corridors create habitats that contain high amounts of edge, which can influence seed predator behavior, I also examined this interaction within patches, near and away from edges. I found that corridors and patch type do not increase seed predation by small mammals and arthropods, but within-patch effects show increased seed predation in the centers of habitat patches. Seed predation was higher by small mammals, and was influenced by surrounding vegetation cover, suggesting small mammal foraging may be influenced by anti-predator behavior. These results imply that *B. lanceolata* may be more threatened in locations where small mammals experience less experience less risk from edge-dwelling predators.

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Introduction

Habitat loss is the primary driving force behind the world's decline in biodiversity

(Wilcove et al. 1998; Sala et al. 2000). Occurring at an alarming rate, habitat loss can

fragment land and create isolated patches, while reducing habitat area and altering patch

geometry and edge-to-area ratios. Such habitat alterations are a growing concern for

ecosystem and species conservation and restoration.

One strategy that land managers have implemented to mitigate negative

consequences of fragmentation is by using habitat corridors. Corridors are linear strips of

habitat that connect two otherwise isolated patches (Diamond 1975). They are touted to

buffer against local extinction rates via 'rescue effects' (sensu Brown and Kodric-Brown

1977), as well as increase species abundance and gene flow, but their use has been

controversial because evidence has lagged behind implementation (Rosenberg et al.

1997; Simberloff et al. 1992). Empirical evidence favoring habitat corridors has recently

increased (Gilbert-Norton et al. 2010), supporting hypotheses that corridors can increase

gene flow (Mech and Hallett 2001), individual movement (Gonzalez et al. 1998; Haddad

et al. 2003), species interactions (e.g. Tewksbury et al. 2002) and even increase plant

species richness (Damschen et al. 2006). Corridors can have positive effects on plants,

facilitating mutualistic interactions such as pollination (Townsend and Levey 2005) and

seed dispersal (Tewksbury et al. 2002; Levey et al. 2005). However, corridors may also

have negative effects on plant species at different life history stages, affecting

interactions such as seed predation by small mammals and arthropods (Orrock 2003;

Orrock and Damschen 2005).

For plants, antagonistic interactions, such as seed predation and herbivory can have detrimental effects on plant population dynamics and viability (Louda 1982; Crawley 1992; Maron and Simms 1997; Maron and Crone 2006), and can ultimately lead to shifts in the plant community structure (Brown and Heske 1990; Howe and Brown 2001). Factors such as habitat connectivity and geometry can alter plant consumer distribution or behavior, and may result in differential effects, depending on the plant and consumer of interest (Orrock and Damschen 2005).

Specifically, corridors can affect species distributions and interactions because they can influence between-patch and within-patch processes. Between-patch responses to corridors may result because of "connectivity effects" (i.e. corridors connect two otherwise isolated patches), "area effects" (i.e. amount of area is increased), and "patch shape effects" (i.e. habitat shape and amount of edge is increased). Additionally, corridors can influence within-patch processes. The amount and proximity to edges can influence within-patch habitat quality and in turn impact species behavior and distributions (Fagan et al. 1999; Ries et al. 2004). Proximity to edges and refuge availability can likewise influence species vulnerability to predators, and could impact prey distributions (Lima and Dill 1990). It is therefore essential to differentiate between the between-patch effects and the within-patch edge effects that corridors may influence. Understanding the relative impacts of both positive and negative effects of corridors on focal species, as well as the role of between- and within-patch effects, can inform restoration actions where consequences of antagonistic interactions may outweigh those of beneficial interactions.

In this study, I examine how connectivity, patch geometry, proximity to habitat edges and surrounding vegetation cover affect the seed predation of *Baptisia lanceolata*. While most seed removal studies focus on the predation of common plant species, I present a unique case that attempts to understand the dynamics of seed predation for a threatened species where it may matter the most. I also examine how locations *within* patches can further affect seed removal by different species. As corridors and edges may have differential effects on seed predators, I distinguish levels of seed predation between small mammals and invertebrates in order to inform restoration efforts of this threatened species.

Methods

Study Site

The study was conducted at the National Environmental Research Park (NERP), Savannah River Site near Aiken, South Carolina. Experimental landscapes consisted of five habitat patches that were cleared and burned within a matrix of mature loblolly pine forest. The landscapes were created to study how habitat connectivity and fragmentation affect the longleaf pine ecosystem habitat in a restoration context. Landscapes consisted of one center or source patch (100x100m) surrounded by 4 patches, each 150m away. One peripheral patch was connected to the center patch via a 25m-wide habitat corridor, while the other 3 peripheral patches were separated from the center patch by 150m of habitat matrix. Because corridors inherently change the habitat geometry, adding habitat area and altering edge-to-area ratios, three types of peripheral patches were used to control for such changes. "Winged" patches were 100x100m with two 25x75m corridor-

like strips on the ends that controlled for changes in edge-to-area ratios and "drift fence" effects (sensu Haddad and Baum 1999). "Rectangular" patches were 137.5x100m and controlled for the area added with the application of a habitat corridor (Figure 1.1). Each experimental landscape contained one extra replicate of either a winged or rectangular patch. Though eight experimental landscapes were available at the site, seven were used because of the widespread presence of a more common *B. lanceolata* congener at one experimental landscape. In the seven that were used, four landscapes had a replicated winged patch, and three contained a replicated rectangular patch. In this experiment I randomly selected one replicated patch, using one of each patch type per landscape.

Focal Species

Baptisia lanceolata (Fabaceae) is a legume endemic to the southeastern United States, present in only Alabama, Georgia, Florida and South Carolina (USDA 2010). In South Carolina, where this study was conducted, *Baptisia lanceolata* is listed as rare because it is only found in two counties (Knox and Sharitz 1990; South Carolina DNR 2010). It is of restoration concern because of its association with the longleaf pine ecosystem, which historically dominated the southeastern United States but is now highly fragmented and threatened (Noss 1989). In addition, *Baptisia* is listed as a longleaf pine indicator species (Peet 2006) and may play an important role in ecosystem functioning since it is a nitrogen-fixing early successional plant.

Ecological processes such as seed dispersal, and interspecific interactions including seed predation, may confine the distribution and abundance of *Baptisia lanceolata*. Seeds are dispersed via explosive dehiscence (Knox and Sharitz 1990)

between August and November, and experience secondary dispersal by tumbling or by harvester ants (*Pogonomyrmex spp.*) (Mehlman 1993b). Predispersal seed consumption of *Baptisia* by insect predators can significantly limit the number of seeds available for dispersal (Horn and Hanula 2004; Haddock and Chaplin 1982). Predispersal seed predators such as the weevil *Apion rostrom* and lepidopteran *Grapholita tristrigana* can induce premature pod abortion and consume seeds in the pods directly, reducing the number of viable seeds (Horn and Hanula 2004; M.Simon unpublished data). While studies of predispersal seed predation have shown that insect seed predators can limit *Baptisia* persistence, to my knowledge, there have been no studies examining the sources of seed mortality after seed dispersal.

Post dispersal seed predation

Post dispersal seed predation trials were conducted using pairs of cylindrical plastic trays each 16cm in height, and 18cm in diameter (Mattos and Orrock 2010). Pairs of trays were placed at two distances from one randomly selected patch edge of each patch type. One pair was located within 5m of the patch edge (i.e. "edge" location), and the other 25m from the edge (i.e. "center" location) (Figure 1.1). Trays were filled with ~0.24L of sterile sand, with a similar texture to the sandy soils of the area, and were covered with tight fitting lids to prevent seed loss from wind and rain. For each tray, two 3.8x3.8cm square holes were cut on opposite sides of the containers, 2.5cm from the bottom. One tray at the edge and at the patch center held wire mesh with 1.3cm openings over its holes to exclude small mammals but allow arthropods (hereafter referred to as ARTH), while the other tray was open to both arthropods and small mammals (hereafter referred to as

OPEN). All trays contained 10 *Baptisia lanceolata* seeds placed on top of the sand.

