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Species Composition And Spatiotemporal Pattern Of The Seed Bank And Vegetation In Native And Degraded Florida Rosemary Scrub

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SPECIES COMPOSITION AND SPATIOTEMPORAL PATTERN OF THE
SEED BANK AND VEGETATION IN NATIVE AND DEGRADED FLORIDA
ROSEMARY SCRUB

by

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ABSTRACT

The soil seed bank plays a dynamic role in the regeneration of plant communities after natural and anthropogenic disturbance. In this thesis, I addressed how disturbances influence the vegetation and seed bank of Florida rosemary scrub. In Chapter One I evaluated changes in species composition and spatiotemporal pattern of the vegetation and seed bank along a gradient of disturbance. During the summers and winters of 2007-2009 percent ground cover and seed bank species composition were assessed among replicates of three vegetation types subjected to minimal, moderate, and extreme anthropogenic disturbance (native rosemary scrub, degraded scrub, and agriculturally improved pasture, respectively). These vegetation types shared the same soil and topographic characteristics but differed in disturbance history. I found that species composition and spatial pattern varied with disturbance. In pastures the compositional and structural characteristics of rosemary scrub were lost and only native scrub species able to evade herbivory persisted in this community. Native and degraded scrub differed most from each other in species abundances and spatial pattern. Degraded scrub showed highest abundance of subshrubs and a spike moss species, while rosemary scrub was dominated by shrubs. The seed banks of scrub herbs in degraded scrub had a tendency towards a random spatial distribution that lacked association with aboveground cover. Conversely, rosemary scrub seed banks tended to have an aggregated distribution and were associated with occurrence of conspecific species aboveground, litter, and shrub cover. These results indicated a change in the spatial heterogeneity of the seed banks of scrub herbs in degraded scrub.

In Chapter Two I evaluated changes in seed bank density with time-since-fire in native rosemary scrub. Due to large pulses of recruitment immediately after fire and population decline

with time-since-fire, I predicted seed density with time-since-fire would follow a unimodal function with low density in early and late years post-fire, and highest density at intermediate time-since-fire. I compared seed density data among sites with different time-since-fire: two sites each of three, six, ten and 24 years time-since-fire and three long-unburned sites (> 24 years). Variability in seed bank composition and density increased with time-since-fire and only recently burned stands were distinctly different from the other time-since-fire age classes. Some species and functional groups did exhibit a quadratic or cubic association to time-since-fire (ruderal herbs, subshrubs, *Ceratiola ericoides*, *Lechea cernua*, *Paronychia chartacea*, *Phyllanthus tenellus*); however, timing of the peak in seed density varied depending on life span and age of reproductive maturity. Scrub herbs were the most abundant functional group in the seed bank and showed highest density in the first ten years post-fire. This pattern corresponds to the pattern of aboveground species abundance and suggests abundances above- and belowground are closely linked. Understanding the dynamics of the seed bank in both naturally and anthropogenically disturbed communities in Florida rosemary scrub is important for the restoration of scrub habitat and management of existing populations of endangered and threatened scrub species endemic to the Lake Wales Ridge in central Florida.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

OVERVIEW

Disturbance has long been recognized as a central component shaping ecological systems (Connell 1978, White 1979, Sousa 1984, Pickett and White 1985). Life history attributes determine how species will respond to different frequencies and intensities of disturbance. These characteristics include life span, fecundity, age of reproduction, and dispersal mechanisms (Noble and Slatyer 1980). In this work, I explored how disturbances, both natural and anthropogenic, alter population and community dynamics. I evaluated how plant communities change in response to different types and intensity of disturbance and how life history characteristics influence the ability of a species to cope with diverse disturbance regimes.

This research was conducted at Archbold Biological Station (Township 38S, Range 30E, Sections 5-8,18,19,29-32) and an adjacent property, the Archbold Reserve (Reserve). Archbold is located on the southern end of the Lake Wales Ridge in central Florida. This is a relic sand dune system with a high diversity of endemic animal and plant species (Abrahamson et al. 1984, Christman and Judd 1990). The Reserve was a working ranch and much of the property was converted to cattle pasture. My research focused on three community types that differ in terms of land use history but share the same topography and soil attributes typical of Florida rosemary scrub. Florida rosemary scrub is a type of scrub which is characterized by the presence of *Ceratiola ericoides* (an allopathic obligate seeding shrub) and open sand gaps which harbor a high number of endemic herbaceous species. Florida scrub is a xeric upland shrub-dominated community found on low nutrient, well drained sandy soils and is characterized by moderate to low frequency fires (Menges 1999).

My study evaluated changes in species composition and spatial-temporal pattern of the vegetation and seed bank along a disturbance gradient which included three community types: (1) *native Florida rosemary scrub* (located on the original Archbold property) which has been subject to natural fire and controlled burns, (2) *degraded scrub* (Reserve) which until recently was subjected to mechanical disturbance and light cattle grazing, and (3) *semi-improved pastures* (Reserve) which was previously subjected to introduction of non-native forage grasses, nutrient additions, hydrological changes, and, until recently, heavy cattle grazing (Figure 1). Understanding the dynamics of the soil seed bank is particularly important in Florida rosemary scrub because it has many obligate seeding species that rely on post-fire recruitment from the seed bank (Menges and Kohfeldt 1995, Menges and Hawkes 1998, Clemente et al. 2007). Likewise, information regarding the species composition, spatial distribution, and seasonal variation of the seed bank will be useful for managing existing scrub populations and for guiding restoration of the many degraded Florida scrub areas now being protected, including the Archbold Reserve.

This thesis is organized in two chapters. Chapter One focuses on changes in species composition and spatial pattern of the soil seed bank and vegetation along an anthropogenic disturbance gradient in Florida rosemary scrub. Chapter Two evaluates changes in the seed bank with time-since-fire in native rosemary scrub. Chapter Two combines my research efforts with those of Nancy Kohfeldt and Eric Menges. The overall goal of my research was to broaden our understanding of the role of disturbance in altering compositional and spatial aspects of plant communities and to provide information that will be useful for the management and restoration of an endangered habitat, Florida rosemary scrub.

CHAPTER ONE: SPECIES COMPOSITION AND SPATIAL PATTERN OF THE SEED BANK AND VEGETATION ALONG A DISTURBANCE GRADIENT IN FLORIDA ROSEMARY SCRUB

Abstract

In plant communities, disturbance plays an influential role in determining species composition and spatial structure. I evaluated how species composition and spatiotemporal pattern of the vegetation and the soil seed bank change along a disturbance gradient in Florida rosemary scrub. I hypothesized that changes in species composition will reflect contrasting abilities of species to cope with disturbance. I expected that increasing anthropogenic disturbance would favor stress tolerant species and would reduce habitat spatial heterogeneity. During the summers and winters of 2007-2009, I assessed percent vegetation cover and soil seed bank species composition in nine grid plots located in three vegetation types: native rosemary scrub, degraded scrub (cleared during the 1970's and 80's), and agriculturally improved pasture (converted during the 1970's). Across all sites, aboveground vegetation was dominated by long-lived perennials while the seed bank was dominated by short-lived species. Pasture and native scrub had the greatest differences in composition and spatial structure above- and belowground. Species richness and composition were similar between degraded and rosemary scrub but abundance and distribution of some species and functional groups differed. The vegetation was aggregated across all sites and larger more homogenous patch sizes were observed in species with relatively high abundance in the degraded scrub (e.g *Licania michauxii*). Abundance of scrub herbs above- and belowground was highest in native scrub, lower in the degraded scrub, and absent in the pastures. Spatial aggregation was less frequent in the seed bank than the vegetation, especially among species that were not present aboveground. In native scrub the seed

banks of scrub plants were spatially aggregated and were positively associated with conspecific species aboveground and litter cover. These patterns were not observed for the same scrub species in degraded scrub. In this study, increased human disturbance first disrupted the spatial structure in the degraded scrub and more severe disturbance in the pastures eventually led to elimination of many of the component scrub species.

Introduction

Disturbance is a main driver of community change (Sousa 1984, Pickett and White 1985). While disturbances at intermediate levels are presumed to maintain biotic diversity and spatiotemporal heterogeneity (Levin and Paine 1974, Connell 1978), disturbances that are outside of the historic range can alter community composition and species spatial distribution (Zedler et al. 1983, Laycock 1991, Knapp 1996, Stylinski and Allen 1999). Disturbance and spatial pattern are often closely linked: disturbance creates spatial heterogeneity within the landscape; however, its occurrence is frequently determined by the structure of the physical environment (Turner 1989).

Spatial pattern has long been recognized as a major determinant of plant community dynamics and processes (Watt 1947, Nathan and Muller-Landau 2000). While the majority of studies demonstrating the function of spatial pattern in influencing ecological processes have been based on models (Tilman and Kareiva 1997), a growing number of empirical studies are now showing that the spatial aggregation commonly found in plant communities plays a dynamic role in maintaining species coexistence and biodiversity (Bergelson 1990, Stoll and Prati 2001, Tirado and Pugnaire 2003). The significance of spatial pattern raises questions of how anthropogenic disturbances, which frequently alter species composition and spatial distribution, will influence the ecological processes in disturbed communities. It has been shown that

4

differences in spatial pattern can modify inter- and intraspecific species interactions, change dispersal patterns, and render habitats unsuitable for fauna with specific structural requirements (Bergelson 1990, Mladenoff et al. 1993, Stoll and Prati 2001, Tirado and Pugnaire 2003).

While some studies have shown differences in disturbance history and intensity can alter the amount of spatial heterogeneity at various spatial scales (Collins 1992, Mladenoff et al. 1993, Adler et al. 2001), there is currently insufficient information to fully predict how different types and severities of disturbance will alter habitat spatial structure. This work evaluates changes in species composition and spatial structure of the vegetation and seed bank along a disturbance gradient. The soil seed bank plays an important role in sustaining local plant populations after disturbance (Thompson and Grime 1979, Johnson 1982). If mortality results from the disturbance event, the seed bank is particularly vital for species that have limited dispersal distance and rely on seeds for recruitment (Noble and Slatyer 1980). Spatial distribution of the seed bank can contribute to species distribution aboveground by influencing where recruitment will occur (Rusch 1992). Loss of spatial heterogeneity in the seed bank could possibly alter species aboveground distributions or lead to population decline if seeds are dispersed away from areas suitable for germination.

Understanding how the seed bank and vegetation change in response to diverse disturbance regimes may lend insight into how resilient a community is to perturbations, which mechanisms drive regeneration, and what steps should be taken to restore community composition and structure (Hopfensperger 2007). I compared species composition and spatial distribution among three vegetation types: native rosemary scrub, degraded scrub, and agriculturally improved pasture. I hypothesized: (1) changes in composition of the seed bank and vegetation will reflect contrasting abilities of species to cope with disturbance, and (2) an

increase in disturbance intensity will homogenize the spatial distribution of those species favored by the disturbance regime. In this study I evaluated how seed bank and vegetation vary along a disturbance gradient in terms of: (1) species composition, (2) spatial structure, (3) temporal pattern (seasonal variation in species composition and spatial pattern), and (4) the relationship of the seed bank to standing vegetation (both spatial and compositional) (for predictions see Figure 2).

Methods

Study Site

This research was conducted at Archbold Biological Station (Archbold) and an adjacent property, the Archbold Reserve (Reserve). Archbold is located near the southern end of the Lake Wales Ridge in Highland County, central Florida (Township 38S, Range 30E, Sections 5-8,18,19,29-32) (Figure 1). The region experiences temperatures ranging from a mean of 8.33^{o} C in the winter to 34.05^{o} C in the summer and receives an average annual rainfall of 1364 mm (Archbold weather data, 1932-2009). Archbold includes a wide variety of vegetation types (southern ridge sandhills, sand pine scrub, rosemary scrub, scrubby flatwoods, flatwoods, swale, bayhead and seasonal ponds) (Abrahamson et al. 1984). Approximately 85% of Lake Wales Ridge has been lost due to commercial, agricultural, and residential development (Weekley et al. 2008), making the 2101.5 ha station important for the conservation of many threatened and endangered species that are endemic to the ridge.

I evaluated the vegetation and seed bank in replicated sites (n=3, total 9 sites) of three communities that differ in disturbance history, but share similar topography and soil attributes typical of rosemary scrub: native rosemary scrub, degraded scrub, and agriculturally improved

pasture. The native scrub sites were located on the original Archbold property. The degraded scrub and pasture sites were located on the adjacent Reserve.

Native rosemary scrub sites (plots 4-6) have been subjected to natural fires and controlled burns (historic fire return interval between 15-100 years; plots 4 and 6 = 10 years time-since-fire, plot 5 = long-unburned) and were found in areas with locally high elevation and well drained low nutrient Archbold or St Lucie soils (Menges 1999). This habitat is dominated by Florida rosemary (*Ceratiola ericoides*), an allelopathic shrub, but also includes patches of shrub species such as palmettos (*Serenoa repens*, *Sabal etonia*), and various clonal oaks (*Quercus chapmanii*, *Q. inopina, Q. geminate*) (Hunter and Menges 2002, Menges et al. 2008). After fire most shrub species resprout from rhizomes or roots (Menges and Kohfeldt 1995), and most obligate seeders (species killed by fire) such as *C. ericoides* and several herbaceous species recruit seedlings from the soil seed bank (Menges and Hawkes 1998, Clemente et al. 2007).

Degraded scrub sites (plots 7-9) were subjected to roller chopping but the time this occurred is uncertain. My study sites were cleared in the early 1970's (plot 8) and early 1980's (plots 7 and 9). Exact fire history of the degraded scrub was unknown but it was presumed from both vegetation structure (tall overgrown shrub patches) and what has been reported from previous land owners that these sites were long-unburned. These areas were also lightly grazed and cattle were present on site until 2002. Species composition of degraded and rosemary scrub are similar; however, relative species abundance and distribution of some species differ between the two vegetation types.

Agriculturally improved pasture sites (plots 1-3) were cleared and planted with non-native forage grasses in the 1970's. These sites were heavily grazed and in the 12 year period

from 1990-2002 the pastures were overstocked and overgrazed, often year round. The pastures are dominated by three non-native grass species (*Paspalum notatum*, *Digitaria eriantha*, and *Cynodon dactylon*); although some unpalatable shrub species still persist (*S. repens*, *S. etonia*, *Sideroxylon tenax,* and *Asimina obovata*).

I selected degraded scrub and pasture sampling locations based on soil and elevation attributes characteristic of rosemary scrub patches: locally highest relict dunes in areas containing Satellite soils. Once all suitable sampling locations were identified, stratified random sampling was used to determine the final location of each plot.

<div align="center">Aboveground Cover Sampling</div>

Between May and July 2007, I established nine 16 x 16 m macroplots, which provided three replicates per vegetation type (Figure 1). I sub-divided each macroplot into 2 x 2 m subplots and each subplot into 40 x 40 cm quadrats. In the summer 2007 (May and June), I sampled aboveground cover in a checkerboard pattern. I collected data from every other 2 x 2 m subplot (32 per macroplot) and every other 40 x 40 cm quadrat (13 per subplot, 416 sample units per macroplot) within each of the selected subplots (Figure 3). Within each quadrat I made ocular estimates of percent cover in whole tenths of a percent (< 10% = trace amount). I assigned cover to the following categories: bare sand, litter, herbs, lichens, graminoids, subshrubs, shrubs, spike moss, and subcanopy (> 3 m). I also assessed percent cover for each species of vascular plant and ground lichen.

I re-sampled percent cover in the winter 2009 (February) in a subset of the initially sampled plots. Ten subplots were randomly selected from among those previous sampled in 2007. Within each subplot, all 13 quadrats were sampled as described above (130 sample units

per macroplot). In the winter, I grouped dormant grasses into a single category because grasses died back and individuals could not be identified at the species level.

Seed Bank Sampling

In summer 2008 (August) and winter 2009 (January), I collected soil samples from all nine macroplots using the same subset of subplots described in the previous section. I collected and aggregated five 1.92 cm diameter by 3 cm deep soil cores from each quadrat (130 subsamples per macroplot, 1,170 samples in total). During both sampling periods I collected the soil cores in a regular pattern within each quadrat and this pattern was alternated each season to avoid coring the exact same locations.

Greenhouse Monitoring

I used the seedling emergence method to determine species composition of the soil seed bank. I sieved each soil sample to break up soil structure and large litter and potted them on top of white sand substrate collected from firelanes in Archbold Biological Station. All sand was heated to 85° C to kill any seeds that may have been present in the soil. I placed the potted samples into several shade houses (covered on all sides to reduce contamination by exogenous seeds) and watered as needed to keep the soil moist. Placement of the samples within the shade houses was randomized and I regularly changed the seedling flat locations to minimize the effect of micro-environmental differences. Controls of heated sand were also randomly interspersed among the soil samples to both ensure all seeds in the sand bed were killed during heating and to account for potential contamination of samples by exogenous seeds. I recorded minimum and maximum temperatures daily. The soil samples were monitored at monthly intervals for seedling emergence. I removed seedlings once they had been identified to the species level. For each sampling season, I monitored the soil samples for seedling emergence for eight months to one

year. During both seasons, germination rates had leveled off before I discontinued germination monitoring.

Data Analysis

I used Mantel tests to correlate vegetation and seed bank data across seasons, above- and belowground, and with spatial coordinate locations (correlation indicates presence of spatial structure). The Mantel test compares two matrices and then determines their association (Legendre and Fortin 1989). The standardized Mantel statistic (mantel r) is used to determine the strength of the correlation between two symmetrical matrices and it ranges from 1 (a complete positive association) to -1 (a complete negative association); a value near zero indicates no correlation (McCune and Grace 2002). The significance of the correlation was tested with Monte Carlo randomization (10,000 permutations). Comparisons were made between seasons for the vegetation and the seed bank (comparison of summer and winter vegetation in the pastures was not made because species identification of dormant grasses was not possible during the winter). I also evaluated potential spatial pattern using the spatial coordinates. I divided the species into functional groups based upon growth habit and, for herbaceous species, habitat preference. I identified the following functional groups: (1) grasses (2) sedges (3) ruderal herbs (species typical of disturbed habitats, generally not found growing aboveground in Florida scrub) (4) scrub herbs (species typically found in scrub habitat) (Menges and Kohfeldt 1995)(5) other herbs (6) shrubs (7) subshrubs (8) lichens and (9) spike moss. Analyses were conducted in R 2.9.1 (see Appendix S1, S2, S3 for scripts).

I used Moran's *I* spatial autocorrelation to evaluate spatial pattern of the vegetation and soil seed bank. When neighbors at different focal distances are more similar or dissimilar than would be expected at random, the spatial pattern is said to be spatially autocorrelated (Sokal and Oden

1979). The value for the Moran's *I* index ranges between -1 to 1, where a value near 0 indicates a random spatial pattern, a positive value indicates aggregated distribution, and a negative value indicates overdispersion. Moran's *I* was conducted on percent cover vegetation data from summer 2007 and seed bank count data from winter 2009 because these seasons represent peaks in vegetation and seed abundances. Vegetation and seed bank data were log + 1 transformed to better meet the assumptions of the tests (Fortin and Dale 2005). Significance of the Moran's *I* value at each distance class (60-810 cm, 16 classes, increasing by 50 cm for the vegetation; 60-1060 cm, 11 classes, increasing by 100 cm for the seed bank) was assessed using a Monte Carlo randomization test with 10,000 permutations (Legendre and Legendre 1998). Significance levels were corrected using progressive Bonferroni. Analyses were conducted in R 2.9.1 (see Appendix S4 for scripts).