Trays were placed in the field for approximately one month (28 September 2008 - 27

October 2008) to help control for factors such as moonlight, which can affect rodent

foraging (Kotler 1984; Bowers 1988). Upon retrieval, contents of the trays were sifted

and the remaining seeds were counted. I assumed that seeds removed from the containers

were consumed, as supported by other studies in this system (Orrock et al. 2003), and

because of visual evidence of seed predation, such as partially consumed seeds, in 9% of

the trays.

Vegetation and ground cover characteristics were also recorded in a 1m radius

around seed tray pairs on 28 September 2008. Percent bare ground, average vegetation

height, and distances to the four closest potential small mammal refuges were measured

by a single observer (M.J.S.). In this study, small mammal refuges were classified as

downed logs, piled woody debris and dense shrubs, all of which can play a role in small

mammal distribution (Tallmon and Mills 1994; Loeb 1999; McCay 2000) and seed

consumption by small mammals (Hulme 1997; Mason and Stiles 1998; Orrock et al.

2004).

Statistical analysis

I used a generalized linear mixed model (proc GLIMMIX) to determine how patch type

and location (i.e. at the patch edge or center) affected the post-dispersal seed predation by

arthropods and small mammals (Littell 2002). I used a binomial error distribution with a

log link function to model the fixed effects of patch type (connected, winged, or

rectangular), location (edge, center), exclosure type (ARTH or OPEN) with experimental

landscape as a random effect. To explore factors that could co-vary with seed removal, I

conducted a principal component analysis between the proportion of remaining seeds and

the surrounding vegetation and substrate data (i.e., percent bare ground, average

vegetation height, and distances to nearest refuges). Correlation analysis indicated that

PCA1 was highly correlated with percent bare ground (correlation coefficient 0.71,

P<0.001). Therefore, percent bare ground was used as a covariate in the mixed model.

All analyses were conducted using SAS Version 9.1 (SAS Institute 2002). Data from

containers that were disturbed or moved from their original location (perhaps by feral

pigs) were not included in the analysis (n=5).

Results

Seed removal by small mammals and arthropods did not significantly differ between

patch types (P>0.05). There was, however, a significant effect of location and exclosure

type (Table 1.1). Overall, seed removal was 15% higher in the centers of patches than

near edges ($F_{[1,91]}= 25.2$, P<0.01) and about 10% fewer seeds remained when small

mammals had access to trays than when excluded ($F_{[1,91]} = 8.8$, P<0.01) (Fig 1.2).

Percent of bare ground also had a significant effect on the proportion of seeds remaining

($F_{[1, 91]} = 10.17$, P>0.01), specifically for small mammals (Figure 1.3). The proportion of

seeds remaining was significantly lower when small mammals had access compared to

when only arthropods had access, especially when percent bare ground was lower than

80% (at 40% bare ground P>0.01, at 60% bare ground P>0.01, at 80% bare ground

P<0.05).

Discussion

Habitat corridors are a popular method used for conservation and restoration that create changes in the landscape geometry (via connectivity) and in edge-to-area ratios. In this study, I investigated how connectivity, patch geometry and distance from patch edge effect the seed predation of a threatened legume. My results indicate that connectivity and patch shape do not have significant effects on the seed predation of *Baptisia lanceolata*. Rather, I foundd that within-patch location and percent bare ground have significant influences on seed predation, and that these effects may be a function of edge-induced changes on patch microclimate, and seed consumer behavior.

The implementation of corridors increases the amount of edge in a habitat patch, which can affect species distributions (Haddad and Baum 1999; Mabry et al. 2003; Orrock et al. 2010 *in review*), their behavior (Levey et al. 2005) and interactions (Orrock and Damschen 2005). High levels of edge can influence microhabitat shade and temperature (Cadenasso et al. 1997) and can influence the species that persist and their interactions (Reis et al. 2004). As Louda et al. (1996) found for the mustard *Cardamine cordifolia*, shade was a major abiotic factor that determined the plant's persistence by buffering against shade-avoiding herbivores. Invertebrates are known to directly respond to habitat temperatures, core area and edges (Didham et al. 1998; Haddad and Baum 1999; Didham and Ewers 2008). In this system, I have found that temperatures increase with distance from the habitat edge (data not shown), suggesting that greater post-dispersal seed predation in the centers of patches may be a result from increased invertebrate activity and seed predation in response to increased temperature and solar load (also see Orrock et al. 2003; Orrock and Damschen 2005).

The spatial distribution of seed predation by small mammals may also be a result of habitat edges and small mammal behavior. Habitat corridors can alter the abiotic microhabitat and can induce anti-predator behavior, resulting in increased activity in habitat centers (Lima and Dill 1990; Mills 1995; Orrock and Danielson 2005) as I have seen in this study. Previous studies have shown that old-field mice (*Peromyscus polionotus*), a small mammal species common at the study site (Orrock and Danielson 2005), is more likely to be captured in the center of habitat patches (Mabry et al. 2003). Such habitat preferences may explain the increased level of seed removal by small mammals in patch centers, as similarly seen by Orrock and Danielson 2005. Microhabitat choice, however, must also be considered as complex cover and refuge availability may be a better predictor of small mammal abundance and activity (Tallmon and Mills 1994; Manson and Stiles 1998; Bowne et al. 1999). Here I found that percent ground cover had a significant impact on the proportion of *B. lanceolata* seeds remaining, specifically for cases where small mammals had seed access (Figure 1.3). My findings indicate that small mammals are able to use surrounding vegetation and debris as refuges, and in turn have a significant effect on seed predation pressure.

Fewer seeds also remained when small mammals had seed access, indicating higher rates of consumption by small mammals. Orrock and Damschen (2005) found seed size was a driving factor that led to differential rates of seed removal, where larger seeds (*Prunus serotina*) were primarily consumed by small mammals, and smaller seeds (*Rubus alleghniensis*) by arthropods. As *Baptisia lanceolata* seeds are comparable in size to *P.serotina*, my results indicate that small mammals are more frequent consumers of *B. lanceolata* than are arthropods. Limiting small mammal consumption at the seed

stage, especially in areas of high surrounding vegetation, may be an effective strategy for increasing the persistence of this species.

Fire is a cue that can initiate *Baptisia* seed germination, allowing individuals to leave the potentially vulnerable seed stage and permitting the regeneration of populations in longleaf pine seed banks (Maliakal et al. 2000; Marshall 2009; Coffey and Kirkman 2006). Though fire may degrade habitat quality for some small mammals, ultimately serving as a habitat sink in longleaf pine ecosystems (Sharp et al. 2009), post burn conditions still tend to promote high abundances of small mammals due to increased availability of seeds and seedling food resources (Torre and Diaz 2004; Sharp et al. 2009; Zwolak et al. 2010). Thus, fire may provide a short window that could allow *Baptisia* to escape from small mammal seed predation. Given these conditions, and the fact that *Baptisia lanceolata* leaves contain herbivore-deterring alkaloids (Cranmer and Turner 1967), restoration via seedling transplants may be among the most viable ways to help reconstruct populations.

Though my findings of how patch geometry and edges can affect the antagonistic interaction of post dispersal seed predation, further research needs to be conducted in order to fully assess how corridors affect this species' demography. The effect of corridors on a species is dependent on the *net* effects of interspecific interactions, both mutualistic and antagonistic. *Baptisia lanceolata* is pollinated by generalist pollinators (Haddock and Chaplin 1982), however its seeds are also consumed by various *pre*-dispersal seed predators, such as weevils and different lepidopeteran species, some of which are host specific (Frost 1945; Horn and Hanula 2004; Simon unpublished data). Pre-dispersal seed predation of *B.lanceolata* can dramatically affect the number of viable

seeds produced, and thus has a significant effect on the persistence of a viable population (Horn and Hanula 2004). Though the effect of corridors and spatial dynamics on pre-dispersal seed predation has yet to be documented, such an interspecific interaction would be critical to incorporate when compiling the effects of multiple interactions. Other sources of seed mortality, such as fungal and microbial attack in the seed bank, could also be included in a model to determine the most sensitive interaction that affect the population dynamics and thus give us a better understanding on how *Baptisia lanceolata* populations can be managed. Understanding how each stage of a plant's life is affected by landscape connectivity and edges is essential for determining the net impact of habitat corridors, and for designing a restoration or conservation plan for focal species.

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Figure and Table Legends

Figure 1.1

Experimental landscape at the Savannah River Site (SRS), near Aiken, South Carolina.

Seven experimental landscapes were used, each containing three patch types: connected,

winged and rectangular. Seed trays that allowed arthropods only (ARTH) or arthropods

plus small mammals (OPEN) were paired and randomly oriented at patch edge and

center.

Table 1. 1

Summary of general linear mixed model analysis of the removal of *Baptisia lanceolata*

seeds by arthropods (ARTH) and arthropods and small mammas (OPEN) in connected,

winged, and rectangular patches, and at patch edges and centers with percent bare ground

used as a covariate.

Figure 1.2

Proportion of seeds remaining in seed trays in each patch type at patch edge and center.

Black bars represent ARTH treatments that allowed arthropods only, where grey bars

represent OPEN treatments that allowed both arthropods and small mammals.

Figure 1.3

Mean proportions of seeds remaining as a function of percent bare ground and exclosure type. Proportion of seeds remaining is significantly lower when small mammals have access (dashed line) at 0.40 and 0.60 bare ground (denoted by asterisks $P<0.01$) as compared to when only arthropods had access. At 0.80 bare ground, $P>0.05$.

Figures and Tables

Figure 1.1
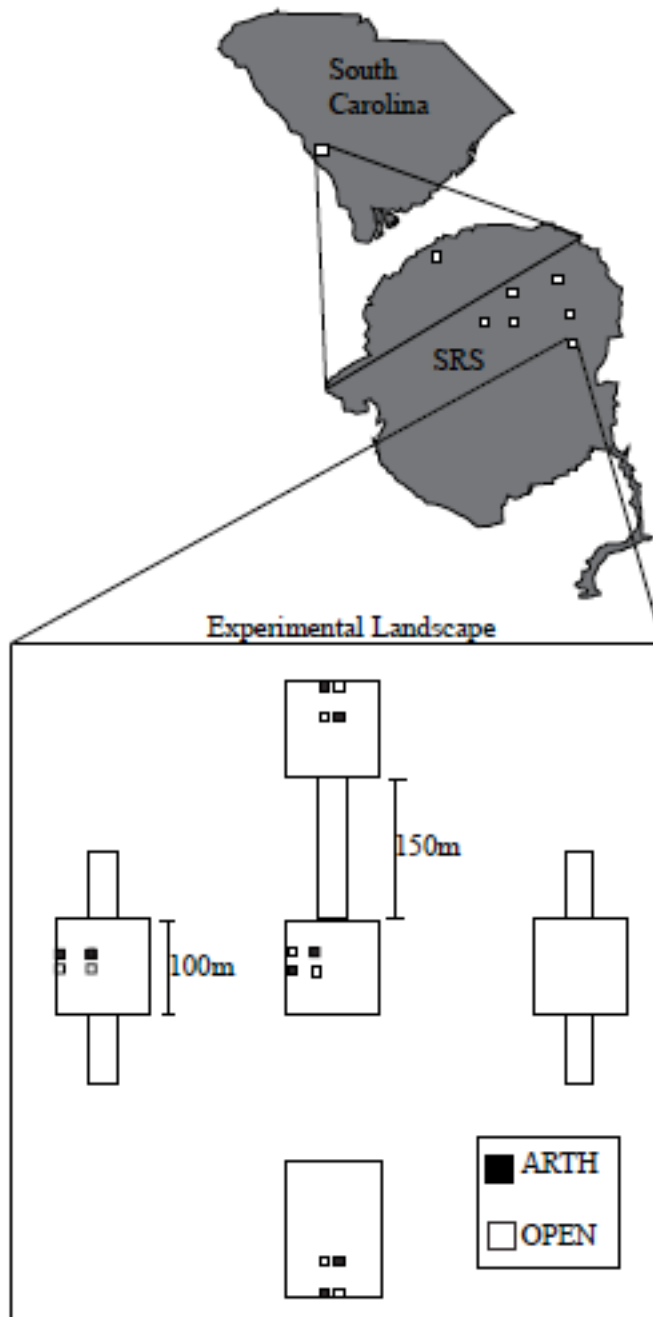
Table 1.1

Effect	F	df	P
Patch Type	1.97	2, 91	0.15
Location	25.2	1, 91	<0.01
Exclosure	8.8	1, 91	<0.01
% Bare Ground	10.17	1, 91	<0.01
Patch Type*Location	1.35	2, 88	0.27
Patch Type*Exclosure	0.27	2, 88	0.76
Location*Exclosure	0.36	1, 88	0.55
Bare Ground*Exclosure	2.54	1, 88	0.11

Figure 1.2
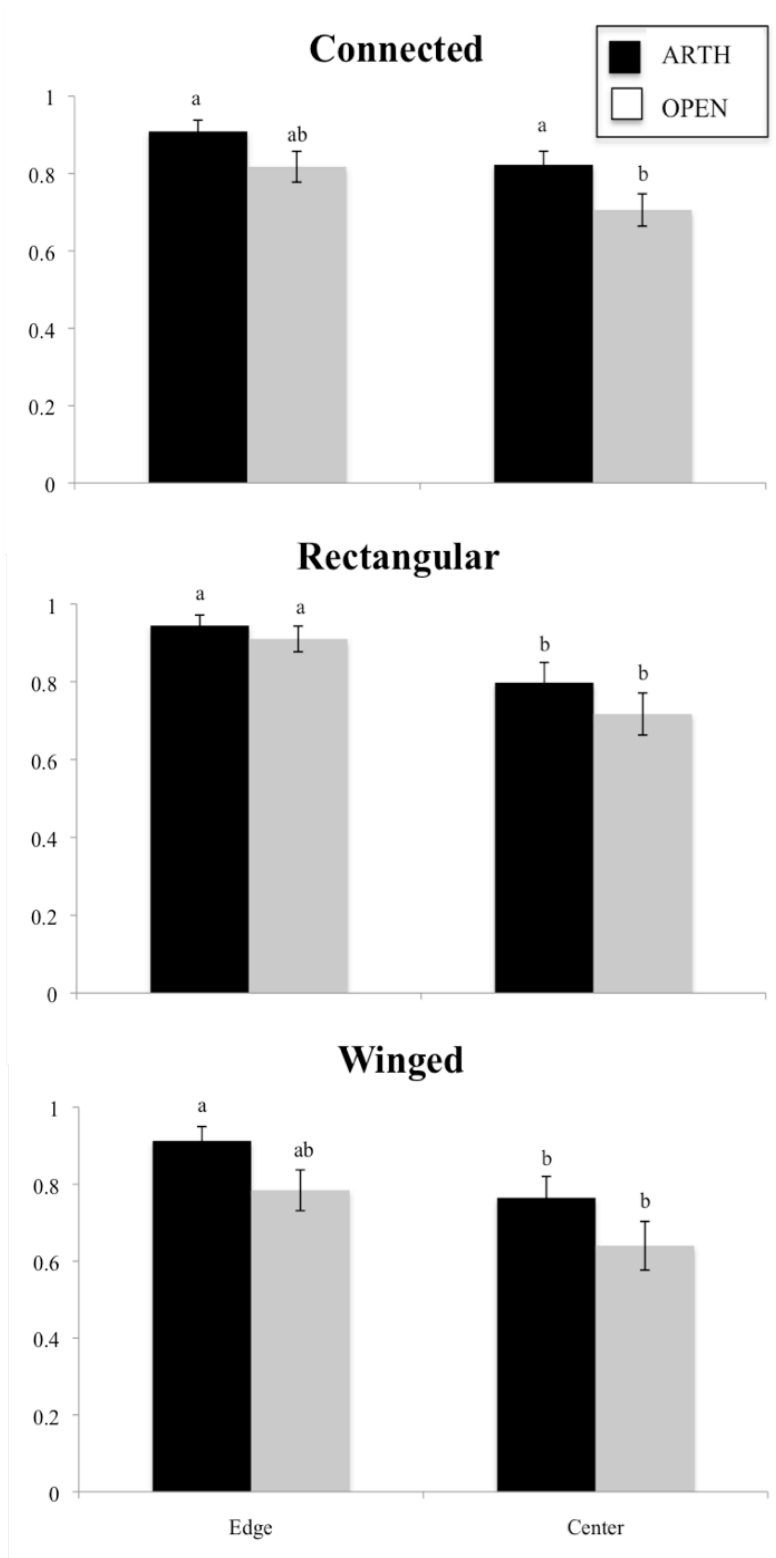
Figure 1.3
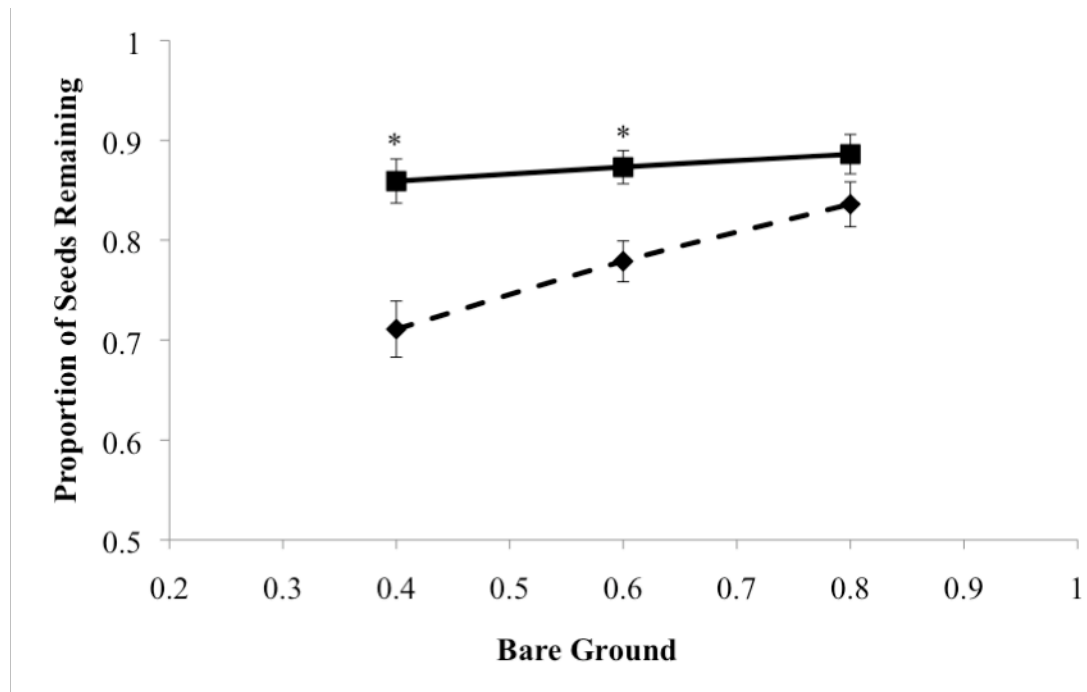
Chapter 2