I used the Morisita Index of dispersion to evaluate the spatial distribution of the seed bank at the level of the quadrat. Deviation from random expectation was tested by creating confidence intervals using the critical value of a Chi-squared distribution with n-1 degrees of freedom (Hairston et al. 1971, Krebs 1999). Analyses were conducted in R 2.9.1. (Appendix S5 for scripts).

I used the Sorensen similarity coefficient to assess similarity of species composition. The Sorensen similarity coefficient was calculated as S=2a/(b+c), where **a** is the number of species shared in common between two samples, **b** is the total number of species in the first sample, and **c** is the total number of species found in the second sample (Sorensen 1948). I used Non-metric Multidimensional Scaling (NMS) ordination with Sorensen distance measure to evaluate community level differences in percent vegetation cover and seed bank seed counts among the three communities (Kruskal 1964, Mather 1976). Data from summer and winter were analyzed

11

independently and together to emphasize differences among the three vegetation types and differences among vegetation and seed bank across seasons. Rare species were removed (occurrence ≥ two sites) from the analysis to reduce noise in the data set (McCune and Grace 2002). The data were analyzed using PC-ORD 5.0. I started with a random configuration and performed 200 runs with real data. Dimensionality of the data was assessed using autopilot and the stability of the solution was evaluated using NMS scree plot. I tested for significant differences in species abundances (vegetation only) among the vegetation types using non-parametric Kruskal-Wallis one way analysis of variance (Sokal and Rohlf 1995).

Results

Species Composition

<u>Vegetation</u>

Overall the standing vegetation included 76 species (69 at reduced sample, 71 without lichens) in summer 2007 (May and June) and 57 (53 without lichens) in winter 2009 (February). During the summer and winter seasons respectively, pastures had 35 (23 at reduced sample) and 19 species, degraded scrub 56 (50 at reduced sample) and 45 species, and the rosemary scrub 50 (47 at reduced sample) and 42 species (Table 1). Seasonal decline in species richness largely resulted from aboveground absence of seasonally dormant and annual herbaceous species during the winter months.

The vegetation was dominated by long-lived perennials across all vegetation types; however, the dominant functional groups varied (Figure 4). Shrubs were the dominant vegetation in rosemary scrub during both seasons. Shrub cover between degraded and rosemary scrub sites was statistically different in summer and winter, but was not statistically different among all

three vegetation types due to one pasture with high shrub cover (plot 1). Approximately half of the vegetation cover in the degraded scrub plots was comprised of two subshrub species (*Licania michauxii* and *Polygonella robusta*) and a club moss (Lycopod) species (*Selaginella arenicola*). During both seasons the combined cover of these three species was significantly higher in the degraded scrub than the rosemary scrub. Subshrub cover was statistically different (highest in degraded scrub) among the three vegetation types in summer, but was not in winter due to reduced cover in the degraded scrub caused by *L. michauxii* dying back. In the pastures, grasses were the dominant vegetation cover. In winter, pasture grasses died back and dormant grass became the dominant vegetation cover (dormant grass and litter were indistinguishable during this season). Grass/dormant grass cover was highest in the pastures and was statistically different during both seasons (see GR vs. DG in Figure 4).

Bare sand and litter did not change substantially between summer and winter; however, litter cover was considerably higher in the pastures during the summer. Bare sand cover was higher in the degraded scrub than the rosemary and was much lower in the pastures than scrub. I have weak evidence of higher litter in native scrub than in degraded scrub. Among all three vegetation types, litter cover was generally slightly higher in the rosemary scrub when compared to the degraded scrub and was statistically different among the three vegetation types in winter due to a seasonal decline in pasture cover. This result does not necessarily signify a decline in litter cover in the pastures during winter, but is a consequence of an inability to distinguish dormant grass from litter (Figure 4).

The NMS ordination of vegetation percent cover showed that the three vegetation types were clearly distinct from one another in both winter (final stress = 5.82; axis 1: $p = 0.004$, $R^2 =$

0.62; axis 2: p = 0.004, R^2 = 0.17) and summer (final stress = 4.60; axis 1: p = 0.004, R^2 = 0.43; axis 2: p = 0.008, R^2 = 0.41) (Figure 5).

Seed Bank

A total of 10,636 seedlings belonging to 52 species were found in the seed bank across all three vegetation types and two seasons of sampling. Collectively, rosemary scrub had 30 species (2,271 seedlings), degraded scrub 36 (2,257 seedlings), and pasture 42 (6,108 seedlings) (Figure 6). The seed banks in all three communities were dominated by short-lived herbaceous species; however, the dominant functional group varied among the communities (Table 2). Across all three vegetation types shrubs were virtually absent from the seed bank and subshrub and grass species exhibited low species richness and seed density. The rosemary scrub was largely dominated by scrub herbs which comprised ~50-76% of the emerging seedlings. Two scrub herbs, *Paronychia chartacea* and *Stipulicida setacea*, were almost exclusively responsible for this pattern; however, *Hypericum cumulicola* had equivalent representation in sites where it was present aboveground. Degraded scrub had more or less equal percentages of scrub herbs, ruderal herbs, and sedges. In this vegetation type, scrub herb densities were lower than in rosemary scrub. Pastures were dominated by ruderal herbs which comprised ~50-70% of the emerging seedlings (Table S12). In degraded and rosemary scrub, propagules of a sporophyte club moss species (*Selaginella arenicola*) emerged from the soil samples. Across all sites seed densities were higher during winter than in summer. Seed bank size was generally equivalent among the three vegetation types; however, aboveground presence of a prolific seeding herb in one pasture plot (*Oldenlandia corymbosa* in plot 1) lead to a near doubling of average seed density of the pastures compared to the two scrub communities.

NMS ordination of seed count data showed that the three vegetation types had distinct seed banks in both winter (final stress = 3.25; axis 1: p = 0.004, R^2 = 0.46; axis 2: p = 0.004, R^2 = 0.42) and summer (final stress = 4.95; axis 1: p = 0.004, R^2 = 0.37; axis 2: p = 0.004, R^2 = 0.53). However, in winter, plot 5 (long-unburned rosemary scrub) and plot 9 (degraded scrub) had a similar seed bank. This similarity was not observed in the summer likely due to lower overall seed density at this time of year (Figure 5).

Spatial Structure

<u>Ground cover</u>

Across all vegetation types the microhabitats exhibited an aggregated distribution. The two scrub communities showed a more heterogeneous spatial distribution of bare sand and litter than the pastures. Spatial pattern of bare sand, litter and lichens showed no distinct differences between the rosemary and degraded scrub (Moran's *I* values and shape of the correlogram were similar) (Figure 7 and Figure S17). The pastures exhibited smaller and more sparsely distributed bare sand patches than in the scrub, as indicated by lower Moran's *I* values and points that were significant to shorter distances. Moran's *I* values for litter were slightly lower in the pastures than scrub, indicating a reduced tendency for a clumped spatial distribution.

<u>Vegetation</u>

Across all sites the vegetation exhibited an aggregated distribution; however, the degree of aggregation and shape of the correlograms differed among species and vegetation type. For most species and functional groups degraded scrub site 8 showed a distinct pattern of larger more homogenous patch size which was indicated by correlograms with higher Moran's *I* values and points that were significant for greater distances (e.g. bare sand, litter, lichen, shrubs, grasses,

15

subshrubs, *L. michauxii,* and *S. arenicola*). This plot is close in proximity to the pastures, has had a more intense disturbance history than the other degraded scrub sites, and has been invaded by non-native grasses (*D. eriantha* and *Melinis repens*).

Among functional groups, Moran's *I* correlograms revealed some difference among vegetation type for grasses, scrub herbs, shrubs, and palmettos. For grasses, patch size was larger in the degraded scrub than rosemary scrub (Figure 8). Grasses in the pastures generally had intense clumping indicated by higher Moran's *I* values which declined rapidly. Most rosemary and degraded scrub sites had a grass distribution that was more spread out and sparse than in the pastures. Spatial pattern for shrubs was most similar between degraded scrub and pastures which showed a stronger pattern of spatial aggregation than rosemary scrub (Figure 8). Scrub herbs in degraded scrub tended to have slightly larger patch size than in rosemary scrub. This was indicated by slightly higher Moran's *I* values that were significant for greater distances (Figure 9). Palmettos typically showed a stronger pattern of aggregation in the pastures than in rosemary scrub (Figure S18).

At the species level, Moran's *I* correlograms showed some differences among the vegetation types for *Aristida sp., P. chartacea* and *L. michauxii* (Figure 9). *Aristida sp.* and *P. chartacea* exhibited a larger more homogenous spatial distribution in the degraded scrub and smaller patch size in rosemary scrub. *L. michauxii* showed a small patchy spatial distribution in rosemary scrub and a larger homogenous distribution in the degraded scrub. Another notable spatial distribution was observed for *C. ericoides* (Figure S17). Lager more aggregated clumps were observed in plots with populations of mature adults (rosemary 5 and degraded 8) versus a population of younger individuals (rosemary 4).

The Mantel test which was used to evaluate overall spatial structure of the vegetation revealed a positive correlation between vegetation cover and spatial location in three rosemary scrub sites, degraded scrub 8, and pasture 3 (Table S13). Correlation between vegetation cover and spatial location indicates that vegetation was not randomly distributed through space.

Seed Bank

When compared to the vegetation, spatial autocorrelation was less common in the seed bank especially among species that were absent from aboveground vegetation. Seeds of sedges generally showed a random distribution or were aggregated in small patches (Figure S19). Seeds of ruderal herbs had random distributions, but did show aggregation if the species was present aboveground (Figure S19). Seeds of scrub herbs generally showed a stronger pattern of aggregation in rosemary than degraded scrub (Figure S20 and Figure S21).

At the species level, seeds of *P. chartacea*, *S. setacea*, and *H. cumulicola* (scrub herbs) were generally aggregated in small patches in rosemary scrub and randomly distributed in degraded scrub (Figure 10). A random distribution was observed across all plots and vegetation types for wind dispersed ruderal herbs that were never recorded aboveground (*Eupatorium capillifolium, Gamochaeta purpurea*, and *Scoparia dulcis*). Seeds of *Linaria floridana, O. corymbosa*, and *Richardia brasiliensis* showed an aggregated distribution at sites where they were present aboveground (Figure S22 and Figure S23).

Similar results were found when seed distribution was evaluated with the Morisita index (Table 3). Overall, the Morisita index showed that the majority of species had an aggregated distribution in the seed bank. Only three species were randomly distributed (*Lechea cernua, Bulbostylis ciliatifolia*, and *Melinis repens*). Scrub herbs had a greater tendency to be aggregated

17

than ruderal herbs. Scrub herbs had an aggregated distribution at all rosemary scrub sites, while aggregation occurred less frequently in degraded scrub. The Mantel test evaluating the correlation between the seed bank and spatial location showed a weak positive correlation in two rosemary scrub plots and two degraded scrub plots (Table S13).

Temporal Pattern

Vegetation

Across most sites, richness was lower in the winter than summer. High Sorensen similarity coefficients indicated that species composition did not differ substantially between seasons. Sorensen values were similar across all but two pasture plots which exhibited lower similarity coefficients (Table 4). NMS ordination of vegetation cover from summer and winter showed clear separation among the vegetation types and, for most plots, close similarity between winter and summer samples from the same site (final stress = 14.20; axis 1: $p = 0.004$, $R^2 = 0.613$) (Figure S24). Grouping among winter and summer pasture plots is largely due to grass dormancy during the winter. Degraded scrub summer plot 8 is also close in proximity to the pasture sites. This plot is near pastures and has a large proportion of non-native grass cover. Spatial pattern of the vegetation was positively correlated between seasons across all sites, with no visible trend among community type (Table 4).

Seed bank

Species richness in the seed bank was equivalent between rosemary and degraded scrub and did not change substantially across seasons. Pastures had the highest seed bank species richness, which declined by 3-5 species in the summer. Sorensen values between summer and winter were relatively high, indicating that species composition did not change substantially

18

across seasons. Sorensen values were slightly lower in rosemary scrub when compared to degraded scrub and pasture (Table 4). NMS ordination of seed bank count data from summer and winter showed clear differences among vegetation types and high similarity between winter and summer samples from the same site (final stress = 8.73; axis 1: p = 0.004, R^2 = 0.462; axis 2: p = 0.004, R^2 = 0.370) (Figure S25). The Mantel test comparing the consistency of spatial distribution of the seed bank across summer and winter showed a weak positive correlation at all three rosemary scrub sites, no correlation at the degraded scrub sites, and a positive correlation at two pasture sites (Table 4).

Relationship Above- and Belowground

Species composition aboveground and belowground was dissimilar across all sites. While Sorensen values across vegetation types were similar, pasture sites generally had the lowest similarity between the vegetation and seed bank, rosemary scrub sites had a slightly higher range of similarity, and the degraded scrub sites had the highest (Table 5). In terms of structural association above and belowground only two rosemary scrub plots showed a weak correlation (analyzed as functional groups). The pasture plot with high shrub cover (plot 1) had a positive correlation (analyzed by species) (Table 5). The three plots that showed a significant spatial association above and belowground (plot 1, 5, and 6) were the plot with the highest percent shrub cover (Table 5).

The seed banks of some species and functional groups were correlated with aboveground microhabitats (bare sand, litter, shrub cover) (Table 6, for full table see Table S14). The seed banks of scrub herbs, both as a functional group and as individual species, were positively associated with aboveground vegetation, litter cover and, in a few cases, shrub cover; degraded scrub sites showed few correlations. Aside from a few exceptions, sedges and grasses were not

19

correlated with aboveground microhabitats. Ruderal herbs typically had the highest amount of correlation with microhabitats in degraded scrub and associations were found with aboveground vegetation, bare sand, and shrub cover. One rosemary scrub and one pasture plot showed a positive correlation between the ruderal herb seed bank and shrub cover (Table S14).

The seed bank of *H. cumulicola* was correlated with aboveground vegetation, litter, and shrub cover in rosemary scrub. The seed bank of *L. floridana* was correlated with aboveground vegetation and shrub cover in the high shrub cover pasture plot, bare sand and shrub cover at one degraded scrub site, and litter at one rosemary scrub site. The seed bank of *O. corymbosa* was correlated with aboveground vegetation and shrub cover at the high shrub cover pasture plot. The seed bank of *P. chartacea* was correlated with aboveground vegetation, litter, and shrub cover across the three rosemary scrub plots. The seed bank of *S. setacea* was positively correlated with aboveground vegetation (two sites) and litter (one site) in rosemary scrub and with litter at one degraded scrub site.

Discussion

In this study, differences in disturbance history influenced community composition, species relative abundance, and species spatial distribution. Increased anthropogenic disturbance homogenized spatial structure and increased abundances of functional groups with lower vertical canopy heights (i.e. grasses in the pasture, subshrubs and *S. arenicola* in degraded scrub). Alteration of habitat structure can impact animal use of a site because many species have habitat preferences with certain structural requirements (Breininger and Smith 1992, Mladenoff et al. 1993, Cork and Catling 1996, Doster and James 1998).

Loss of spatial heterogeneity in rosemary scrub could also have consequences for the herbaceous scrub endemics that inhabit open sand gaps. While differences in spatial structure of the native and degraded scrub were weakly demonstrated in scrub herbs aboveground, a clear lack of spatial pattern of the seed bank was observed in degraded scrub. Seeds were not found to be aggregated around mother plants or in litter patches as they were in native scrub. Dispersal of seeds away from mother plants may lead to more homogeneous spatial distribution of new recruits and/or result in population decline if seeds are transported to areas away from safe sites. Change from an aggregated to homogeneous distribution could influence the genetic structure of the population, modify seed and pollen distributions, alter plant interactions with pollinators, or change inter- and intraspecific species interactions (Levin and Kerester 1975, Antonovics et al. 1997, Hassell and Wilson 1997, Lehman and Tilman 1997).

Species Composition

I found differences in species abundances and growth forms in the seed bank and vegetation among the three plant communities. Changes in disturbance type and intensity are known to alter species composition, select for plant morphological characteristics tolerant of the disturbance regime, and change suitable microhabitat availability (Halpern 1988, Diaz et al. 1992, Jimenez and Armesto 1992, Kinucan and Smeins 1992, O'Connor and Pickett 1992, Lavorel et al. 1999, Quintana-Ascencio et al. 2009). Species composition is altered as disturbance frequency and intensity increase because the recovery potential of sensitive species diminishes (Collins et al. 2001).

Although changes in species abundances and dominant growth forms were observed across the disturbance gradient, I found species characteristics such as life span and primary reproductive method were not; long-lived perennial species reliant upon vegetative/colonial

21

reproduction were dominant aboveground (e.g. shrubs, subshrubs, grasses), while short-lived annual/perennial species reliant upon sexual reproduction were dominant in the seed bank (e.g. herbs, sedges). Dominance by long-lived species aboveground and short-lived species in the seed bank is frequently reported in the literature (Schneider and Sharitz 1986, Vlahos and Bell 1986, Kitajima and Tilman 1996, Figueroa et al. 2004, Shaukat and Siddiqui 2004).

While classic life history theory predicts increased disturbance frequency will select for short-lived annual species with high fecundity and quick maturity (Cole 1954, Iwasa and Cohen 1989), other studies have found that proportion of clonal spreading perennials increases with greater disturbance frequency (Fahrig et al. 1993, Fahrig et al. 1994). While disturbance type, frequency and intensity differed across the sites in this study, both degraded scrub and pastures had been removed from their historic disturbance regimes. Particularly in the pastures, removal from grazing (one year prior to initiation of this study) has likely given a competitive advantage to perennial grasses and lead to near complete absence of short lived species aboveground (Bertiller 1992, Marco and Paez 2000).

Species composition of the seed bank and vegetation differed most between the pastures and the two scrub communities. In the pastures, only a few native scrub species persisted in the aboveground vegetation (*Opuntia humifusa*, *S. etonia*, *S. tenax*, and *Smilax sp.*) likely due to their ability to evade herbivory, and scrub species were rarely found in the seed bank. The perennial grasses dominant aboveground were absent from the seed bank. This result is not surprising since the three dominant grass species aboveground rely primarily on vegetative reproduction for propagation (Shaukat and Siddiqui 2004). Grasses commonly form transient seed banks even among species that propagate only from seed (Bertiller 1992, Russi et al. 1992) and perennial grasses that reproduce vegetatively often have low seed production (Champness

and Morris 1948). Emergence of *M. repens* (invasive species that has invaded degraded scrub and the pastures) during only one sampling period (winter 2009) likely indicates that this species does not form a persistent seed bank.

Between the rosemary and degraded scrub species identity was roughly equivalent aboveground; however, species abundances were substantially altered. Shrubs were the dominant functional group in rosemary scrub. In degraded scrub, subshrub species (which were relatively rare in rosemary scrub) had a substantially higher percent cover. *L. michauxii* and *P. robusta* were the two species primarily responsible for this increase in abundance. *S. arenicola*, a club moss, also had higher cover in degraded scrub. One possible reason for greater abundance of these species in degraded scrub may be that rollerchopping (the primary disturbance) may have favored species growing close to the ground that could reproduce from vegetative structures (e.g. *L. michauxii* and *S. arenicola*). Reduced cover of taller shrubs and thus reduced competition may also explain why obligate seeding subshrubs (e.g. *P. robusta*) have increased in abundance in degraded scrub.

Cover of ground lichens was also substantially higher in degraded scrub than either the pastures or rosemary scrub. Differences with rosemary scrub are likely due to fire suppression in degraded scrub and reduced shrub cover which allows more opportunities for lichens. Lichens are known to increase in abundance with time-since-fire (Hawkes and Menges 1996). While the exact fire history of the degraded scrub is not known it is presumed the area is long-unburned. As a functional group, scrub herbs also had higher cover in the degraded scrub; however, this pattern was largely due to an increase in one species, *Chapmannia floridana*, which is less frequent in rosemary scrub. Species most common aboveground and in the seed bank in rosemary scrub (e.g. *S. setacea* and *P. chartacea*) had reduced abundance in the degraded scrub.

23

This difference is likely due to fire suppression since the long-unburned rosemary scrub site (plot 5) had comparable cover and seed densities of these two species in degraded scrub. Scrub herbs are known to decline aboveground and in the seed bank as time-since-fire-increases (Hawkes and Menges 1996, Schafer et al. 2010). Scrub herbs inhabit open sand gaps, and as time-since-fire increases, gaps close as shrubs, litter and lichen cover increase (Menges and Hawkes 1998). Decline in microhabitat availability in long-unburned stands does not appear to be the only reason for herb decline. High occurrence of allelopathic chemicals leached from roots and leaves of *C. ericoides* may be a contributing factor (Hunter and Menges 2002, Hewitt and Menges 2008); however, only two sites had *C. ericoides* present aboveground (rosemary 5 and degraded 9) and all four long-unburned sites (rosemary 5 and degraded 7, 8, 9) had lower seed densities of scrub herbs. Although bare sand gaps are present even in long-unburned stands, reduced herb density may be due to a decline in microhabitat quality as gap area decreases and distance from shrubs is reduced (Menges et al. 2008, Schafer et al. 2010). My data showed a slight increase in the amount of bare sand cover and decline in shrub cover in degraded scrub and aerial photos of the area also reveal reduced shrub cover and greater open space than native scrub. While aboveground bare sand cover may be greater in degraded scrub, gap quality may not be equivalent since belowground conditions (e.g. competition with roots) also influence microhabitat suitability (Schafer et al. 2010).

Species composition of the seed bank and vegetation was dissimilar. Lack of correspondence of both compositional (Thompson and Grime 1979, Kinucan and Smeins 1992, Kitajima and Tilman 1996, Crawford and Young 1998, Maliakal et al. 2000, Tekle and Bekele 2000, Shaukat and Siddiqui 2004) and structural attributes (Henderson et al. 1988, Arroyo et al. 1999) between the vegetation and seed bank have been found in other plant communities.

Correspondence between abundance and composition of the seed bank and standing vegetation is more commonly found in communities with a large portion of annuals (Zammit and Zedler 1994, Olano et al. 2005). In this study, dominance of vegetatively reproducing species aboveground likely explains the lack of correspondence of species composition above- and belowground.

Among scrub species, presence in the seed bank was well predicted by fire adaptive strategy (Navarra, Chapter 2). In general obligate seeders or seeding and resprouting species were present in the seed bank, while resprouters and clonal spreaders were absent (Menges and Kohfeldt 1995). Across the disturbance gradient ruderal species, particularly wind dispersed species (e.g. *Conyza canadensis*, *E. capillifolium*, *G. purpurea*, *S. dulcis*), were rarely present in the aboveground vegetation. In the pastures, non-wind dispersed ruderal herbs were possibly more abundant aboveground when grazing occurred (e.g. *Houstonia procumbens*, *O. corymbosa*, *Oldenlandia uniflora*, *Polypremum procumbens*) and competition with grasses was reduced (Manier and Thompson Hobbs 2006, Williams et al. 2007). Many of the ruderal species found in this study have also been found in the seed banks of native Florida habitats such as flatwoods (*G. purpurea*, *L. floridana*, *O. uniflora*, *P. procumbens*) and sand pine scrub (*Cyperus spp.*, *C. canadensis*, *E. capillifolium*, *L. floridana*) (Carrington 1997, Maliakal et al. 2000). These species are likely well dispersed due to seed structures that promote wind dispersal and/or small seed size. Also, the discovery of seeds emerging from rabbit feces in this study (e.g. *O. corymbosa*) suggests animal dispersal may be an additional mechanism by which ruderal species are introduced into the seed banks of areas where they do not occur aboveground. Sedge species in particular had high species richness and density in the seed bank but only two sedge species were found growing aboveground (e.g. *Cyperus croceus*, *Cyperus retrorsus*). Sedges are known to produce large seed banks, have high seed production of very small well-dispersed seeds, and are

dispersed by animal feces (Kinucan and Smeins 1992, Leck et al. 1998, Weiterová 2008, Brescacin *unpublished data*).

Spatial Structure

Spatial aggregation was ubiquitous among the vegetation and microhabitats but aggregated distribution of the seed bank was less frequent. While differences in species abundances across the disturbance gradient were apparent, demonstration of aboveground differences in spatial pattern among the vegetation types was less conclusive. That said, some spatial pattern differences were found among the sites, but in most cases dissimilarity among the vegetation types were not universally observed among all three replicates. One reason for this is that disturbance intensity among the degraded scrub plots and time-since-fire among the rosemary scrub plots differs. Degraded scrub plot 8 was cleared 11 years prior to the other sites and aerial photos appear to show a history of greater disturbance intensity. This site stands out as having a larger, more homogenous patch size for most species and functional groups. Aerial photos also indicate that one degraded site (plot 9) is less disturbed than the others. Spatial pattern for one rosemary scrub site (plot 5) was more similar to the degraded scrub for some species (e.g. *C. ericoides*) expectedly because this plot is long-unburned and has higher cover of species that are known to increase in abundance with greater time-since-fire (Menges and Kohfeldt 1995).

Differences in spatial pattern were observed for species and functional groups with altered aboveground abundances. For example, those species with increased abundance in the degraded scrub (e.g. *L. michauxii*) generally showed larger more homogeneous patch size. Surprisingly, spatial patterns of bare sand and litter did not differ between the rosemary and degraded scrub. Failure to detect strong spatial pattern differences for the vegetation and ground

cover could be partially explained by scale (Turner 1989, Fortin and Dale 2005). The macroplot size (16 x 16 m) used in this study was not large enough to capture the larger scale structural differences that occur between the rosemary and degraded scrub. Arial photographs show the degraded scrub has increased cover of bare sand gaps and reduced shrub cover compared to rosemary scrub. Larger gap sizes with uniform distribution have been found to increase dispersal distance (Bergelson et al. 1993). A change in the bare sand gap structure in the degraded scrub may explain why there is less spatial aggregation of species in the seed bank.

Spatial pattern differences among the vegetation types were more apparent at the finer scale of the seed bank. Spatial distribution of the seed bank had a greater tendency to be random as disturbance intensity increased; however, spatial structure at the species level was largely dependent upon dispersal mechanism and presence of species aboveground. Species absent from the aboveground vegetation, such as wind dispersed ruderal species, showed a random distribution (e.g. *Eupatorium capillifolium*, *G. purpurea*, *Scoparia dulcis*) across all sites.

The greatest differences in seed bank spatial structure were observed for scrub herbs in rosemary versus degraded scrub. Several analyses of the structural attributes of the seed bank indicated presence of spatial pattern in rosemary scrub and a lack of pattern in the degraded scrub. The results indicated a greater tendency for the seed banks of scrub herbs in rosemary scrub (1) to have an aggregated distribution (indicated by Moran's *I* and Morisita indices), (2) to show spatial pattern (3) to have correspondence in the spatial distribution of seeds across seasons (4) and to have association with aboveground vegetation/microhabitat cover (presence of species aboveground, litter cover, and shrub cover). Canopy structure, aboveground species composition and distribution, and microhabitat cover are known to influence seed bank spatial pattern (Olano et al. 2002). In rosemary scrub, seeds tended to cluster around mother plants but were also

dispersed away from plants and were potentially trapped in litter patches. Accumulation of seeds under litter patches but infrequent detection under shrubs was unexpected. Seeds are commonly found to aggregate beneath shrubs due to their restriction of lateral seed movement and to the contrasting inability of bare ground to retain seeds (Fuentes et al. 1984, Price and Reichman 1987, Zammit and Zedler 1988, Aguiar and Sala 1997, Moro et al. 1997, Bullock and Moy 2004, Caballero et al. 2008). Higher rates of depredation occurring under shrub patches may explain the lack of association between the seed bank and shrub cover. While direct association between shrub cover and the seed bank was infrequent, amount of shrub cover appeared to be an important predictor of the structural correlation between the vegetation and seed bank since the plots with the highest amount of shrub cover (plots 1, 5 and 6) showed correlation above and belowground. Lack of association between the seed bank of scrub herbs and litter in the degraded scrub may be due to the fact that litter and shrub cover were reduced and that overall seed densities of scrub herbs were lower.

The pasture plot with high proportion of shrub cover also showed structural correlation above- and belowground. The seed banks of species present aboveground (e.g. *L. floridana*, *O. corymbosa*) were correlated with mother plants and shrub cover. Herbs and sedges may be facilitated by the presence of shrubs in the pastures which excluded grasses from growing directly beneath them. Shrubs are known to outcompete grasses in other systems (McPherson and Wright 1990, Köchy and Wilson 2000, Lett and Knapp 2003). Because herbs and sedges were generally only observed growing beneath shrubs, the presence of perennial grasses seems to alter the competitive interaction between shrubs and herbs. In scrub, herbaceous species are negatively impacted by shrubs, which is evident from their decline in abundance as shrub cover

increases (Menges and Hawkes 1998). On the other hand, herbs in the pastures appear to be facilitated by the presence of shrubs since shrubs are able competitively exclude grasses.

Broader Implications

Understanding how differences in disturbance history will alter community composition, abundance, and spatial distribution may allow for the accurate prediction of how communities will change under diverse disturbance regimes. Anthropogenically disturbed communities, in many cases, will not follow predictable recovery sequences due to drastic changes imposed on the biotic and abiotic environment (Stylinski and Allen 1999). These changes include complete destruction of native biomass and/or seed bank, intentional introduction of non-native (often long-lived) species, and alteration of hydrology and/or soil properties. Knowledge of which life history and morphological characteristics will be favored by the historic disturbance regime will better enable land managers to pinpoint which anthropogenically disturbed systems will follow a trajectory towards the reference community and which will require active restoration.

In this study, an increase in disturbance intensity led to a loss of species sensitive to disturbance and an increase in abundance of tolerant species. Changes in species abundances across the disturbance gradient have resulted in structural changes in the community, particularly to the vertical canopy structure and to the fine scale spatial heterogeneity of the seed bank for scrub herbs. What long term effects these structural changes will have on community dynamics and how these communities will change over time remains unclear. Passive restoration of scrub in pastures seems unlikely due to the presence of non-native perennial grasses (D'Antonio and Vitousek 1992, Christian and Wilson 1999, Stylinski and Allen 1999, Davis et al. 2005, Domènech et al. 2005, Kulmatiski 2006). It is unknown whether passive restoration of native species abundance and distribution in the degraded scrub can occur. To predict trajectories of

recovery, it is necessary to know what mechanisms are responsible for maintaining species

abundances and spatial structure in native rosemary scrub. While fire and elevation are known to

be two important components (Hawkes and Menges 1996), there are certainly other contributing

factors. While restoration projects often emphasize reintroducing species absent from the

disturbed community, an even greater challenge is presented in determining how to restore native