The effects of corridors and edges on the fungi-mediated seed mortality

of *Baptisia lanceolata*

Abstract

   Seed mortality in the seed bank can lead to significant declines in viability, and
ultimately affect the survival and persistence of plant populations. In the soil seed bank,
much of this loss can be attributed to microorganisms such as pathogenic fungi. Seed
loss from pathogenic fungi has been shown to be dependent on abiotic factors such as
shade, relative humidity, soil moisture, and pH that allow microorganisms to persist,
survive and attack seeds. Landscape changes can affect abiotic conditions, which can
alter the distribution and impact of seed-deteriorating fungi in the seed bank. Corridors
can ameliorate the impact of habitat fragmentation but also create more edge habitat,
which could influence fungal seed attack. I used a replicated, large-scale experiment to
test how corridors and edges affect fungi-mediated seed mortality for the threatened
legume, *Baptisia lanceolata*. Three types of measurements were used to test for the
viability of dormant and non-dormant seeds. Corridors, patch shape and edges had no
effect on fungi-mediated mortality of *B. lanceolata.* Amount of patch edge and soil
moisture holding capacity influenced the proportion of seeds that germinated, suggesting
that amount of edge could impact the ability of seeds to break dormancy. Though the
distribution of pathogenic fungi may be influenced by landscape configuration and edge,
my results suggest that this threatened legume is able to withstand the presence of seed-
deteriorating microorganisms, permitting long term residency in the soil seed bank.

Introduction

Seed banks can play a vital role in the maintenance of plant populations (Leck et al. 1989; Kalisz and McPeek 1992; Baskin and Baskin 1998, Thompson 2000). For example, seed banks can affect the recovery of species after disturbances such as fire (Maliakal et al. 2000), allow for the coexistence of species in varying environments (Chesson 1986) and maintain genetic diversity in populations (McCue and Holtsford 1998). Understanding seed bank dynamics and the factors that influence seed persistence can therefore, be important for conservation and restoration, especially in fragmented habitats that may have reduced seed sources (Bakker et al. 1996). Specifically, such studies could be valuable for the longleaf pine ecosystem of the southeastern United States. Since only 2-3% of the longleaf pine ecosystem still intact (Noss 1989), little has been documented about the ecosystem's seed bank dynamics (but see Maliakal et al. 2000; Cohen et al. 2004; Coffey and Kirkland 2006; Andreu et al. 2009).

A large component of the seed mortality is experienced within the seed bank (Burdon 1987), where seeds are exposed to seed-deteriorating microorganisms that can reduce viability (Christiansen 1972; Halloin 1986; Burdon 1987; Baskin and Baskin 1998; Chee-Sanford 2006). Specifically, fungal pathogens within the soil are likely to be a significant factor responsible for the death of seeds in the seed bank (Leishman et al. 2000; O'Hanlon-Manners and Kotanen 2006), however, relatively few studies have examined this, especially in natural systems as compared to agricultural ones (Lonsdale 1993; Chambers and MacMahon 1994; Baskin and Baskin 1998; Gilbert 2002; Shafer and Kotanen 2003; Chee-Sanford et al. 2006).

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Several factors can influence the distribution and effect of fungal attack by pathogens in the seed bank soil. Abiotic factors, such as previous land use, soil texture, organic matter, water availability, pH, and temperature can affect microorganism development, persistence, longevity, and distribution (Burdon 1987; Ingham 2000; Zhou et a. 2002; Chee-Sanford 2006), which can in turn affect the viability of seeds within the seed bank soil. Some ecological studies that have examined fungi-mediated seed mortality in natural systems, have observed soil moisture and microhabitat shading to be influencing factors. For example, pathogenic fungi demonstrated to have higher levels of seed or seeding attack rates in mesic versus dry meadows (Schafer and Kotanen 2003), wetland versus drier upland habitats (Blaney and Kotanen 2001), and in moist, shaded versus open light-gap habitats (Augspurger 1993; Augspurger and Kelly 1984). This suggests that variability in soil moisture or habitat type may lead to the spatial variation in the distribution and impact of fungal pathogens in the soil. Spatial variation in abiotic factors, such as soil moisture can be a result of comparing different soil types or habitats, but can also be a result of anthropogenic factors such as habitat fragmentation.

Habitat loss is the primary cause of global biodiversity loss (Wilcove 1998). Habitat loss often leads to the fragmentation of habitats and reduces the amount of previously contiguous land, creating habitat edges that inherently alter abiotic factors, such as solar load, temperature and moisture, which can lead to changes in species distributions and interactions (Chen et al. 1999; Ries et al. 2004). Edges and reduced habitat area by fragmentation have even shown to impact the soil microbial community (Didham 1998).