spatial structure and species abundance in degraded habitats.
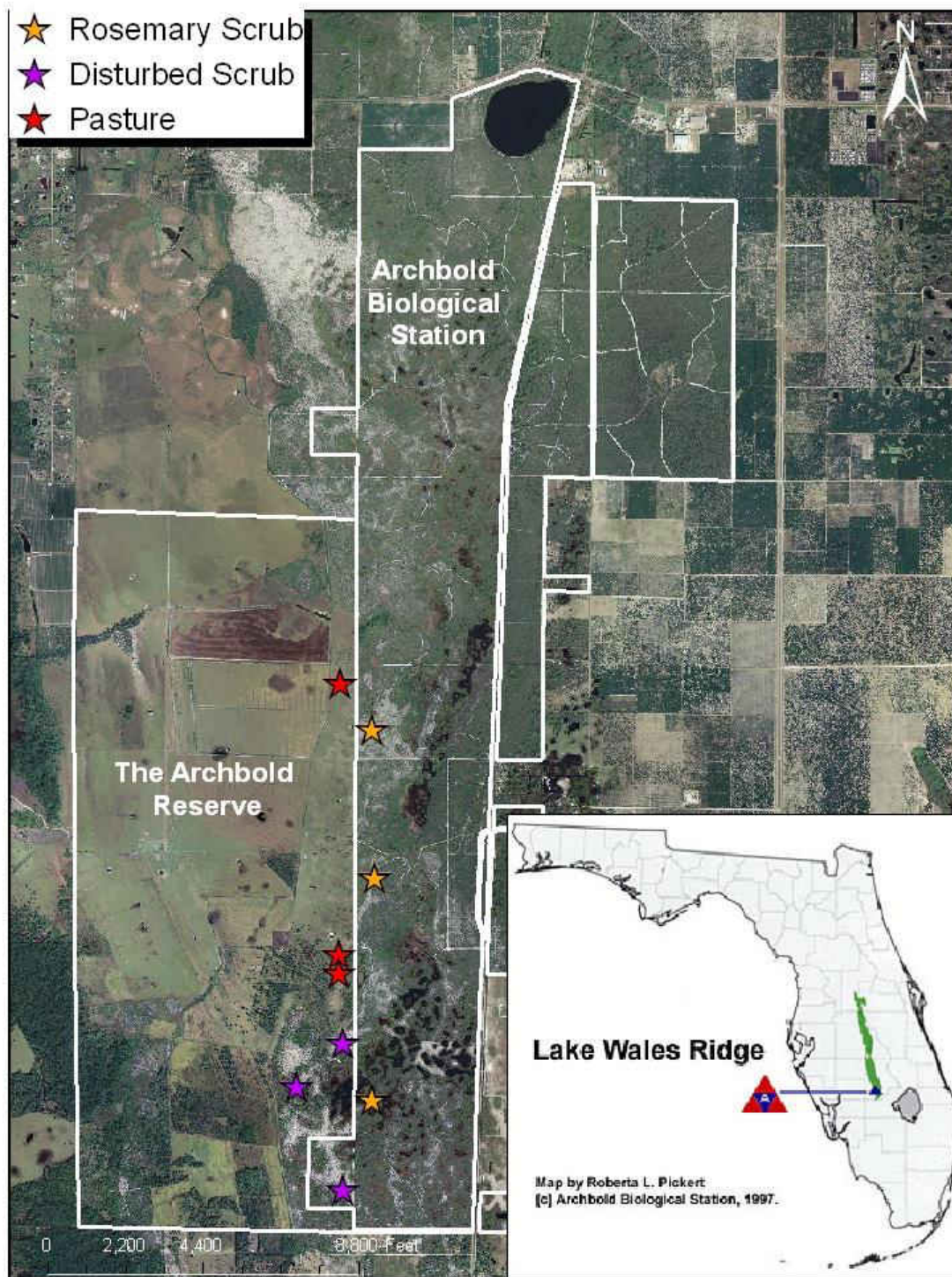
Figure 1. Map of macroplot locations at Archbold Biological Station and the Archbold Reserve.
Yellow = rosemary scrub, purple = degraded scrub, red = pasture.
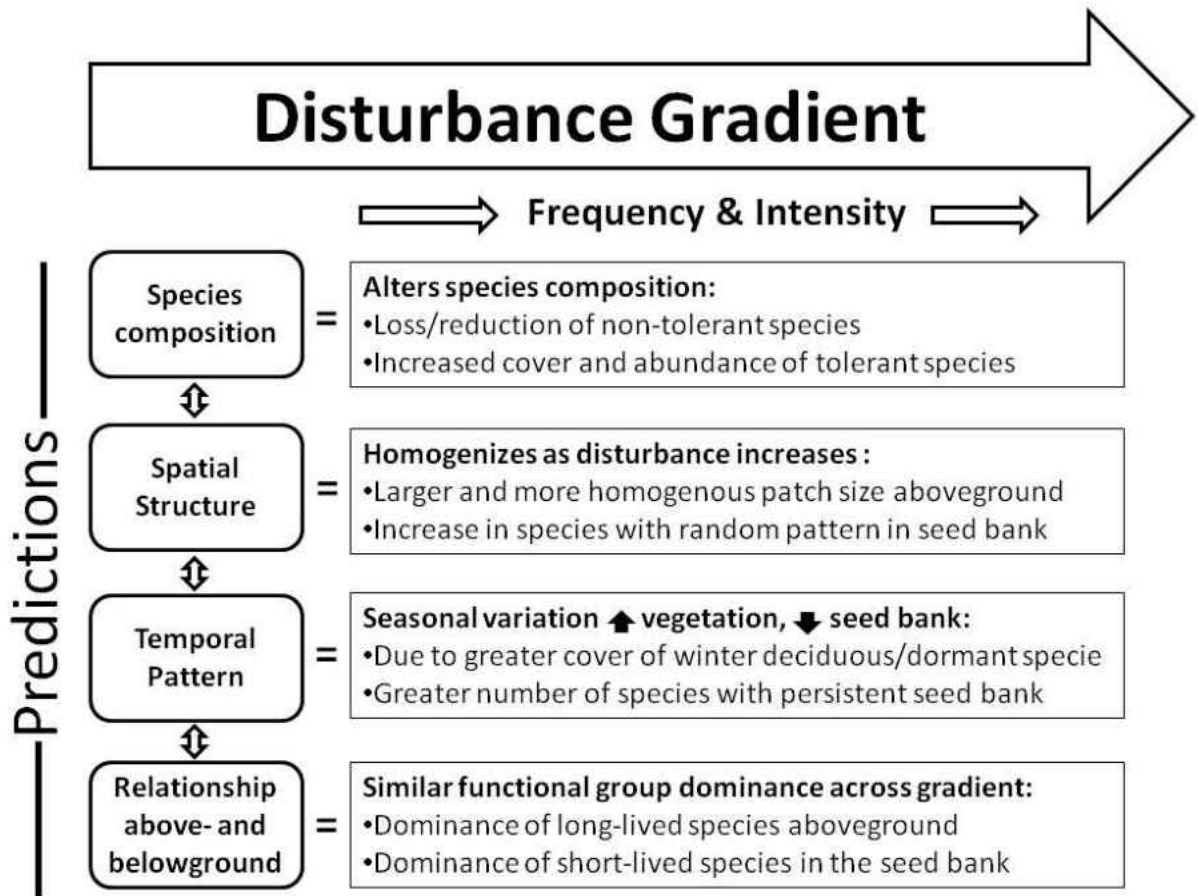
Figure 2. Prediction of how species composition, spatial structure, temporal pattern and the relationship above- and belowground will change across a disturbance gradient with increased frequency and intensity.
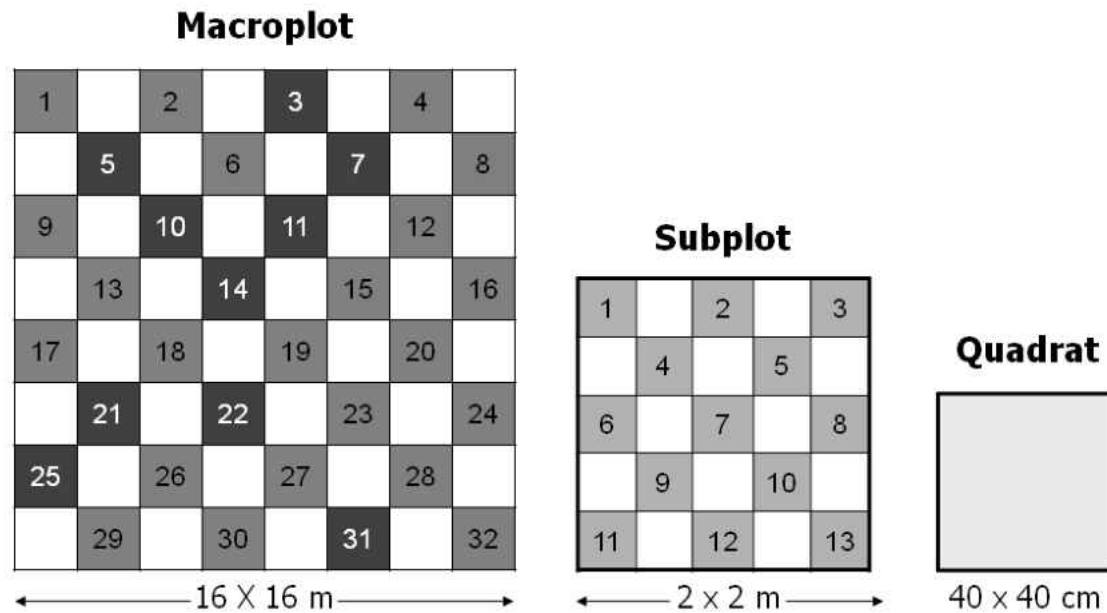
Figure 3. Sampling design for vegetation and seed bank sampling. Thirty-two subplots were sampled in summer 2007 (416 sample units). For the remainder of the study sample size was reduced to 10 randomly selected subplots (dark grey squares, 130 sample units). Shaded areas indicate sampling locations.
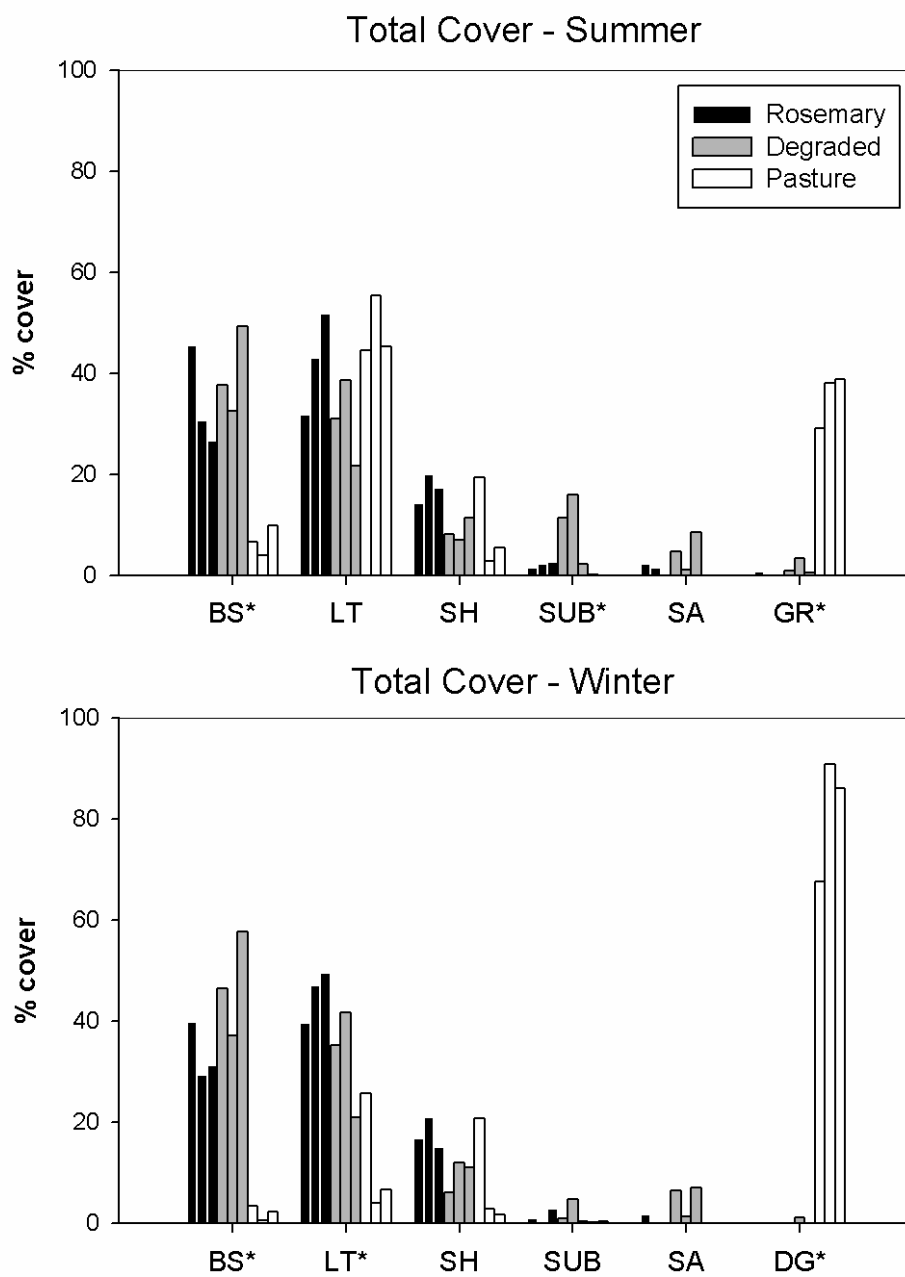
Figure 4. Percent total aboveground cover in summer 2007 and winter 2009. SU = sample unit, * = α < 0.05, SH = shrub, SUB = subshrub, SA = *S. arenicola*, GR = grasses, BS = bare sand, LT = litter, DG = dormant grass.
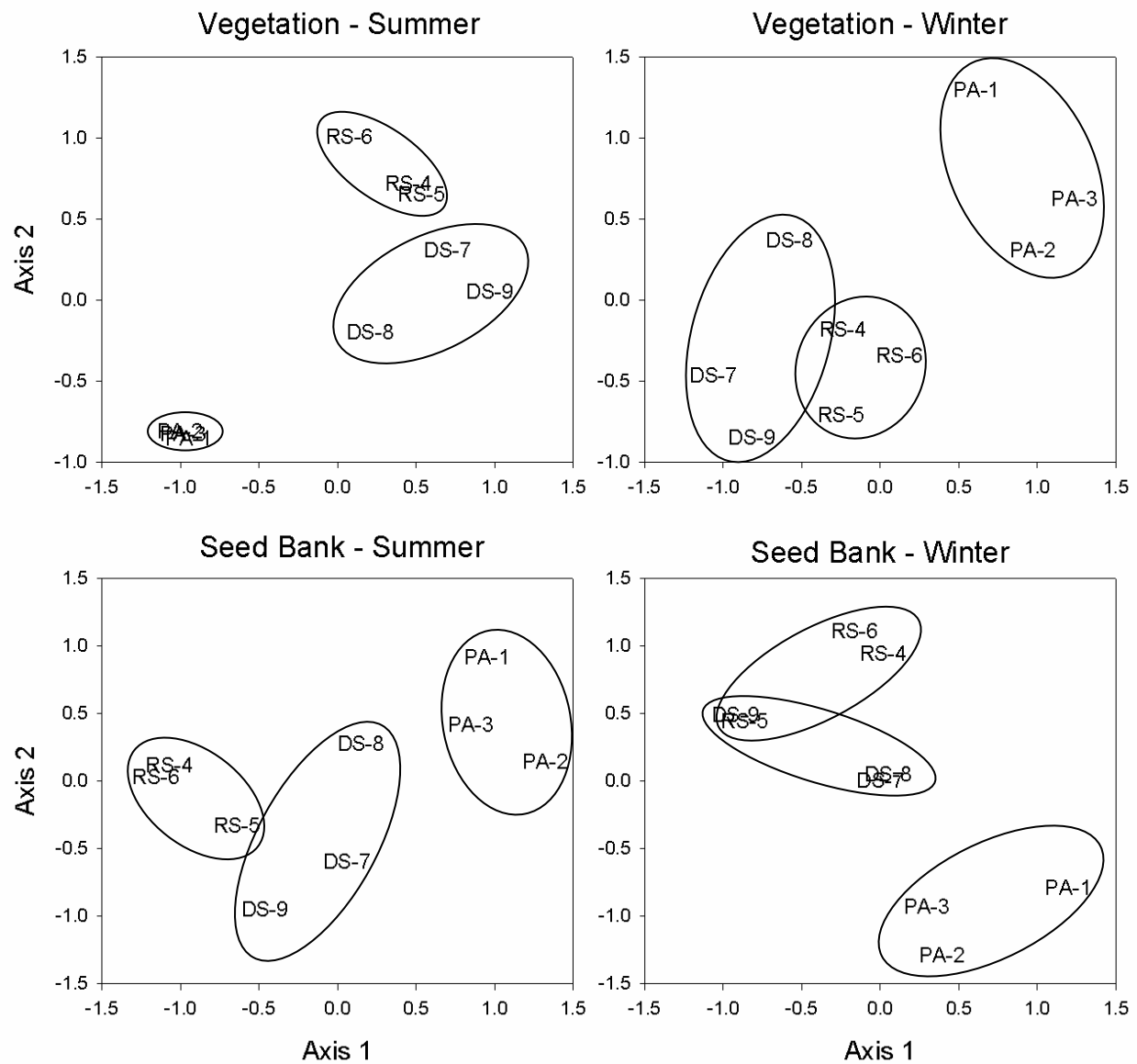
Figure 5. NMS ordination plots of the vegetation and seed bank in summer and winter. RS = rosemary scrub, DS = degraded scrub, PA = pasture, number denotes site ID.
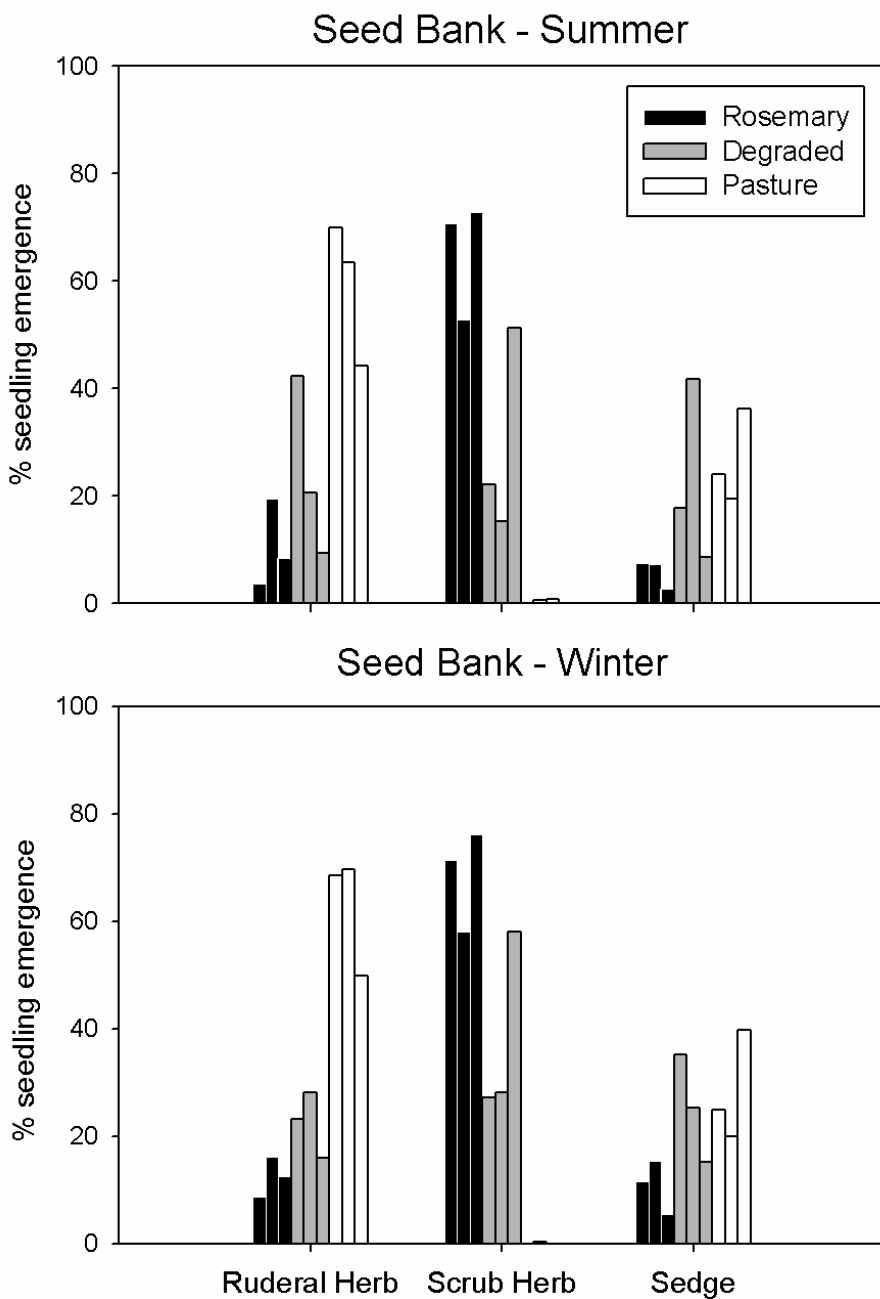
Figure 6. Percentage of emerging seedlings of ruderal herbs, scrub herbs, and sedges in summer 2008 and winter 2009.
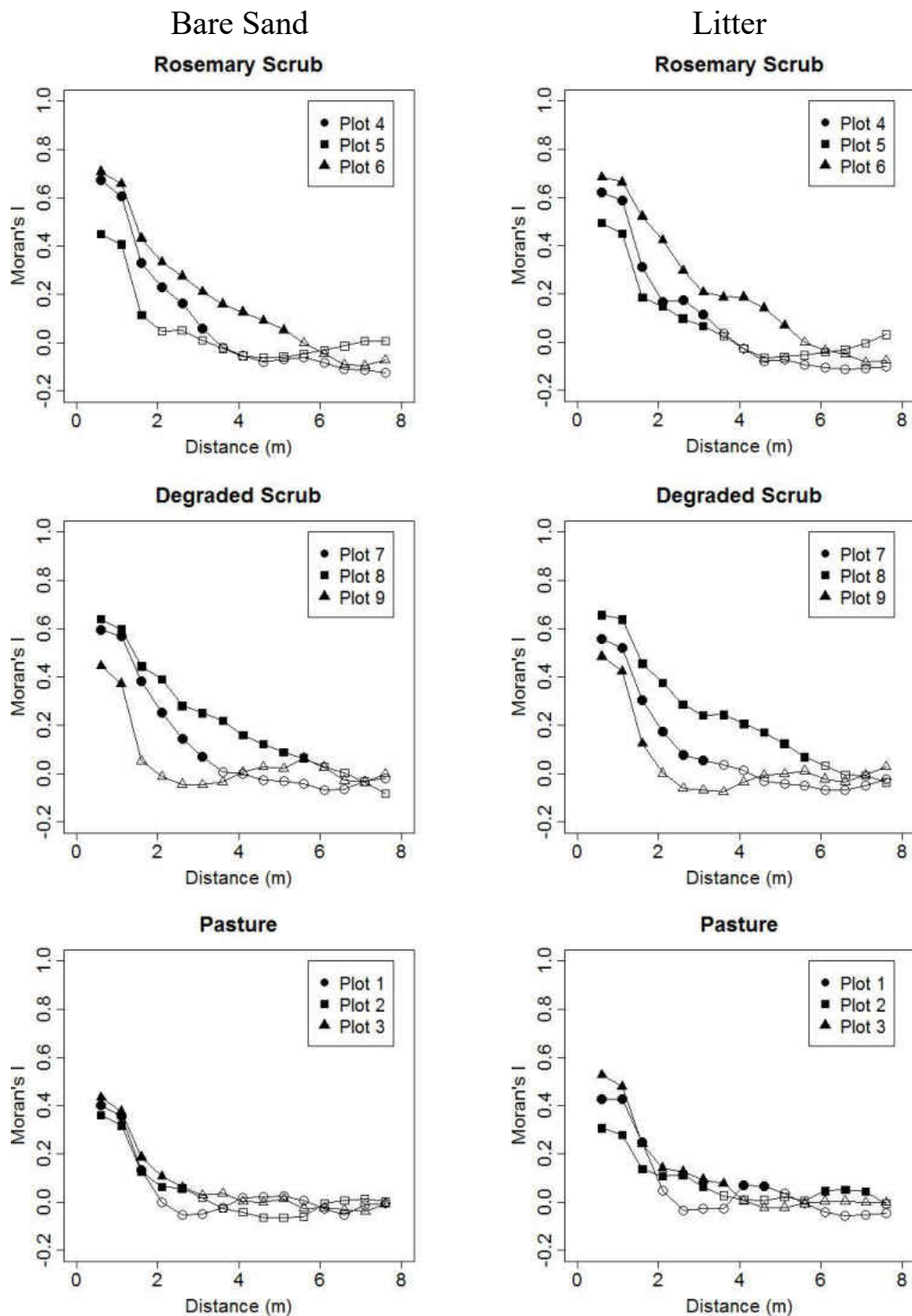
Figure 7. Bare sand (right) and litter (left) - Moran's *I* correlograms of ground cover in rosemary scrub, degraded scrub, and pasture. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.
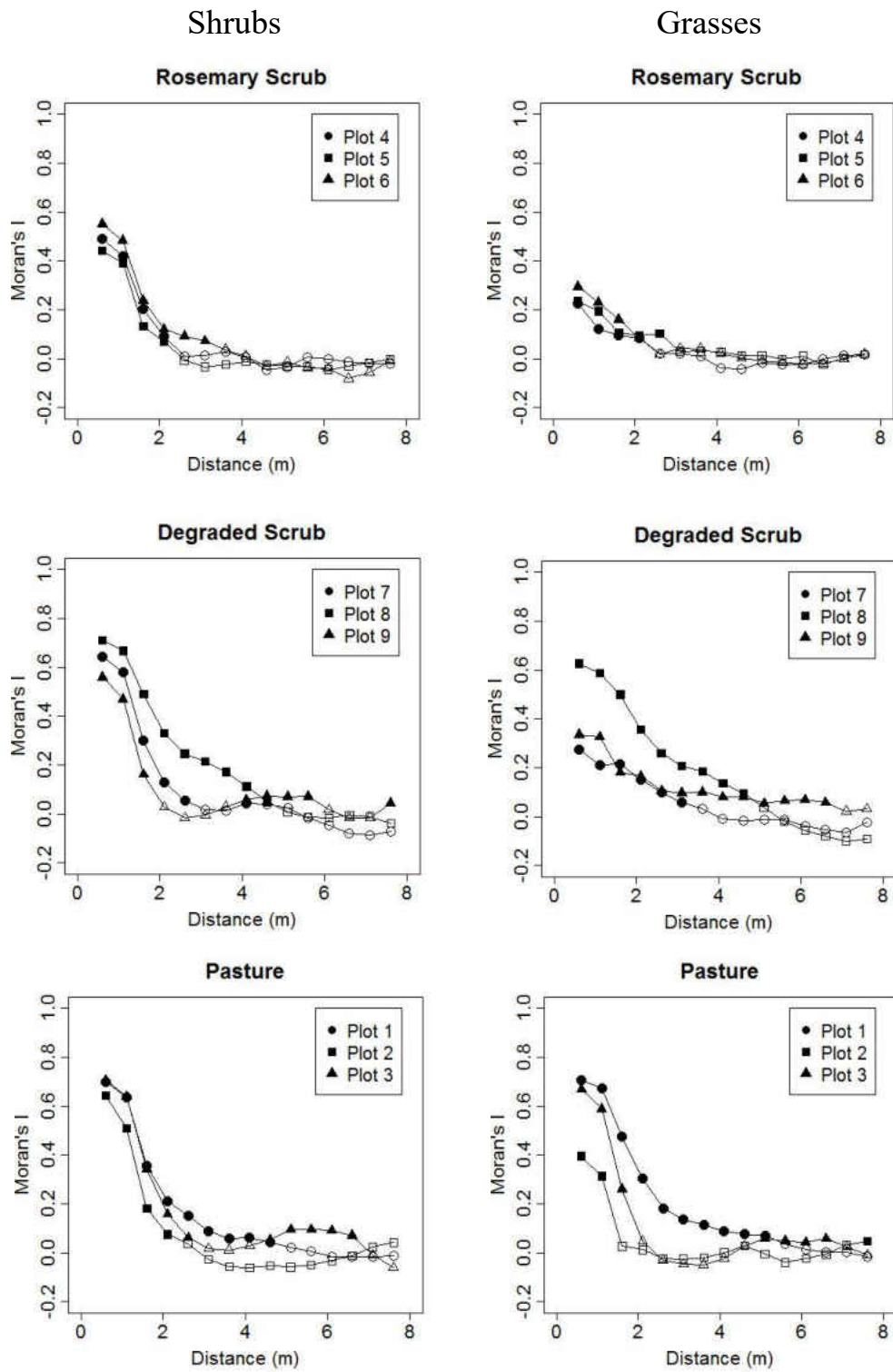
Shrubs   Grasses

Figure 8. Moran's *I* correlograms of shrubs (left) and grasses (right) between the rosemary and degraded scrub. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.
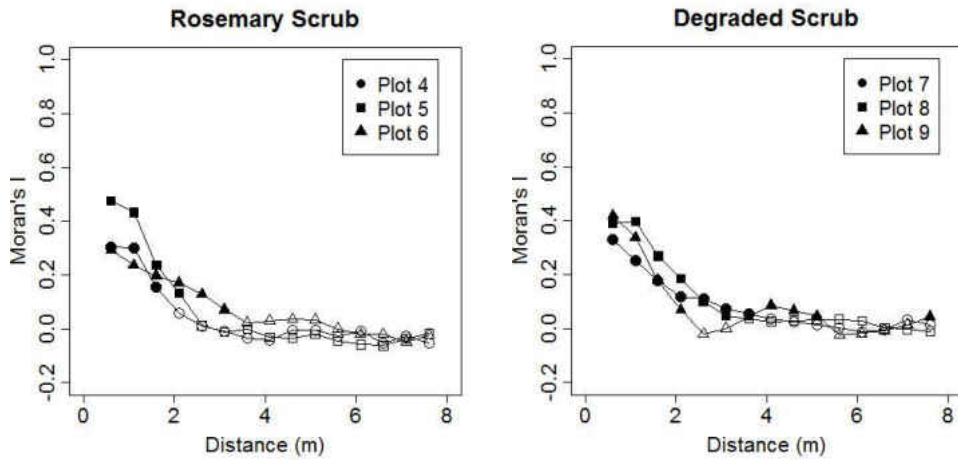
Scrub Herbs

Aristida sp.
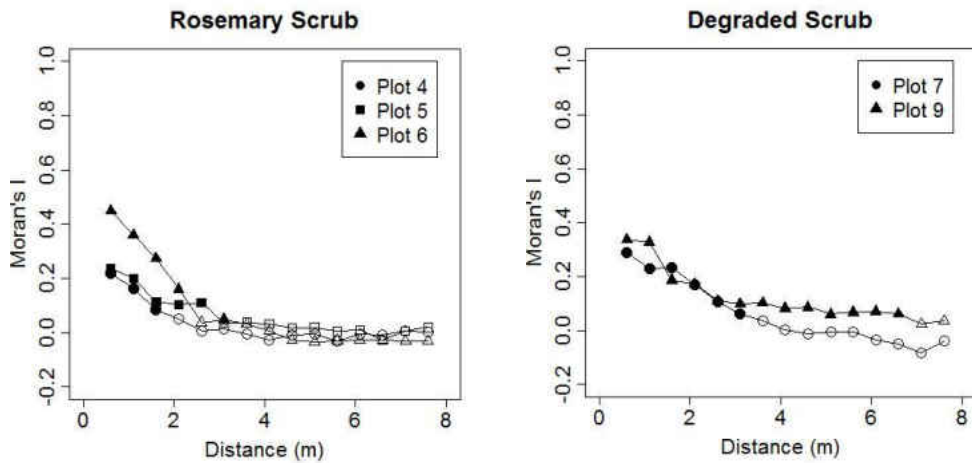
Licania michauxii
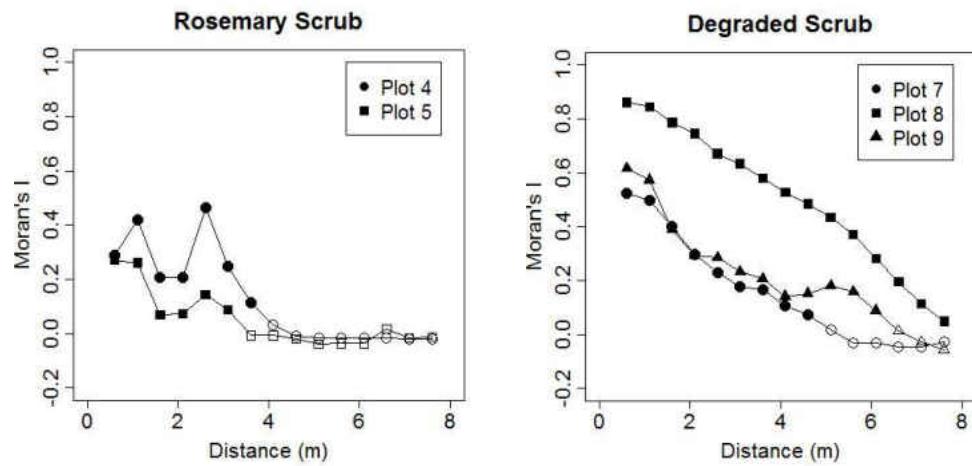
Figure 9. Moran's *I* correlgrams of scrub herbs (top), *Aristida sp.* (middle), *L. michauxii* (bottom) between the rosemary and degraded scrub. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.

39

Paronychia chartacea
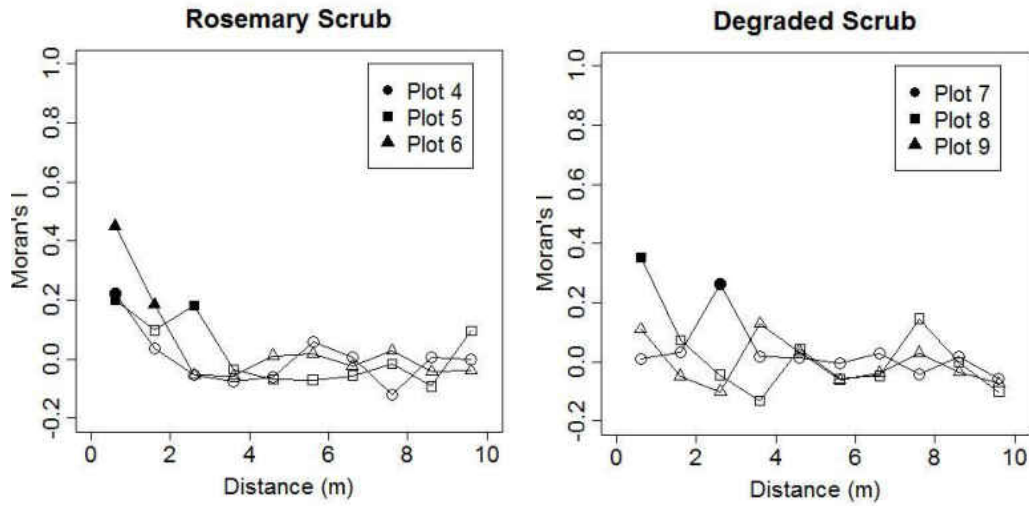
Stipulicida setacea
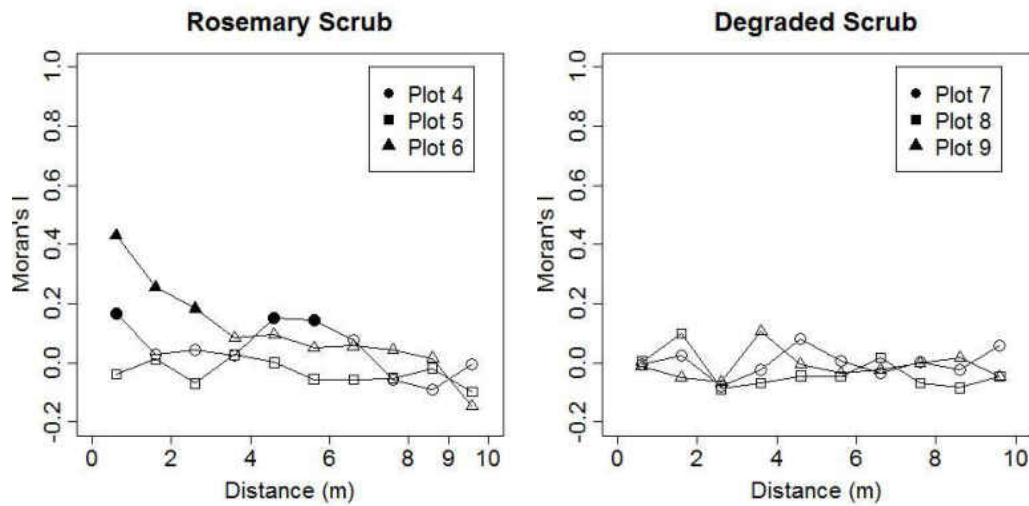
Hypericum cumulicola
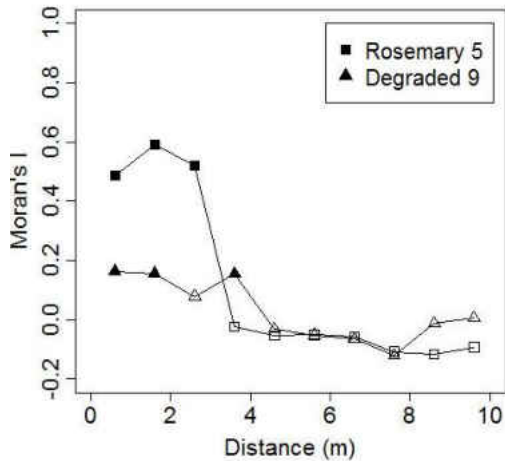
Figure 10. *P. chartacea* (top) and *S. setacea* (center), *H. cumulicola* (bottom left) - Moran's I correlograms of seed bank in rosemary scrub and degraded scrub. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.

40

Table 1. Mean percent cover (± standard error) of ground cover and vegetation across the three vegetation types in summer 2007 and winter 2009. A complete species list can be found in the appendix (Table S11).

	SUMMER 2007			WINTER 2009		
	Rosemary	**Degraded**	**Pasture**	**Rosemary**	**Degraded**	**Pasture**
Ground Cover						
Bare Sand	34.23 (5.71)	39.87 (5.0)	6.7 (1.73)	33.43 (3.81)	47.2 (5.87)	9.2 (3.27)
Litter	42.23 (5.79)	30.5 (4.92)	48.33 (3.54)	45.33 (2.95)	32.7 (6.24)	46.23 (1.70)
Vegetation						
Grasses	1.73 (0.57)	5.02 (2.91)	79.2 (10.5)	1.19 (0.24)	4.43 (2.63)	39.3 (16.3)
Sedges	0.14 (0.07)	0.19 (0.16)	0.28 (0.13)	0.91 (0.53)	0.36 (0.29)	0.03 (0.03)
Ruderal Herbs	-	0.14 (0.12)	0.18 (0.18)	0.01 (0.01)	0.73 (0.55)	0.18 (0.18)
Scrub Herbs	1.69 (0.39)	3.52 (1.74)	0.45 (0.41)	1.40 (0.33)	2.11 (0.65)	0.02 (0.02)
Other Herbs	0.10 (0.06)	0.14 (0.06)	0.25 (0.16)	0.11 (0.07)	0.33 (0.19)	0.08 (0.04)
Shrubs	72.5 (5.36)	29.7 (4.84)	19.4 (10.1)	82.3 (3.37)	47.8 (7.68)	57.5 (16.0)
Subshrubs	13.0 (2.54)	34.9 (13.9)	0.29 (0.08)	7.98 (4.51)	12.1 (6.11)	3.04 (2.34)
Lichens	3.39 (1.93)	10.6 (4.25)	-	2.45 (1.63)	7.29 (1.79)	-
S. arenicola	5.00 (2.75)	15.9 (7.35)	-	3.38 (2.36)	24.9 (9.29)	-
Total Veg. Cover	**23.6 (1.38)**	**29.7 (0.77)**	**45.0 (2.38)**	**21.2 (1.25)**	**20.1 (0.91)**	**45.0 (4.28)**

Table 2. Mean seed bank density (m^{-2}) (± standard error) across the three vegetation types in summer 2008 and winter 2009. A complete species list can be found in the appendix (Table S12).

	SUMMER 2008			WINTER 2009		
	Rosemary	**Degraded**	**Pasture**	**Rosemary**	**Degraded**	**Pasture**
Grasses	25 (5)	32 (9)	41 (13)	23 (13)	25 (4)	128 (88)
Sedges	60 (19)	266 (147)	588 (234)	131 (46)	368 (132)	877 (418)
Ruderal Herbs	96 (28)	266 (118)	1513 (786)	143 (14)	337 (139)	2226 (1243)
Scrub Herbs	708 (162)	255 (34)	7 (4)	886 (265)	452 (70)	2 (2)
Subshrubs	4 (4)	51 (30)	-	5 (3)	105 (89)	-
S. arenicola	37 (17)	319 (141)	-	2 (2)	27 (21)	-
Unidentified	159 (30)	143 (8)	198 (20)	71 (12)	89 (34)	135 (12)
Total	**2141 (320)**	**2345 (357)**	**4694 (2033)**	**2520 (670)**	**2776 (792)**	**6734 (3488)**

Table 3. Results of the Morisita index of seed bank during summer 2008 and winter 2009. Table includes number of plots where the functional group/species occurred (#plots) and the number of plots within each vegetation type that the Morisita index indicated a statistically significant aggregated seed distribution. RS = rosemary scrub, DS = degraded scrub, PA = pasture.

	Summer 2008				Winter 2009			
	# plots	RS	DS	PA	# plots	RS	DS	PA
Functional Groups								
Ruderal herbs	9	2/3	3/3	3/3	9	2/3	2/3	3/3
Scrub herbs	6	3/3	3/3	-	6	3/3	3/3	-
Sedges	9	2/3	2/3	3/3	9	2/3	2/3	3/3
Graminoids								
Bulbostylis ciliatifolia	1	-	0/1	-	1	-	0/1	-
Melinis repens	1	-	-	0/1				
Ruderal herbs								
Conyza canadensis	1	-	-	1/1	-	-	-	-
Eupatorium capillifolium	4	1/1	-	1/3	3	-	-	2/3
Gamochaeta purpurea	7	0/3	0/1	2/3	2	-	-	0/2
Linaria floridana	4	0/1	3/3	1/1	2	-	1/1	1/1
Oldenlandia corymbosa	2	-	-	2/2	1	-	-	1/1
Oldenlandia uniflora	2	-	-	2/2	3	-	-	2/3
Polypremum procumbens	1	-	-	0/1	3	-	-	1/3
Richardia brasiliensis	1	-	-	1/1				
Scoparia dulcis	3	-	-	3/3	3	-	-	3/3
Scrub herbs								
Hypericum cumulicola	2	1/1	1/1	-	2	1/1	1/1	-
Lechea cernua	-	-	-	-	1	-	0/1	-
Paronychia chartacea	6	3/3	2/3	-	5	3/3	1/2	-
Polygonella robusta	-	-	-	-	1	-	1/1	-
Selaginella arenicola	-	-	-	-	2	-	2/2	-
Stipulicida setacea	6	3/3	2/3	-	6	3/3	2/3	-

Table 4. Comparison of vegetation and seed bank spatial structure, species richness, and composition between summer and winter. Table includes mantel r values and associated p-value, species richness in winter and summer, and Sorensen similarity coefficients (Sorensen) of species composition between summer and winter.

| Habitat | Spatial Pattern | | Species richness | | |
	Mantel r	p	Summer	Winter	Sorensen
Vegetation					
Rosemary 4	0.711	0.0001*	36	28	0.84
Rosemary 5	0.697	0.0001*	29	26	0.95
Rosemary 6	0.558	0.0001*	26	26	0.85
Degraded 7	0.534	0.0001*	36	31	0.87
Degraded 8	0.430	0.0001*	29	29	0.83
Degraded 9	0.616	0.0001*	27	22	0.86
Pasture 1	-	-	21	15	0.67
Pasture 2	-	-	10	7	0.82
Pasture 3	-	-	8	5	0.46
Seed Bank					
Rosemary 4	0.064	0.002*	17	17	0.59
Rosemary 5	0.094	0.041*	17	15	0.69
Rosemary 6	0.125	0.009*	17	15	0.56
Degraded 7	-0.004	0.546	17	18	0.74
Degraded 8	0.004	0.385	21	20	0.73
Degraded 9	-0.054	0.878	14	15	0.69
Pasture 1	0.235	0.0001*	27	22	0.9
Pasture 2	0.01	0.24	23	20	0.7
Pasture 3	0.044	0.026*	25	21	0.7

Table 5. Comparison of species composition and spatial structure of vegetation versus the seed bank. Analysis was conducted using summer 2007 vegetation data and winter 2009 seed bank data. The table shows percent shrub cover (%SH), Sorensen coefficients (Sorensen) for species composition, and mantel r values with the data organized by functional group and species.