Corridors, linear strips of habitat that connect two previously isolated patches, are popular tools that land mangers use to help mitigate the negative consequences of habitat fragmentation (Diamond 1975). Evidence to date suggests that corridors affect species in mostly positive ways (Haddad et al. 2003; Gilbert-Norton 2010). Though some have examined the effects of corridors on plants, few have explored how corridors can facilitate interactions that may be detrimental to plant populations. Among these are studies on post dispersal seed predation of common plant seeds by small mammals and insects (e.g. Orrock et al. 2003; Orrock and Damschen 2005). Corridors have shown to have a positive influence on the soil fungi at small scales (Rantalainen et al. 2005). To my knowledge, no study has examined the effects of corridors and edges on fungi-induced seed mortality at a large scale.

I used replicated experimental landscapes to test if corridors and edge effects influenced the seed mortality of a rare plant in the longleaf pine ecosystem. Since longleaf pine habitats are characterized by having sparse tree densities with open understories, the habitat patches of this study were created to mimic these conditions with open, clear cut areas surrounded by a dense matrix of longleaf and loblolly pine trees. The addition of corridors not only changes patch connectivity, but it also inherently adds habitat area and changes habitat geometry by altering edge-to-area ratios. To control for the confounding effects of area and patch shape, two types of unconnected peripheral patches were incorporated in each experimental landscape (see *Methods: Study Site below*). These between patch types (i.e., patch shape) and within-patch type effects (i.e., proximity to edge) may play a role in the persistence and distribution of pathogenic fungi due to changes in the abiotic factors. I hypothesized that the amount and proximity to

patch edge will influence rates of fungus-mediated seed mortality because edges can

create more shady and humid microhabitats (Cadenasso et al. 1997), which may be more

favorable to pathogenic fungi (Augspurger 1983; Augspurger and Kelly 1984; Shafer and

Kotanen 2003; O'Hanlon-Manners and Kotanen 2004). Understanding how

microclimate changes due to between and within-patch effects influence seed bank

mortality can help guide conservation and restoration plans so that more effort can be

applied in locations where it is needed most.

Methods

Study site and Experimental landscape

This study was conducted at the Savannah River Site, a National Environmental

Research Park (NERP), located near Aiken, South Carolina. The study area consisted of

seven "experimental landscapes", each of which contained five habitat patches cut into a

mature longleaf and loblolly pine matrix used to study the efficacy of habitat corridors.

Each experimental landscape contained one 100x100m center or source patch,

surrounded by four peripheral patches, each 150m away from the center patch. One

peripheral patch was 100x100m and connected to the source patch via a 25x150m habitat

corridor. This "connected" patch explicitly tests for the effect of connectivity via a

habitat corridor. Since habitat corridors inherently add habitat area and changes patch

shape, "winged" and "rectangular" patches are used to test for patch shape effects and

area effects in absence of connectivity. Winged patches consisted of 100x100m patches

with two 25x75m blind-end corridors to control for the change in edge-to-area ratios or

"drift fence effects" (sensu Haddad and Baum 1999) that a corridor may induce.

Rectangular patches consisted of 137.5x100m that control for area added by the corridor. Each experimental unit was randomly oriented in one cardinal direction. Though each experimental landscape included either a duplicated winged or rectangular patch, only one patch of those with a duplicate patch type was selected for the experiment.

Focal species

For this study, I used *Baptisia lanceolata* (Fabaceae) as the focal species. As a plant of state concern (Knox and Sharitz 1990; South Carolina DNR 2010), *B. lanceolata* is endemic to the southeastern United States. It is affiliated with longleaf pine habitats and is present in Alabama, Georgia, South Carolina and Florida (USDA NPDC 2010). Listed of state concern in South Carolina, it can only be found in two counties (Knox and Sharitz 1990) in the state. Ecological processes such as predispersal seed predation by invertebrates (e.g. weevils, microlepidopera) and postdispersal seed predation by small mammals and seed predators may limit the plant's persistence, and can play a significant role in population dynamics (Horn and Hanula 2004; Haddock and Chaplin 1982; Simon unpublished data). While the causes of pre-dispersal seed mortality have been examined for this species in a number of studies (Mehlman 1993a; Horn and Hanula 2004), the causes of post-dispersal seed mortality of *B. lanceolata* have not been examined. Since the post-dispersal source of seed mortality by small mammal and invertebrate seed consumption have been addressed elsewhere (Simon et al. Chapter 1), this study seeks to explore seed mortality via pathogenic fungi.

Baptisia lanceolata disperses via explosive dehiscence between August and November (Knox and Sharitz 1990), and experience secondary dispersal via tumbling or

by harvester ants (Mehlman 1993b). Seeds have a thick, hard seed coat, characteristic to legume species, and may stay dormant for up to eight years (Baskin and Baskin 1998). Seed coat thickness may serve as an adaptation to allow seeds to persist in the seed bank for long periods of time, creating a physical barrier that allows seeds to withstand physical contact with detrimental organisms in the soil (Halloin 1986; Baskin and Baskin 1998). However, some fungi are able to infiltrate through small pores or seed cracks, while others can penetrate through seed coats (Burdon 1987).

Seed mortality in the seed bank

On 28 September 2008, seed bank mortality trials were conducted using mesh envelopes made of fiberglass window screening with 1mm openings to allow seeds to have contact with seed bank soil. Envelopes were 3.75x3.75cm, and contained 10 *Baptisia lanceolata* seeds. Seed envelopes were buried roughly 5cm beneath the soil surface (Cohen et al. 2006) in pairs along a random transect within 5m of the habitat edge (hereafter "edge" locations) and 25m from the edge (hereafter "center" locations) (Figure 2.1). One seed envelope at the edge and at the center of each patch type was treated with a fungicide powder (hereafter "fungicide" treatment), while the others were not (hereafter "untreated"). Captan (*N*-trichloromethylthio-4-cyclahexene-1,2-dicarboximide) is a fungicide effective against a wide range of Oomycetes, Ascomycetes, and Basidiomycetes (Torgeson 1969; Neergaard 1977) that does not directly affect rates of seed germination (Schafer and Kotanen 2003), and has been used successfully in similar ecological studies (e.g. Schafer and Kotanen 2003; Orrock and Damschen 2005; Mitschunas et al. 2009).

Seed viability

Seed viability was tested in three ways after they were exhumed: field germination, greenhouse germination, and the total viable seeds. First, to test for field germination, seeds were exhumed in early January 2009. Upon retrieval, seeds were categorized as germinated, unviable, or intact for the "Field Germination" measurement. Germinated seeds with an emerged radicle were considered viable and quantified. Rotted seeds, soft to the touch were quantified and considered unviable (Leishman et al. 2000; Schafer and Kotanen 2004). Hard, filled seeds that were still intact and did not germinate were further tested for viability in the greenhouse and lab for "Greenhouse Germination" and "Total Viable Seed" measurements. Since seed requirements that break dormancy can be highly specific, the remaining seeds received a two-step treatment in order to initiate germination in the greenhouse. *Baptisia* experiences low rates of germination, high rates residual of dormancy, and may require intense scarification to induce germination (Barbour 2006; Coffey and Kirkman 2006). Also, certain legumes with thick seed coats like *Baptisia lanceolata* often need fire or the heating of dormant seeds in order to initiate germination (Stoddard 1936; Martin et al. 1975; Marshall 2009). Using a protocol similar to Marshall (2009), seeds were first exposed to a heat treatment of 95°C for 8 minutes to simulate fire, then treated with 500ppm concentration of gibberellic acid, a rooting hormone, to further initiate germination. These seeds were then placed in the greenhouse atop of approximately 6cm of soil and were lightly dressed with soil to cover exposed seeds. All seeds, regardless of field treatments, were treated with a Captan solution to prevent further fungal growth in the greenhouse. For eight weeks, germinated seeds were quantified and collected twice a week. Non-germinated

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seeds that remained from the greenhouse were treated in the lab with tetrazolium assays to test for viability, following the protocol as described by Grabe (1970). The measurement of "Total Viable Seeds" was defined as the sum of all viable seeds from each of the three methods - field germination, greenhouse germination, and tetrazolium assays. This method of inducing germination, then testing via tetrazolium assays has been successfully used in similar ecological field studies to test for total viability (e.g. O'Hanlon-Manners and Kotanen 2006).

Soil Moisture Holding Capacity

Soil moisture holding capacity can influence the amount of water available to a seed, possibly playing a role in germination (Baskin and Baskin 1998), and the soil microbial composition (Halloin 1986; Burdon 1987; Chee-Sanford). In a previous experiment (Damschen et al. 2006), soil moisture holding capacity was tested from soil cores collected from subplots in each patch from six of the experimental landscapes used. In center patches, 24 subplots were used, while in peripheral patches 34 subplots were used, yielding a total of 756 subplots. Average soil moisture holding capacity at patch edges and centers was calculated by quantifying the potential moisture a soil could hold by weight (Damschen et al. 2006). This value was used as a covariate in the analysis as it may influence the soil microbial community, and thus seed survival (Halloin 1986; Burdon 1987; Chee-Sanford).

Statistical Analysis

I used a generalized linear mixed model (Proc GLIMMIX, SAS v.9.1) to test the effect of patch type, location and treatment on field seed germination (Littell 2002). I used a binomial distribution with a log link function to model the fixed effects of patch type (connected, winged, rectangular), location (edge, center), treatment (control, fungicide) and the experimental landscape as random effect with average soil moisture holding capacity as a covariate. I ran similar tests for analyzing the total proportion of seeds germinated in the greenhouse (i.e. seeds that germinated in the seed bank + greenhouse), as well as for the total proportion of viable seeds (i.e., those germinated in the seed bank + germinated in the greenhouse + viable with tetrazolium assay). When significant interactions were found, I used linear contrasts to test the importance of simple effects (Littell 2002). Means are presented with ±1 standard error. Analyses were all conducted using SAS Version 9.1 (SAS Institute 2002).

Results

Differential results were found based on when seed viability was measured. In general, I found that there was no significant effect of the fungicide treatment, indicating that seed mortality was not attributed to pathogenic fungi (Tables 2.1, 2.2, 2.3).

Field Germination

Seed germination or viability was not significantly different among connected, winged or rectangular patches. In addition, there was no significant effect of location

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within patch (i.e. at patch edge or center), seed treatment, nor average soil moisture holding capacity (Table 2.1).

Greenhouse Germination

By summing the number of seeds germinated in both the seed bank and in the greenhouse, I determined the proportion of seeds that were able to break dormancy and germinate. This value is of ecological importance in this study as seeds that germinate leave the seed bank and escape from potential seed attacking fungal pathogens. After germination was induced, there was a significant effect of patch type, and with the average soil moisture x patch type interaction (Table 2.2). Specifically at low and moderate soil moisture holding capacities, seed germination was not significantly different between patch types, while at high soil moisture holding capacity, there was a trend of significance between connected and rectangular patches (P = 0.06; Figure 2.2). Since connected and winged patches contain relatively the same amount of edge (and thus edge-to-area ratios), I used a linear contrast to compare the mean proportion of germinated seeds of rectangular versus connected and winged patches to find a significant difference between the two (linear contrast: $F_{[1,19.4]} = 8.50$; P < 0.01).

Total viability

Tetrazolium assays measure seed viability for seeds that did not break dormancy and germinate. In this study, the total proportion of viable seeds was measured by quantifying the number of viable seeds via tetrazolium testing in addition to seeds that germinated in the field and greenhouse. I found that there was no significant effect of

patch type or treatment (Table 2.3). However, there was a significant effect of location

(P<0.01), average soil moisture holding capacity (P<0.01) and the interaction average

soil moisture holding capacity x location (P>0.01). There was also a trend of significance

with the interaction of location x treatment (0.10>P>0.05). Total seed viability was

significantly higher in patch centers than patch edges at a low soil moisture holding

capacity (P > 0.01). By separating the data by patch location (i.e., center, edge), I was

able to further analyze the relationship between soil moisture holding capacity and

fungicide treatment. In patch centers only, there was no significant difference between

treated and untreated seeds along the soil moisture gradient (Figure 2.3a). However, at

patch edges only, fungicide treated seeds had significantly lower viability than untreated

seeds, especially at 29.91 (i.e. low) percent soil moisture holding capacity (P = 0.02).

Whereas at 30.94 and 32.72 percent soil moisture holding capacities, fungicide treated

and untreated seed viability was not significantly different (P = 0.09 and P = 0.92,

respectively; Figure 2.3b).

Total viability of untreated seeds

The deleterious effect of fungicide treatment on seed viability led us to rerun the analysis

using only untreated seeds. More ecologically relevant, untreated seeds experience the

natural soil conditions that allow us to ask how seed viability is affected with the

presence of soil fungi. Using only untreated seeds there was no significant effect of patch

type, location, or soil moisture holding capacity (Table 2.4).

Discussion

The most vulnerable stage of a plant's life is the seed stage, where the majority of plant mortality occurs (Cook 1980; Chambers and MacMahon 1994). While much of this mortality occurs while seeds are in the seed bank (Burdon 1987), studies of seed bank mortality by fungi and other microorganisms have been predominantly in agricultural systems, and remain relatively uncommon in natural systems (Chambers and MacMahon 1994; Baskin and Baskin 1998; Gilbert 2002; Chee-Sanford et al. 2006).

Habitat corridors are used as management tools and can facilitate both beneficial and antagonistic interactions, however, their application can also induce abiotic changes that can affect species distributions and interactions since corridors are linear strips of habitat that increase the amount of edge relative to area. Edges can alter abiotic factors and microhabitats by increasing shade and relative humidity (Cadenasso et al. 1997). Since pathogenic fungi can respond positively to abiotic factors such as moisture and shading (Augspurger 1983; Augspurger and Kelly 1984; Shafer and Kotanen 2003; O'Hanlon-Manners and Kotanen 2004), I hypothesized that pathogenic fungi would thrive and therefore increase seed mortality levels at the edges of habitat patches and in patches with high levels of edge.

Fungus-induced mortality

Even though fungal pathogens can have a range of effects on seed morality of different species (Londsdale 1993; Leishman et al. 2000; Orrock and Damschen 2005; O'Hanlon-Manners and Kotanen 2006; Mitschunas et al. 2009), I found no significant difference in the viability of seeds treated and untreated with the Captan fungicide. This

indicates that, at least for the duration of this study, *Baptisia lanceolata* is able to withstand contact with soil fungal pathogens. *Baptisia* are thick seeded legumes can remain viable for up to eight years in the seed bank (Baskin and Baskin 1998). Their hard impermeable seed coat likely affords the seeds immunity to fungal infection experienced through its long life in the seed bank (Halloin 1987; Baskin and Baskin 1998).

Effects of landscape on seed germination

Our results provide evidence that patch type and average soil moisture holding capacity have a significant influence on the germination of *Baptisia lanceolata* seeds. Based on the proportion of seeds that germinated in both the field and in the greenhouse, *B. lanceolata* experienced significantly higher rates of germination in connected and winged patches versus rectangular patches (linear contrast: $F_{[1,19.4]} = 8.50$; $P < 0.01$), indicating that patches with high amounts of edge had proportionally more germinated seeds than the patch type with lower amounts of edge. When examining total germination in conjunction with average soil holding moisture capacity, I found a trend toward the proportion of germinated seeds in connected patches being higher than rectangular patches at high soil moisture holding capacity (Figure 2.2). This suggests that high edge, and thus potentially more moist conditions (Cadenasso et al. 1997), in addition to soil moisture may provide more optimal conditions for *B. lanceolata* seed germination. It is possible that at even high soil moisture holding capacities, low-edge rectangular patches do not retain as much moisture as high-edge patches, inducing

slightly more water stress which can lead to increased dormancy in some plant species (Baskin and Baskin 1998).