				Vegetation vs. Seed bank			
				Functional Groups		Species	
Habitat	ID	%SH	Sorensen	Mantel r	p	Mantel r	p
Rosemary	4	14.2	0.226	0.014	0.208	0.023	0.242
Rosemary	5	19.9	0.178	0.107	0.009*	0.080	0.031*
Rosemary	6	17.2	0.140	0.030	0.046*	0.013	0.334
Degraded	7	8.0	0.226	0.018	0.267	0.041	0.189
Degraded	8	6.9	0.408	0.017	0.193	-0.026	0.785
Degraded	9	11.4	0.293	0.021	0.278	-0.040	0.826
Pasture	1	19.3	0.194	0.044	0.146	0.094	0.003*
Pasture	2	2.7	0.059	-0.084	0.999	-0.089	0.992
Pasture	3	5.4	0.063	-0.003	0.518	-0.023	0.651

Table 6. Mantel test results of correlation of the aboveground microhabitats versus the seed bank of various species and functional groups. Analysis was conducted using summer 2007 vegetation data and winter 2009 seed bank data. Veg = occurrence of same species aboveground, BS = bare sand. Complete table can be found in the appendix (Table S14)

Mantel r									
Habitat	**ID**	**Veg**	**p**	**BS**	**p**	**Litter**	**p**	**Shrub**	**p**
Scrub Herbs									
Rosemary	4	0.005	0.175	-0.006	0.774	-0.003	0.534	0.013	0.104
Rosemary	5	0.366	0.0001*	-0.022	0.723	0.264	0.0001*	0.093	0.005*
Rosemary	6	0.121	0.005*	-0.003	0.503	0.271	0.0001*	0.005	0.359
Degraded	7	0.021	0.134	0.009	0.359	-0.023	0.783	0.003	0.469
Degraded	8	0.048	0.086	-0.007	0.551	0.050	0.083	-0.023	0.707
Degraded	9	0.015	0.284	-0.039	0.867	-0.030	0.963	0.015	0.269
Hypericum cumulicola									
Rosemary	5	0.339	0.002*	-0.050	0.871	0.375	0.0001*	0.122	0.003*
Degraded	9	0.147	0.177	-0.073	0.905	-0.033	0.850	0.005	0.412
Linaria floridana									
Rosemary	6	0.022	0.710	-0.022	0.714	0.154	0.020*	0.023	0.239
Degraded	8	0.053	0.249	0.075	0.011*	-0.062	1.000	0.256	0.0001*
Pasture	1	0.426	0.039*	-0.002	0.540	0.009	0.304	0.089	0.017*
Oldenlandia corymbos									
Pasture	1	0.019	0.028*	0.0001	0.380	-0.006	0.727	0.176	0.0001*
Paronychia chartacea									
Rosemary	4	0.141	0.008*	0.013	0.328	0.047	0.062	-0.016	0.853
Rosemary	5	0.145	0.053	-0.054	0.915	0.175	0.003*	0.079	0.022*
Rosemary	6	0.071	0.363	-0.028	0.774	0.357	0.0001*	-0.047	0.921
Degraded	7	-	-	-0.029	0.629	-0.045	0.745	0.090	0.153
Degraded	8	0.066	0.268	-0.022	0.665	0.024	0.291	-0.041	0.806
Degraded	9	0.108	0.266	-0.035	0.688	-0.038	0.877	0.049	0.158
Stipulicida setacea									
Rosemary	4	0.137	0.002*	-0.034	0.923	-0.003	0.496	-0.017	0.936
Rosemary	5	0.143	0.197	-0.024	0.669	0.021	0.318	-0.010	0.577
Rosemary	6	0.265	0.0007*	-0.040	0.944	0.152	0.005*	0.005	0.378
Degraded	7	0.216	0.007*	0.019	0.337	-0.028	0.711	-0.010	0.571
Degraded	8	0.037	0.480	0.009	0.399	-0.015	0.587	-0.042	0.753
Degraded	9	0.044	1.000	-0.025	0.525	-0.030	0.780	0.044	0.230

CHAPTER TWO: SEED BANK CHANGES WITH TIME-SINCE-FIRE IN FLORIDA ROSEMARY SCRUB

Abstract

Question: How does seed density change with time-since-fire? We predicted that seed density would follow a unimodal function, having low density in recent and long-unburned stands and high density at intermediate time-since-fire.

Location: Florida rosemary scrub, Lake Wales Ridge, Highlands County, FL

Methods: We combined data from two seed bank trials conducted in 1992-1993 and 2008-2009. Seed bank soil samples were collected from a chronosequence of time-since-fire: two sites each of three, six, ten, 24 years post-fire and three long-unburned (> 24 years). The seedling emergence method was used to determine species composition of the seed bank.

Results: Across all time-since-fire age classes scrub herbs dominated the seed bank, while long-lived subshrub and shrubs were present in low densities. Seed banks from sites three years post-fire were distinct from the other sites. Seed densities were associated with time-since-fire for shrubs (cubic), subshrubs (quadratic) and ruderal herbs (quadratic), while densities of scrub herbs and graminoids were independent of time-since-fire. At the species level, densities of two scrub herbs, *Paronychia chartacea* and *Lechea cernua*, were associated with time-since-fire, reaching peaks in density at six and ten years post-fire. Overall seed densities of scrub herbs were highest in the first ten years post-fire. This pattern corresponds to the pattern of aboveground species abundance and suggests that scrub herb abundances above- and belowground are closely linked.

Conclusion: A few species and functional groups showed a cubic or quadratic change in seed

density with time-since-fire. The timing of the peak in seed density varied depending on life span and age of reproductive maturity.

Introduction

Disturbances play a central role in shaping life history strategies of species in habitats subject to frequent perturbations (Pickett and White 1985). Life history characteristics such as dispersal mechanism, ability to establish and grow, and time necessary to reach critical life stages determine if a species will persist in a community during and after disturbance (Noble and Slatyer 1980). Species within the same system often evolve a variety of adaptive strategies to cope with frequent disturbance (Christensen 1985).

One of the most ubiquitous terrestrial disturbances worldwide is fire. Fire influences global vegetation pattern and shapes species characteristics in systems subject to frequent fire (Bond and van Wilgen 1996, Bond et al. 2005). In fire-prone communities like African fynbos, Australian heaths, and California chaparral, species rely upon persistent soil seed banks (seeds remain viable for at least one year) to regenerate after fire (Keeley 1991, Auld et al. 2000, Holmes and Newton 2004). Recruitment from the soil seed bank is essential for obligate seeding species of which aboveground individuals are killed by fire. Fire has been found to stimulate mass recruitment events and seedling densities are generally highest in recently burned stands (Meney et al. 1994, Tyler 1995, Carrington and Keeley 1999, Weekley and Menges 2003). High recruitment post-fire can result from direct cues such as smoke, heat, or chemical leaching which break seed dormancy or indirect effects from increases in microhabitat availability and release from competition or allelopathic chemicals (Christensen 1985, Keeley 1991, Pierce and Cowling 1991, Tyler 1996, Keeley and Fotheringham 1998, Izhaki et al. 2000).

Changes visible in aboveground species composition and abundance as time-since-fire increases may also be reflected in the seed bank characteristics of pyrogenic communities. For example, seed bank size may follow a unimodal function: seed densities are low in years immediately following fire when seedling recruitment is high and seed inputs are low (due to mortality of reproductive plants after fire), peak in size at intermediate years since fire, and decline in size in long-unburned stands as aboveground populations senesce and seeds lose viability (Vaughton 1998, Clemente et al. 2007). Understanding the effects of time-since-fire on the seed bank dynamics of obligate seeders is essential for proper management of plant populations since fire intervals that are either too frequent or infrequent can lead to local species extinctions (Zedler et al. 1983). Species characteristics such as life span (e.g. annual, perennial), fire sensitivity, dispersal mechanism, and timing of reproductive maturity strongly influence how species cope with fire (Keeley 1991, Ooi et al. 2006).

Fire is the most important disturbance in the Florida rosemary scrub and likely plays a central role in determining the dynamics of the seed bank for many species, particularly those endemic to this community. Florida rosemary scrub is a xeric upland sclerophyllous shrubland found on relic sand dunes that harbor a high diversity of endemic plant and animal species (Abrahamson et al. 1984, Christman and Judd 1990). Understanding how species regenerate and respond to fire can contribute to better management of populations of endangered and threatened plant species. One key requirement for maintaining healthy populations in fire-prone habitats is implementation of appropriate fire return intervals. The interval for obligate seeders must be long enough to insure that adult plants reach a reproductive life stage to replenish the seed bank; however, it should not be so long that adult life span and/or the viability of the seed bank have been surpassed (Zammit and Zedler 1988).

In this study we evaluate seed bank changes with time-since-fire using data from two trials conducted in 1992-1993 (trial I) and 2008-2009 (trial II). We address the following questions: (1) Is there an association between time-since-fire and seed density? (2) If so, how does this association vary among different functional groups? (3) Which rosemary scrub species form persistent soil seed banks?

Methods

Study Site

Research was conducted at Archbold Biological Station (Archbold) located near the southern end of the Lake Wales Ridge in Highlands County, Florida (Township 38S, Range 30E, Sections 5-8,18,19,29-32). The station experiences average mean temperatures that range from 8.33^{o} C in the winter to 34.05^{o} C in the summer and has an average annual rainfall of 1364 mm (Archbold weather data,1932-2009). The Lake Wales Ridge is characterized by a mixture of wetlands, mesic scrubby flatwoods, and xeric upland communities found on relic sand dunes in central Florida. Rosemary scrub is found at locally high elevations with well drained, low nutrient, Archbold or St. Lucie soils (Menges 1999). This habitat is dominated by Florida rosemary (*Ceratiola ericoides*), an allelopathic shrub, but also includes patches of shrub species such as palmettos (*Serenoa repens*, *Sabal etonia*), and various clonal oaks (*Quercus chapmanii*, *Q. inopina, Q. geminate*) (Hunter and Menges 2002). Shrub patches are separated by bare sand gaps where many herbaceous endemic species grow (Menges et al. 2008). After fire most shrub species resprout from rhizomes or roots (Menges and Kohfeldt 1995). Obligate seeders such as the dominant shrub *C. ericoides* and other herbaceous species recruit from the seed bank or from nearby unburned areas after fire (Quintana-Ascencio and Menges 2000).

Seed Bank Sampling

Field Sampling

During trial I (1992-1993), we sampled eight rosemary scrub sites that consisted of two sites in each of four age classes of time-since-fire: three years, six years, 24 years, and long-unburned (>24 years) (Figure 11). From each site, we collected twenty soil cores in a stratified random fashion along a 6 meter transect through the longest axis of each rosemary scrub site. Soil cores were collected in tins 10 cm in diameter x 6 cm in depth (surface area per site = 0.0785 m^{-2}). We collected six samples over a one and a half year period in January, April, July, and October of 1992, and January and April of 1993. Over this period we collected a total of 120 soil cores per site.

During trial II (2008-2009), we established three 16 x 16 m macroplots in three separate sites: two at ten years post-fire and one long-unburned (>24 years) (Figure 11). Ten 2 x 2 m subplots were randomly placed within each macroplot. Each subplot was subdivided into 40 x 40 cm quadrats and samples were collected in a checkerboard pattern from every other quadrat (yielding thirteen quadrats per subplot) (Figure 3). In August 2008 and January 2009, we collected five 1.92 cm diameter by 3 cm deep soil cores from each quadrat and the cores were aggregated yielding 130 soil samples per macroplot (surface area per plot = 0.1882 m^{-2}). During both sampling periods, we collected soil cores from the quadrats in a regular coring pattern and this pattern was alternated between the two seasons to avoid coring the exact same locations. In spite of the differences in soil depth employed during the two trials (trial I = 6 cm, trial II =3 cm) the volume of soil per sample unit was approximately equivalent (trial I = 235.62 cm^3, trial II=217.15 cm^3). Species composition has been found to be consistent within this range of soil depth (Navarra, *unpublished data*)

Although the two trials were performed at different times we decided to analyze them together to evaluate the effect of time-since-fire. This comparison assumes that differences among periods of collection had a relatively smaller effect than time-since-fire on seed bank variation across sites. Our analysis assesses the consistency of pattern in the seed bank between trials. If association of seed density with time-since-fire is found, we argue that combining these data strengthens the evidence for the association of seed bank with time-since-fire.

Greenhouse Monitoring

We used the seedling emergence method to determine species composition of the seed bank. During trial I, each soil core was thoroughly mixed and half of the volume of soil was placed into four separate germination trays 4.2 x 5.5 x 2.5 cm in size. In trial II, we sieved each soil sample to break up soil structure and large litter and then potted the soil on top of a white sand substrate. We collected the substrate from firelanes in Archbold Biological Station and heated it to 85° C (minimum of 8 hours) to kill any seeds that may have been present in the soil. We randomized placement of the samples within the greenhouses and the seedling flat locations were regularly changed to minimize micro-environmental differences.

 For both trials, we maintained samples in unheated greenhouses and watered them regularly to keep the soil moist. Sterile soil controls were placed among the samples to detect contamination from outside seed sources and, for trial II, to also ensure all seeds were killed during baking. For trial I, we considered all seedlings in the analysis since a relatively small portion of the emerging seedlings came from the controls (~1% of the total number of seedlings emerged from the controls). For the second trial, we omitted species/seedlings from the analysis that appeared to result from contamination based on the pattern of occurrence in the samples and controls (~ 5% of the total number of seedling emerging from the controls). For both trials, we

monitored the soil samples for germination at monthly intervals. Seedlings were removed once they had been identified to the species level; however, some seedlings died before identification was possible. Nomenclature follows the Atlas of Florida Vascular Plants online database (http://www.florida.plantatlas.usf.edu).

For trial I, we carried out seedling monitoring from the time of soil collection until July 1994 (time max = 18 months, time min = 30 months). For the second trial, we monitored the soil samples for 8-12 months. Although the soil samples were monitored for different lengths of time, this variation was unlikely to bias the results of the study since the majority of seedlings emerged during the first two months after collection. It is not necessary for every seed in the soil to germinate to reveal strong patterns in the data. For all sampling periods, germination rates reached an asymptote before germination monitoring was discontinued (Figure 12).

Assessing long-term persistence

To determine which species form persistent seed banks we used trial I data from all eight sites and six months of soil sample collection. Those species that continued to germinate into the second year of greenhouse monitoring and were present in the seed bank during all six months of soil collection were considered to form persistent seed banks. This dual approach to assessing the persistent seed bank ensured that these species' seeds remained viable for at least one year and that their seeds remained in the seed bank year round (when exposed to other pressures that may result in depletion such as depredation) (Thompson and Grime 1979, Ortega et al. 1997, Arroyo et al. 1999). This approach to assessing seed persistence is conservative and those species that do not meet both criteria may still form persistent seed banks.

Data Analysis

Organizing the data by species and functional groups, we used regression to assess the association of time-since-fire with soil seed bank density (number of seeds/total surface area per m^{-2}) and species richness. We only analyzed seed bank data collected from summer and winter seasons to combine comparable datasets from the two trials (trial I = January and July 1992; trial II = August 2008 and January 2009). We divided the species into functional groups based upon growth habit and, for herbaceous species, habitat preference. We identified the following functional groups: (1) scrub herbaceous species; (2) scrub subshrubs; (3) scrub shrubs; (4) graminoids (sedges, rushes, and grasses), and (5) ruderal herbs (species typical of disturbed habitats, generally not found growing aboveground in Florida scrub). We only analyzed species and functional groups that were present across 50% of the scrub patches to ensure occurrence was high enough along the time-since-fire chronosequence to reveal pattern. Seed density was averaged across seasons within sites to avoid pseudoreplication.

We used a model selection approach for small samples (Akaike's information criterion; AIC_c) to compare linear, quadratic and cubic models (see Appendix S6 for R scripts) (Crawley 2007). Akaike weights were calculated for each model to determine the likelihood of each model given the data (Burnham and Anderson 2002). We assumed negative binomial error distribution for seed counts (Venables and Ripley 2002).

We evaluated whether time-since-fire had an association with seed composition and density at the community level using Non-metric Multidimensional Scaling (NMS) ordination based on Sorensen distances (Kruskal 1964, Mather 1976). Species that did not occur across 20% of the sites and seasons were omitted from the analysis to remove rare species and reduce noise in the data set (McCune and Grace 2002). The data were analyzed using PC-ORD 5.0. We

started with a random configuration and 200 runs with real data. Dimensionality of the data was assessed using autopilot and the stability of the solution was evaluated using NMS scree plot. We evaluated whether a similar final stress could be obtained by chance with Monte Carlo tests (McCune and Grace 2002)

We compared species richness between summer and winter seasons using non-parametric Kruskal-Wallis one way analysis of variance (Sokal and Rohlf 1995). Calculations were done in R 2.9.1 using the "kruskal.test" function.

<center>Results</center>

<center>Species composition</center>

A total of 3,963 seedlings (trial I = 2,647; trial II = 1,316) belonging to 45 species were found in the seed banks of the two trials (summer and winter seasons only) (Table 7). Approximately 15% of the emerging seedlings could not be identified. In both trials, the seed bank was dominated by annual and short-lived perennial herbaceous species (Figure 13). The two most abundant species in the seed bank were *Paronychia chartacea* and *Stipulicida setacea*, which comprised approximately 43% (trial I = 34%, trial II = 62%) of the emerging seedlings (Table 7). The total seed count for long-lived species was significantly lower than for short-lived herbs. A spike moss, *Selaginella arenicola*, comprised approximately 50% of the emergence from the samples collected in trial I (trial II = 1%), however this species was not considered in the regression or NMS ordination analyses since it is a sporophyte (data on density and persistence are presented in Table7 and10). This species is thought to reproduce vegetatively from broken fragments (Menges, *personal communication*).

Species Richness

Species richness ranged between seven and 37 species and had a mean of 14 across all sites and seasons (Table 8). We did not find evidence of association between species richness and time-since-fire; however, mean species richness was slightly higher in three year and long-unburned stands. This slight increase was for the most part due to a greater number of weedy species being present in these two time-since-fire age classes. Species richness was higher in winter than in the summer (Kruskal-Wallis, p= 0.026).

Community Level Association with Time-since-fire

NMS ordination of seed density for species occurring across $\geq 20\%$ of the seasons and sites indicated that time-since-fire does explain some differences among the sites. While both axes were significant (final stress = 11.55, # iteration = 43; axis 1 - p = 0.032, R^2 = 0.562; axis 2 – p = 0.008, R^2 = 0.317), a NMS scree plot showed slight overlap between the stress for real and randomized data indicating a weaker pattern for axis 1. The NMS ordination plot showed clear separation of sites three years time-since-fire, particularly for the winter samples. The other time-since-fire classes exhibited considerable overlap (Figure 14).

Species and Functional Group Association with Time-since-fire

Thirteen species and all five functional groups (graminoids, ruderal herbs, scrub herbs, shrubs, and subshrubs) had high enough occurrences to be considered in the analysis. We identified different associations between time-since-fire and seed densities for several species and functional groups (Table 9). A quadratic model was the best model for ruderal herbs and shubshrubs; their seed densities were highest three year post-fire and declined in the later time-since-fire age classes (Figure 15a and Figure 15c). A cubic model of time-since-fire was found to be the best for shrubs, *C. ericoides*, *Lechea cernua*, *P. chartacea*, and *Phyllanthus tenellus*.

Shrubs, which were almost exclusively comprised of seeds from *C. ericoides*, showed highest seed densities in the recent and long-unburned time-since-fire age classes (Figure 16a). Two scrub endemics, *L. cernua* and *P. chartacea*, showed lowest density in recently burned and long-unburned sites and high densities at intermediate time-since-fire (Figure 16b and Figure 16c). The overall model for scrub herbs was not significant; however, highest seed densities were generally observed at three to ten years post-fire (Figure 15b). *P. tenellus* showed highest density in long-unburned sites (Figure 16d).

<div align="center">Seed Persistence</div>

Six scrub herbs (*Eryngium cuneifolium*, *Hypericum cumulicola*, *L. cernua*, *Lechea spp.*, *P. chartacea*, and *S. setacea*), one subshrub (*Lechea deckertii*), one shrub (*C. ericoides*), two graminoids (*Cyperus spp.*, Poaceae), and five ruderal herbs (*Euthamia caroliniana*, *Eupatorium spp.*, *Gamochaeta purpurea*, *Linaria floridana*, and *Oxalis corniculata*) formed persistent seed banks (Table 10). *S. arenicola*, a club moss species, was also found across all seasons of sampling and continued to emerge after one year.