Effects of edges and fungicide on total viability

Total viability was higher in patch centers of low soil moisture holding capacity, however, this pattern seems to be driven by the trend toward fungicide treated seeds at the patch edge (Figures 2.3a, 2.3b). At patch edges only, fungicide treated seeds were significantly less viable than untreated seeds at low and moderate soil moisture holding capacities. This unexpected result of increased mortality when fungi are excluded at the edge could be due the non-target effects of Captan. Studies have shown that while Captan may effectively eliminate specific groups of fungus, it can also lead to the release of potentially harmful bacteria, or shift the dominance of fungal species in the community (Inghan and Coleman 1984; Ingham 1985; Colinas et al. 1994; Matinez-Toledo et al. 1998). Such non-target effects suggest that *B. lanceolata* seeds may suffer under specific soil moisture and microbial conditions, however, more specific research is needed in order to determine how microbial community composition affect seed mortality.

Total viability of naturally exposed seeds

Since the fungicide treatment seemed to have a negative effect on seed viability (the opposite of what was predicted), I reran the total viability model using only data from untreated seeds. Untreated seeds exposed to the soil community offer the most ecologically relevant results, as these are conditions that seeds would normally experience. I found that patch type (i.e., connected, winged, rectangular), location (i.e.,

edge or center), and soil moisture holding capacity have no significant impact on the viability of *Baptisia lanceolata* seeds. As a species that may spend several years in the seed bank, I provide evidence that for the duration of this study, *B. lanceolata* is able to withstand changes in the abiotic and biotic conditions that are induced by habitat connectivity, added area, increased edge-to-area ratios, and edge effects.

Implications for restoration

Seed banks can play a significant role in maintaining plant population dynamics (Leck et al. 1989; Kalisz and McPeek 1992; Baskin and Baskin 1998, Thompson 2000), and for restoring habitat such as the highly fragmented longleaf ecosystem (Cohen et al. 2004; Andreu 2009).

Corridors are conservation and restoration tools used by land managers that may induce changes in abiotic habitat conditions. Such changes may affect a species' interactions at different stages of its life. From the standpoint of a plant, the seed stage may be considered the most vulnerable life stage (Cook 1980; Chambers and MacMahon 1994). Soil microorganisms can have significant impacts on seed viability (Christiansen 1972; Halloin 1986; Burdon 1987; Baskin and Baskin 1998; Chee-Sanford 2006), and can respond to fragmentation at large scales (Didham 1998). I found that corridors and edge effects do not influence fungi-mediated seed mortality, at least for *Baptisia lanceolata.* While corridors may in fact influence soil microbial communities, such a change is unimportant for *Baptisia lanceolata,* likely due to the species' hard, thick seed coat, which allows for its long term in the seed bank.

Amount of patch edge and soil holding moisture capacity may play a role in the germination of *B.lanceolata* seeds. Optimal germination conditions may be more easily reached in patches with high amounts of patch edge and soil moisture holding capacities, however, this evidence is weak and increasing edge to increase *B. lanceolata* seed germination for restoration is not suggested.

Although corridors show a neutral effect on *Baptisia lanceolata* mortality in the seed bank, it is possible that their net effects of interactions influenced by corridors could benefit their low population sizes. Corridors are likely to facilitate the movement of *Baptisia lanceolata* generalist pollinators (Townsend and Levey 2005) and may also benefit from increased seed dispersal via tumbling. More information, however, is needed to understand how corridors affect interactions for each stage of the species life history.

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Figure and Table Legends

Figure 2.1

Experimental landscape at the Savannah River Site (SRS), near Aiken, South Carolina.

Seven experimental landscapes were used, each containing three patch types: connected,

winged and rectangular. Seeds in envelopes were either treated with fungicide

(FUNGICIDE) or untreated (UNTREATED). Pairs were randomly oriented and were

buried within 5m and 25m from a randomly chosen patch edge.

Table 2.1.

Summary of general linear mixed model analysis of the germinated *Baptisia lanceolata*

seeds from the field seed bank untreated and treated with fungicide in connected, winged,

and rectangular patch types, and at patch edge and center locations with percent bare

ground used as a covariate.

Table 2.2

Summary of general linear mixed model analysis of the seed bank and greenhouse

Baptisia lanceolata seeds untreated and treated with fungicide in connected, winged, and

rectangular patch types, and at patch edge and center locations with percent bare ground

used as a covariate.

Figure 2.2

Mean proportions of seeds germinated seeds from field and greenhouse as a function of average soil moisture holding capacity among patch types. Proportion of germinated seeds did not significantly differ between patch types at 29.9 and 30.4 percent soil moisture holding capacities. Seed germination had a trend of significance of being higher in connected patches than rectangular patches at 32.72 percent soil moisture holding capacity ($P = 0.06$).

Table 2.3

Summary of general linear mixed model analysis of the total viability of *Baptisia lanceolata* seeds untreated and treated with fungicide in connected, winged, and rectangular patch types, and at patch edge and center locations with percent bare ground used as a covariate.

Figure 2.3a

Mean proportions of total viable seeds as a function of average soil moisture holding capacity at patch centers only between UNTREATED (solid line) and FUNGICIDE (dashed line) seed treatments. Proportion of total viable seeds is not significantly different between treatments at 29.9, 30.4, and 32.72 percent soil moisture holding capacities.

Figure 2.3b

Mean proportions of total viable seeds as a function of average soil moisture holding

capacity at patch edges only between UNTREATED (solid line) and FUNGICIDE

(dashed line) seed treatments. Proportion of total viable fungicide treated seeds is

significantly lower at 29.9 percent soil moisture holding capacity ($P = 0.02$). Viability of

treated and untreated seeds did not significantly differ at 30.4, and 32.72 percent soil

moisture holding capacities.

Table 2.4

Summary of general linear mixed model analysis of the total viability of *Baptisia*

lanceolata seeds for untreated seeds only in connected, winged, and rectangular patch

types, and at patch edge and center locations with percent bare ground used as a
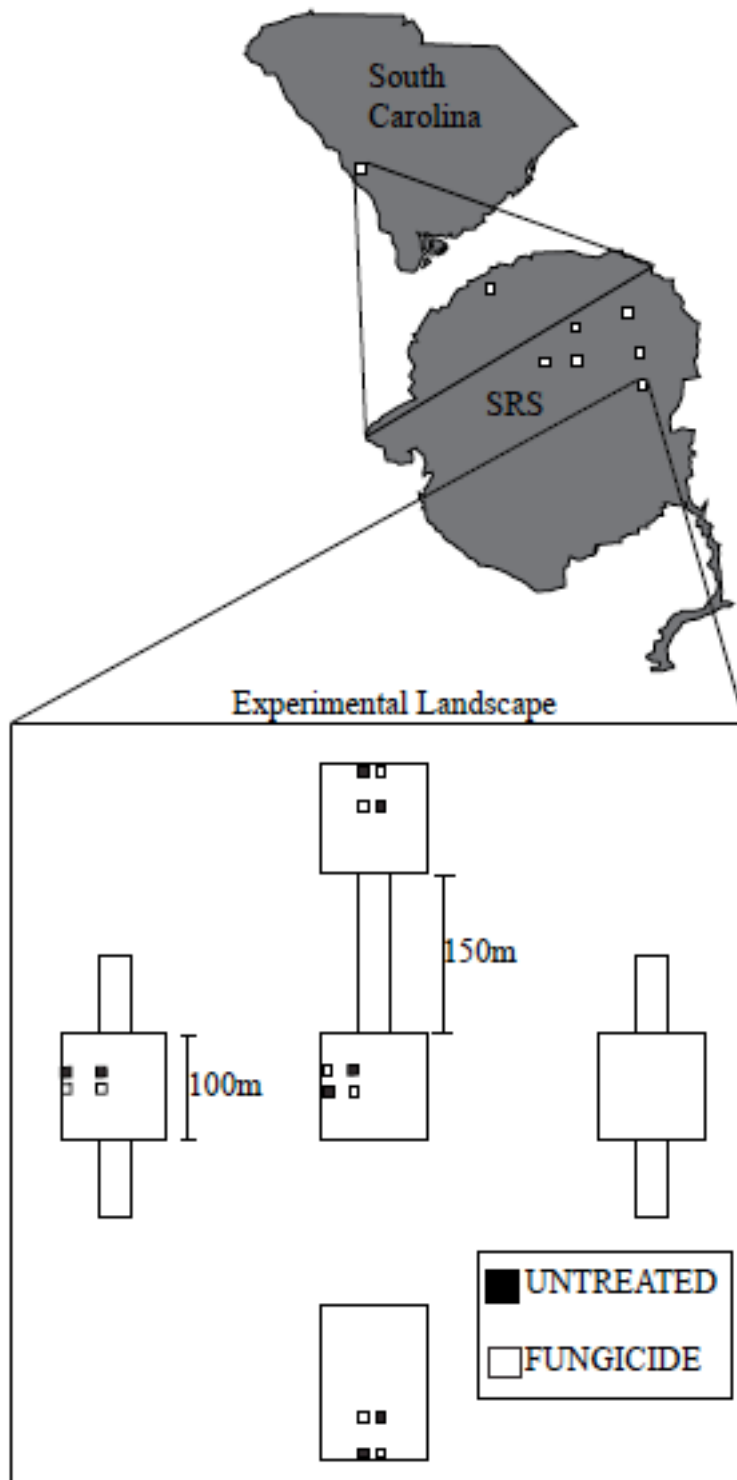
covariate.