<div align="center">Discussion</div>

Our results indicate that disturbances influence seed bank dynamics. In Florida rosemary scrub, time-since-fire affects seed density for some species and functional groups. Previous studies evaluating changes in seed bank characteristics after natural and anthropogenic disturbances have had mixed results. Some studies have found significant relationships between species richness and/or seed density and time since disturbance (Young et al. 1987, Roberts and Vankat 1991, Vaughton 1998, Bekker et al. 1999, Clemente et al. 2007), while others have found no association (Granstrom 1988, Zammit and Zedler 1994, Milberg 1995, Dalling and Denslow 1998, Ne'eman and Izhaki 1999, Figueroa et al. 2004, Wills and Read 2007). Association of the

seed bank with time since disturbance was not well predicted by disturbance or habitat type. Variation due to other factors, both abiotic (e.g. substrate type or elevation) and biotic (e.g. dispersal of exogenous seeds in landscapes with diverse land-use types), can reduce or override any disturbance effect among sites of similar time since disturbance (Zammit and Zedler 1994, Quintana-Ascencio et al. 1996).

Changes in the seed bank with time since disturbance in fire-prone communities may differ when compared to anthropogenically disturbed habitats undergoing secondary succession. In fire-prone communities with a significant association between seed density and time-since-fire, there is a gradual increase in seed bank size in recently burned stands followed by a decline in long-unburned sites (Vaughton 1998, Clemente et al. 2007). Life history characteristics strongly influence how a species will recover after and persist between fires. In shrubland communities, frequent fire has promoted the evolution of a variety of adaptive strategies and has resulted in species strongly reliant upon disturbance for recruitment (Christensen 1985).

Seed Density

In Florida rosemary scrub we did find a short-term change in seed density in response to fire at the community level. Recently burned sites showed distinctive pattern of seed density, while sites ≥ six years post-fire exhibited considerable overlap. This pattern is at least partially explained by large changes in species abundance aboveground in recently burned sites followed by a slow decline as time-since-fire increases. For example, at sites two years post-fire, *E. cuneifolium* showed the highest survival and seed production while sites at intermediate to late years post-fire had lower seed production and more variation (Menges and Quintana-Ascencio 2004). These population increases are probably associated with decreased litter, lichen and shrub cover which reduce competitive interactions in the years immediately following fire (Hawkes

and Menges 1996, Quintana-Ascencio and Menges 2000). With time-since-fire, population density declines and community change slows. Lack of strong pattern with longer time-since-fire intervals could result from more variable seed production and species composition in intermediate and long-unburned communities.

We only found an association of seed density with time-since-fire among a few species and functional groups. Among the functional groups, seed densities of shrubs, subshrubs and ruderal herbs were found to have an association with time-since-fire, while scrub herbs and graminoids did not. *C. ericoides* is the only obligate seeding shrub found in rosemary scrub habitat and was essentially the only shrub found in the seed bank. Seed densities of *C. ericoides* were highest in the later years post-fire. Low seed density or absence of *C. ericoides* at six and ten years post-fire is not unexpected since this species reaches reproductive maturity at ten years (Johnson 1982). Curiously, *C. ericoides* was not found in the seed bank of the long-unburned site of trial II. This may have resulted from difference in sampling design. Sampling methods with smaller core size have been found to be effective for describing spatial distribution of the seed bank but are less effective at detecting low density and large-seeded species with clumped distributions (Bigwood and Inouye 1988, Kemény et al. 2003).

Subshrubs such as *Calamintha ashei* (obligate seeder)*, Lechea deckertii* (seeder and resprouter)*, Palafoxia feayi* (seeder and respouter), and *Polygonella robusta* (obligate seeder) were also rare in the seed bank but in contrast to *C. ericoides* were most abundant in recently burned sites. Absence of other subshrub species present in this system (e.g. *Vaccinium myrsinites*) is likely due to a stronger reliance on resprouting to recover post-fire. Even among obligate seeding subshrubs, such as *C. ashei* and *P. robusta*, seed densities were low. Low seed

density may be explained by relative rarity of subshrubs in rosemary scrub when compared to other functional groups (Menges and Kohfeldt 1995).

Ruderal herbs such as *P. tenellus* had highest seed density in recent and long-unburned sites. The observed pattern for ruderal herbs remains unexplained, as these species are not found aboveground in rosemary scrub. This pattern may be a result of location rather than response to time-since-fire. Archbold Biological Station is surrounded by a variety of human modified habitats (primarily orange groves and pastures). Since sites belonging to the same time-since-fire age class were generally in close proximity to each other, these sites may have also experienced similar rates of dispersal of weedy species from surrounding areas. Ruderal herb diversity was much higher in trial I than trial II and we have reason to believe that some of these species came completely or partially from outside seed sources. Species meeting any of the following criteria were suspected not to have come from the seed bank: occurrence in very low frequency, presence during only a few seasons of sampling, greater seedling emergence in the later months of germination monitoring, or a high proportion of seedling emergence from the controls (e.g. *Emilia fosbergii*, *Euthamia caroliniana*, *Oldenlandia spp.*, *Oxalis corniculata*, *Pilea microphylla*, *Physalis spp.*, *Richardia scabra*).

Unexpectedly, seed density of the scrub herb functional group did not have significant association with time-since-fire; however, highest seed densities were seen in the first ten years post-fire. At the species level *P. chartacea* and *L. cernua* did have a significant association with time-since-fire, both reaching a peak in density at six and ten years post-fire. This pattern corresponds to the changes in abundance for these two species aboveground (Menges and Kohfeldt 1995) and suggests seed densities and vegetation abundances are closely linked. The majority of herbaceous species in rosemary scrub are "gap specialists" and are most abundant,

have the greatest survival, and highest seed production in the years immediately following fire (Hawkes and Menges 1996, Menges and Kimmich 1996, Menges 1999). As time-since-fire increases, gaps close as shrubs, litter and lichen cover increases and herbaceous species are outcompeted (Menges and Hawkes 1998). Gap sizes are smallest in long-unburned areas and largest between six and ten years post-fire; herb cover increases with gap area (Menges et al. 2008). Menges et al. (2008) found sites > ten years post-fire have a wide amount of variation in gap area. Site-to-site variation in microhabitat cover may help to explain variation in seed density among different time-since-fire age classes (Navarra, Chapter 1). Environmental variables such as elevation may explain why some sites retain greater amounts of open space than others (Hawkes and Menges 1996) and thus sustain higher cover of herbs leading to larger yearly seed inputs into the seed bank.

Manipulative experiments conducted in rosemary scrub and California chaparral both showed that recruitment was higher in recently burned versus unburned stands even when microhabitat availability was equivalent between sites (Tyler 1995, Quintana-Ascencio and Menges 2000). These results indicate that microhabitat availability is not the only factor that leads to a decline of species above and belowground in long-unburned sites. An alternative explanation for reduced recruitment in long-unburned stands is higher amounts of allelopathic chemicals leaching from roots and leaves of *C. ericoides* (Hunter and Menges 2002, Hewitt and Menges 2008). Abundance of allelochemicals likely increases in intermediate and long-unburned stands with high cover of *C. ericoides*.

<div align="center">Seed Persistence</div>

Short-lived herbaceous species were found to be the dominant group forming persistent soil seed banks. These results are not surprising since annuals and short-lived perennials have

been widely reported to form persistent seed banks (Thompson et al. 1993). Many of the species, particularly endemic herbs, have small seed size which is a characteristic known to promote formation of persistent seed banks (Thompson et al. 1993, Funes et al. 1999, Moles et al. 2000, Thompson et al. 2001, Stromberg et al. 2008). Of the seven scrub herbs found in the seed bank, five were present year round and germinated into the second year. These results correspond well with what is already known about the demography of some scrub endemic herbs. In *E. cuneifolium* seedling recruitment after fire is much higher than at other times. The plants reach maturity very quickly post-fire and probably replenish the seed bank rapidly. The population declines with time-since-fire and the seed bank likely decays fairly quickly (Menges and Kimmich 1996, Menges and Quintana-Ascencio 2004).

While formation of a persistent seed bank is a common mechanism species used to cope with frequent disturbance, not all obligate seeding herbs were found in the seed bank. For example, *Polygonella basiramia* is known to form a transient seed bank and relies on dispersal from unburned areas to re-colonize post-fire (Menges 1999, Quintana-Ascencio and Menges 2000). Rarity of *Balduina angustifolia* and other common scrub herbs in the seed bank may suggest these species also rely on dispersal to rebound after fire.

Knowledge of obligate seeding species that do not form persistent seed banks and changes in seed availability of species forming persistent seed banks as time-since-fire increases has important implications for implementing controlled fire regimes that accommodate a wide variety of species. Due to differences in species' life histories such as juvenile period, fire sensitivity and microhabitat requirements, not all species will be favored by the same fire regime (Quintana-Ascencio and Menges 2000, Ooi et al. 2006). Implementation of low intensity patchy fires has been suggested as a solution that allows for coexistence of species with varying fire

requirements because smaller portions of the aboveground populations will be killed (Ooi et al. 2006). This fire regime is suited to obligate seeding species that do not form persistent seed banks and rely on dispersal for post-fire recruitment, as well as for species with long juvenile periods before reaching reproductive maturity and replenishing the seed bank (e.g. *C. ericoides*).

Overall, long-lived obligate seeding species were rare in the rosemary scrub seed bank. While all of the subshrub species found in the seed bank germinated into the second year, only one was found in the seed bank year-round. Since these species are present in extremely low densities, their detection was likely difficult in seasons when the species were not seeding. Absence of long-lived species in the seed bank is not uncommon because adult-longevity has been found to be negatively correlated with seed persistence (Rees et al. 1996, Clemente et al. 2007). The majority of long-lived species in Florida scrub habitats resprout after fire and are less dependent on sexual reproduction (Menges and Kohfeldt 1995). These results contrast with other fire-prone communities such as the California chaparral and Australian heaths which report higher species richness and seed densities of resprouting and obligate seeding shrubs (Zammit and Zedler 1994, Wills and Read 2007); however, a study conducted in the fire-prone Mediterranean Aleppo pine forest also reported absence of long-lived species in the seed bank (Ne'eman and Izhaki 1999).

Seed densities of long- and short-lived obligate seeders may have been underestimated in this study due to seed dormancy. Physical seed dormancy has been studied in other fire-prone communities and fire cues such as heat and smoke have been reported to increase germination (Zammit and Zedler 1988, Zammit and Zedler 1994, Keeley and Fotheringham 1998, Wills and Read 2007). While fire cues that directly stimulate germination have not been extensively studied in scrub species, smoke and heat did not affect germination rates of many rosemary scrub

species (Quintana-Ascencio and Menges 2000, Lindon and Menges 2008). These findings may suggest that high recruitment in scrub species post-fire results from indirect effects such as increased microhabitat availability, release from allelopathic chemicals, or nutrient release from burnt plant biomass. Indirect effects of fire such as mechanical shrub or lichen removal and opening of gap space are known to promote germination (Pierce and Cowling 1991, Hawkes and Menges 2003, Ooi et al. 2007).

Conclusion

The results of this study support previous findings that obligate seeding species indirectly respond to time-since-fire. Greatest seed densities were observed in the first ten years post-fire; however, significant site-to-site variation did occur even in recently burned stands. Even though sample size for this study was small (N=11 sites), patterns were detected for some species and for several functional groups. Many of the obligate seeding species in Florida rosemary scrub rely on persistent soil seed banks to recover after fire. Considerable variation in seed bank size in relationship to time-since-fire are likely linked to differences in life history characteristics such as plant life span, dispersal mechanism, seed size, germinability, and juvenile period (Pierce and Cowling 1991). The majority of studies evaluating seed bank dynamics in fire-prone communities have reported dominance of obligate seeding shrubs. In contrast, herbaceous species appear to dominate the seed bank in rosemary scrub. While these findings have broadened our understanding of how rosemary scrub changes with time-since-fire, further research is necessary to fully understand the role of the seed bank in this unique pyrogenic community. Future research should focus upon determining whether indirect or direct fire cues promote recruitment from the seed bank in recently burned sites. This knowledge will help to