Figures and Tables

Figure 2.1

Table 2.1

Effect	P
Patch Type	0.32
Location	0.87
Treatment	0.55
Soil Moisture	0.38
Patch Type x Location	0.57
Patch Type x Treatment	0.52
Soil Moisture x Patch Type	0.32
Location x Treatment	0.52
Soil Moisture x Location	0.82
Patch Type x Location x Treatment	0.89

Table 2.2

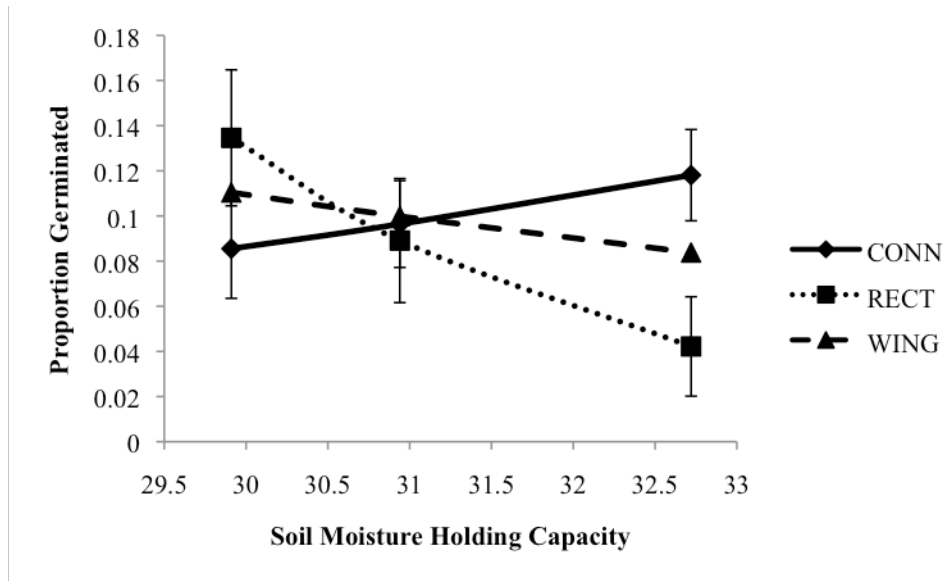| Effect	P
Patch Type	<0.01
Location	0.64
Treatment	0.23
Soil Moisture	0.08
Patch Type x Location	0.21
Patch Type x Treatment	0.11
Soil Moisture x Patch Type	<0.01
Location x Treatment	0.18
Soil Moisture x Location	0.57
Patch Type x Location x Treatment	0.25
Soil Moisture x Treatment	0.33

Figure 2.2

Table 2.3

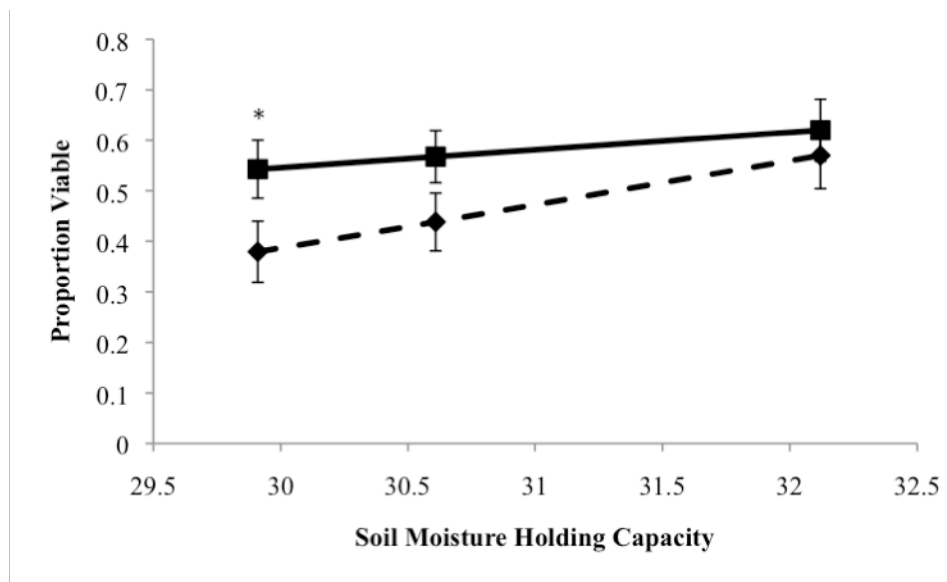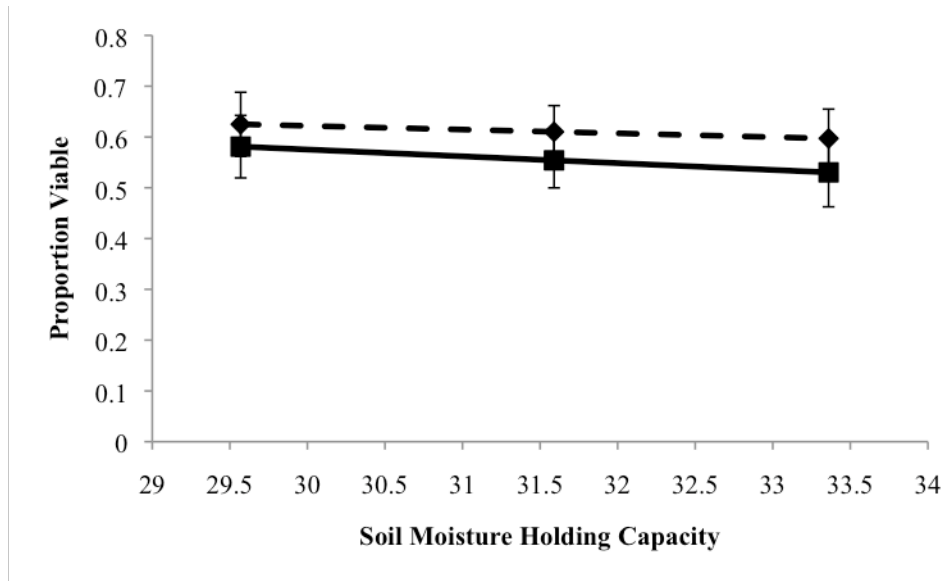| Effect	P
Patch Type	0.78
Location	<0.01
Treatment	0.24
Soil Moisture	0.02
Patch Type x Location	0.10
Patch Type x Treatment	0.17
Soil Moisture x Patch Type	0.74
Location x Treatment	0.06
Soil Moisture x Location	<0.01
Patch Type x Location x Treatment	0.93
Soil Moisture x Treatment	0.26

Figures 2.3a, 2.3b

Table 2.4

Effect	*P*
Patch Type	0.31
Location	0.08
Soil Moisture	0.18
Patch Type x Location	0.47
Soil Moisture x Patch Type	0.3
Soil Moisture x Location	0.08
Soil Moisture x Patch Type x Location	0.44