determine whether seed densities in rosemary scrub are being underestimated due to seed dormancy.
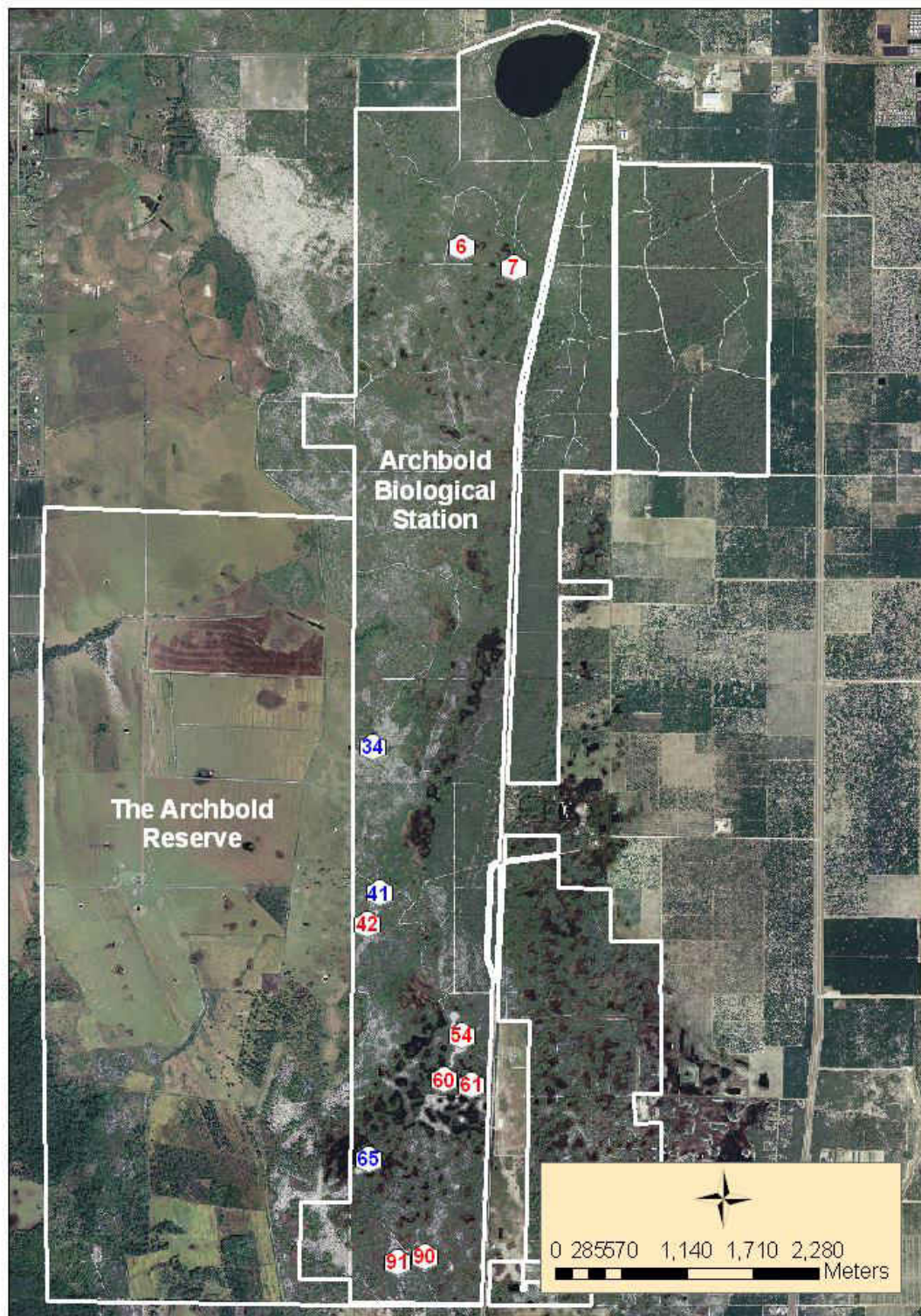
Figure 11. Map of sampling locations. Red numbers = Trial I sampling locations, blue numbers = Trial II sampling locations. Sites six and seven = three years time-since-fire, 90 and 91 = six years time-since-fire, 34 and 65 = ten years time-since-fire, 54 and 60 = 24 years time-since-fire, and 41, 42 and 61= long-unburned.
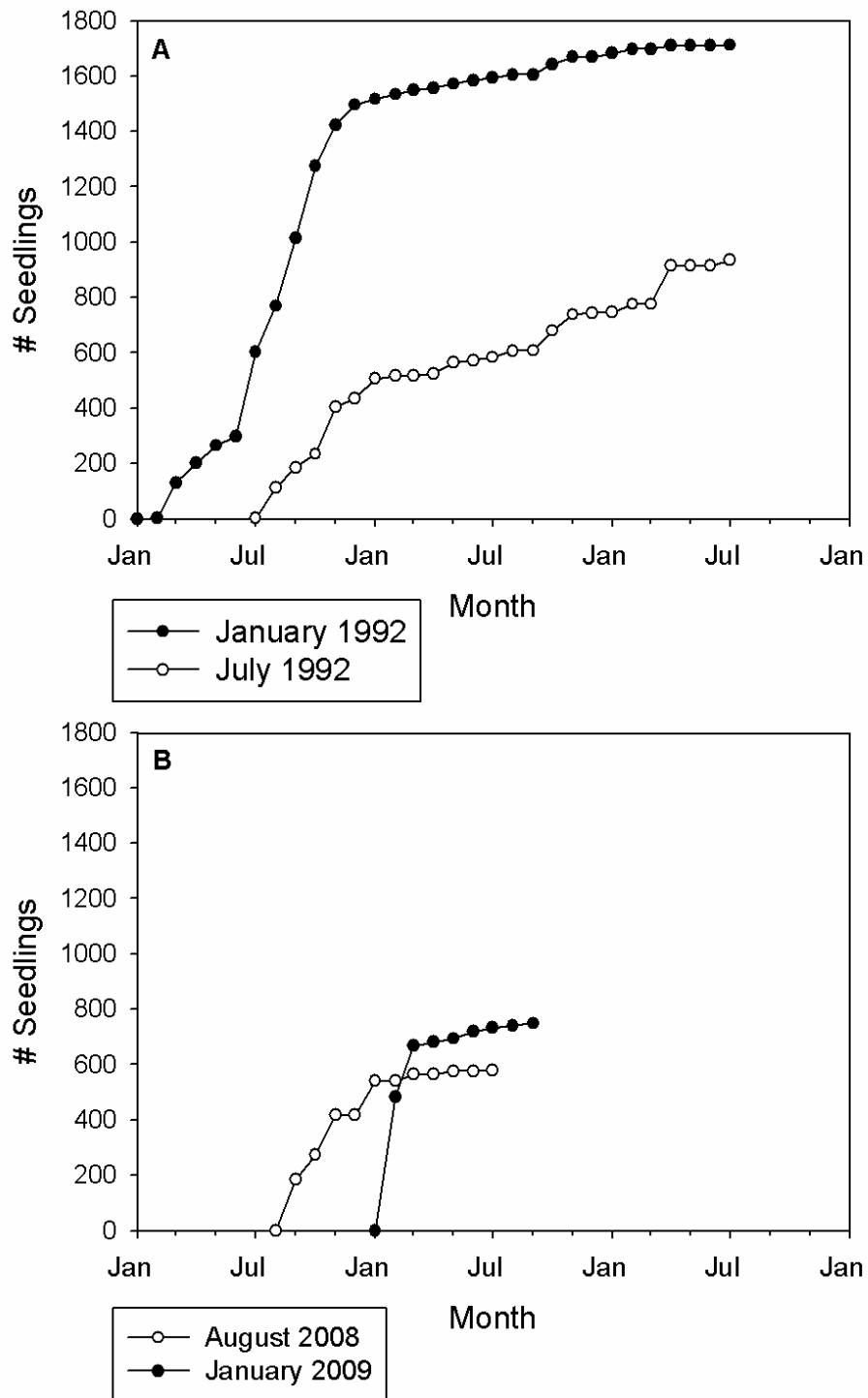
Figure 12. (A) Trial I cumulative seed emergence across the months of monitoring for samples collected in January 1992 and July 1992. (B) Trial II cumulative seed emergence across the months of monitoring for August 2008 and January 2009.
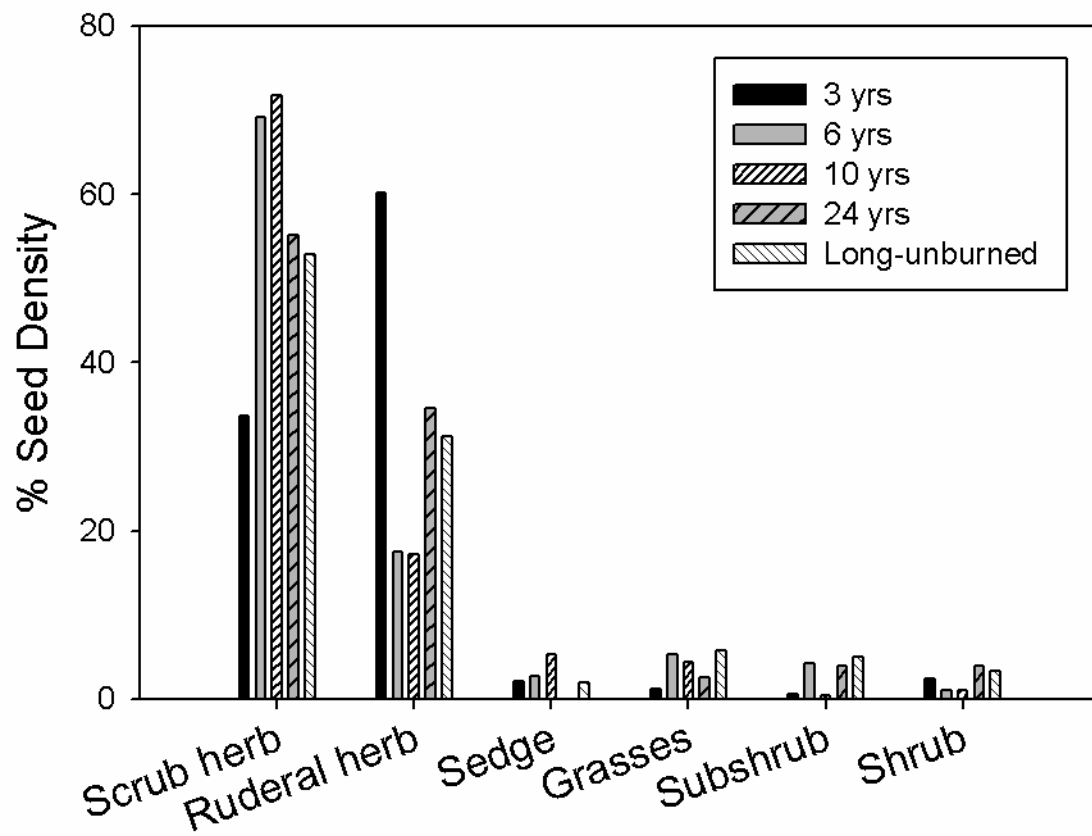
Figure 13. Percent seed density of each functional group at each time-since-fire age class.
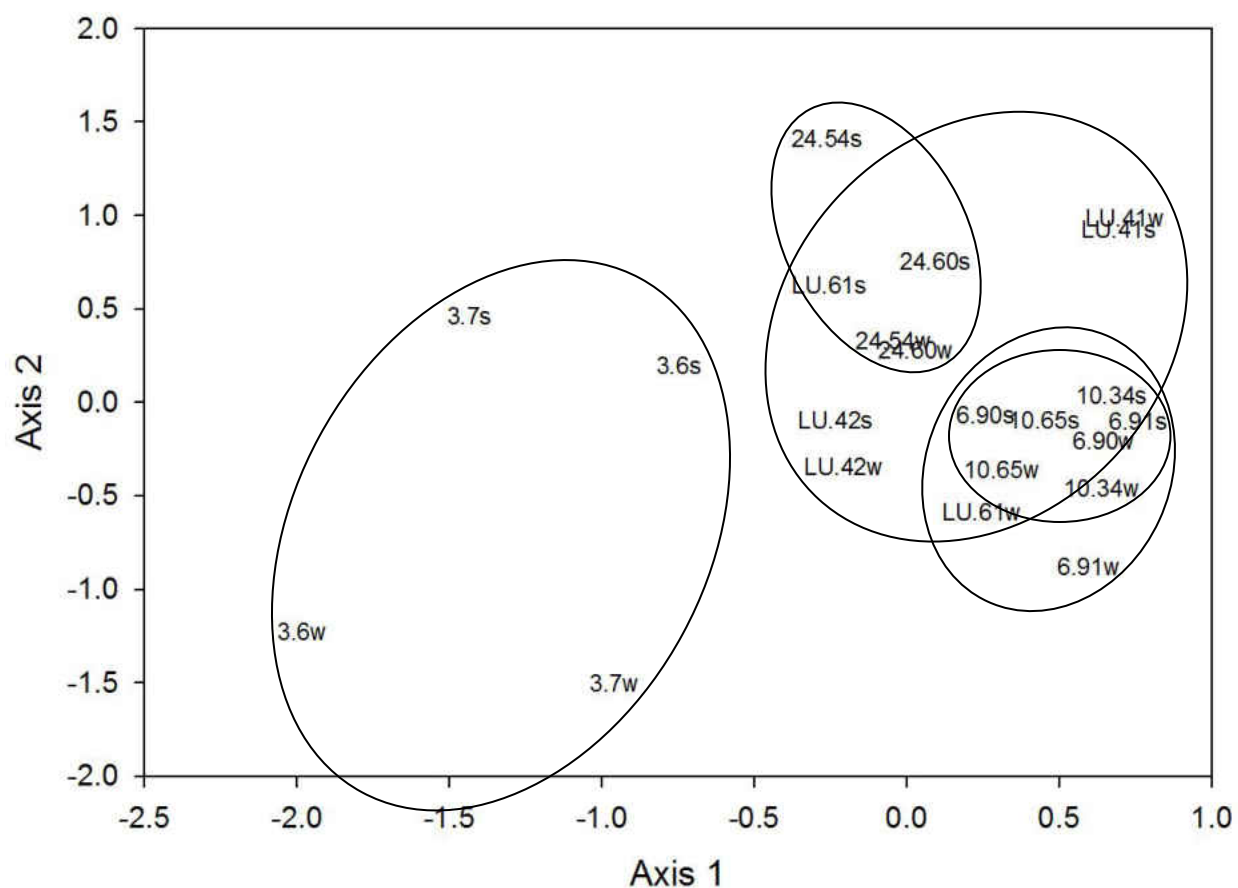
Figure 14. NMS ordination of species seed density. Abbreviation before period: three = three years time-since-fire, six = six years time-since-fire, ten = ten years time-since-fire, 24 = 24 years time-since-fire, LU = long-unburned; all numbers after the period indicate site identification number; letters indicate season of sampling, s = summer, w = winter.

A   Ruderal Herbs

B   Scrub Herbs

N.S.

C   Subshrubs
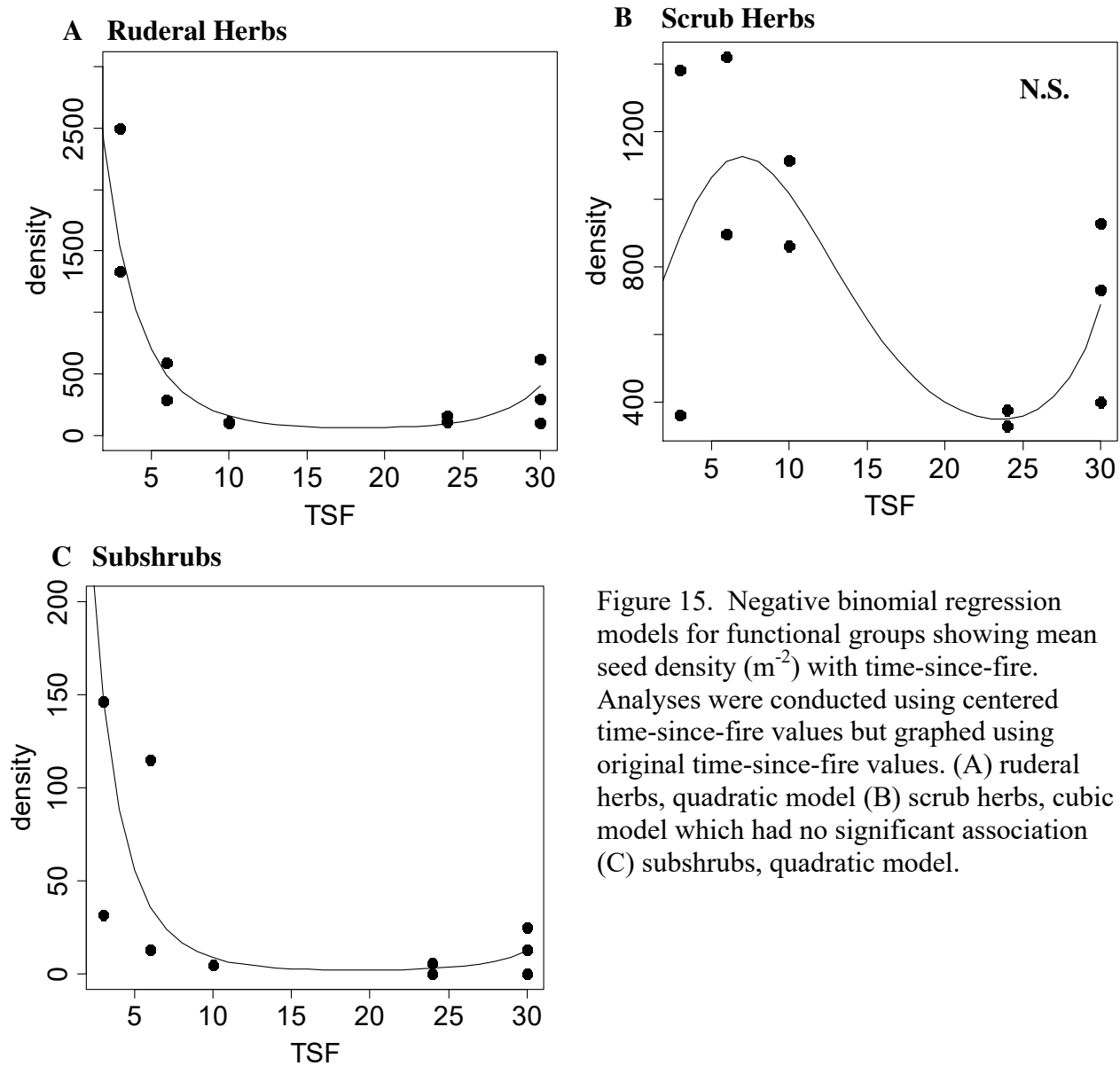
Figure 15. Negative binomial regression models for functional groups showing mean seed density (m^{-2}) with time-since-fire. Analyses were conducted using centered time-since-fire values but graphed using original time-since-fire values. (A) ruderal herbs, quadratic model (B) scrub herbs, cubic model which had no significant association (C) subshrubs, quadratic model.
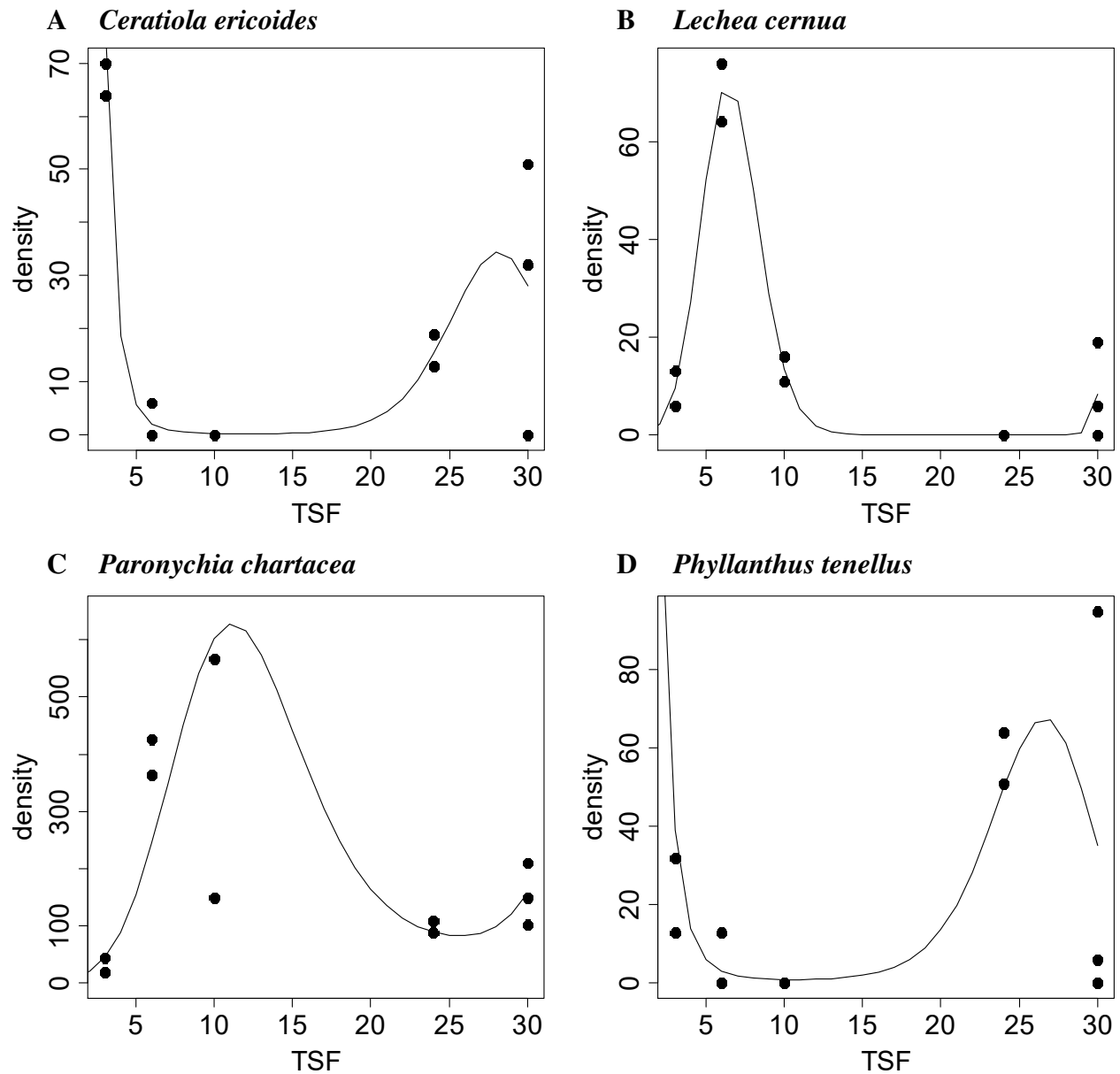
Figure 16. Cubic negative binomial regression models for species showing significant association between mean seed density (m^{-2}) and time-since-fire. Analyses were conducted using centered time-since-fire values but graphed using original time-since-fire values (A) *C. ericoides* (B) *L. cernua* (C) *P. chartacea* (D) *P. tenellus*.

Table 7. Average seed density (m^{-2}) rounded to the nearest integer (± standard error) for species in different time-since-fire age classes. Three, six, 24 years time-since-fire, and two long-unburned sites contain data from trial I. Both ten year sites and one long-unburned (LU) site contain data from trial II. LU (I, II) shows separate averages of seed density for trials I and II. Overall total excludes *S. arenicola*.

Species	Time-Since-Fire					
	3 years	6 years	10 years	24 years	LU	LU (I, II)
Scrub Herbs						
Balduina angustifolia	3 (3)	-	-	-	-	-
Eryngium cuneifolium	38 (38)	3 (3)	-	16 (16)	2 (2)	(3, 0)
Helianthemum nashii	38 (38)	-	-	-	-	-
Hypericum cumulicola	3 (3)	57 (29)	3 (2)	13 (13)	86 (29)	(57, 143)
Lechea cernua	10 (5)	70 (41)	13 (3)	-	8 (4)	(3, 19)
Lechea spp.	13 (9)	60 (56)	-		2 (2)	(3, 0)
Paronychia chartacea	32 (11)	395 (71)	357 (134)	99 (26)	154 (38)	(156, 149)
Polanisia tenuifolia	-	-	3 (3)	-	1 (1)	(0, 3)
Polygonella basiramia	-	-	3 (2)	-	-	-
Stipulicida setacea	735 (639)	573 (135)	610 (69)	226 (56)	435 (170)	(608, 88)
All scrub herbs	**872 (611)**	**1159 (166)**	**988 (115)**	**353 (65)**	**688 (161)**	**(831, 401)**
Subshrubs						
Calamintha ashei	-	-	-	-	2 (2)	(3, 0)
Lechea deckertii	10 (3)	60 (29)	-	-	6 (6)	(10, 0)
Palafoxia feayi	41 (20)	-	5 (2)	3 (3)	4 (3)	(6, 0)
Polygonella robusta	38 (38)	3 (3)	-	-	-	-
All subshrubs	**89 (38)**	**64 (32)**	**5 (2)**	**3 (3)**	**13 (6)**	**(1 9, 0)**
Shrubs						
Ceratiola ericoides	67 (17)	3 (3)	-	16 (6)	28 (12)	(41, 0)
Lyonia sp.	-	-	-	-	2 (2)	(3, 0)
All shrubs	**67 (17)**	**3 (3)**	-	**16 (6)**	**30 (13)**	**(45, 0)**
Spike Moss						
Selaginella arenicola (scrub spp.)	621 (201)	1458 (154)	13 (10)	2136 (1067)	826 (462)	(1222, 32)
Graminoids						
Bulbostylis warei	3 (3)	3 (3)	-	-	-	-
Cyperus spp. (total)	22 (10)	51 (25)	100 (38)	29 (17)	51 (18)	(35, 82)
Cyperus polystachyos						
Cyperus retrorsus						
Cyperus surinamensis						
Dichanthelium spp.	3 (3)	-	-	-	-	-
Juncus spp.	-	-	8 (3)	-	2 (2)	(0, 5)

Graminoids	3 years	6 years	10 years	24 years	LU	LU (I, II)
Panicum repens	6 (6)	-	-	3 (3)	-	-
Paspalum notatum	3 (3)	-	-	-	-	-
Paspalum setaceum	10 (6)	-	-	-	-	-
Poaceae	45 (24)	16 (8)	7 (3)	48 (6)	45 (26)	(67, 3)
All graminoids	**92 (48)**	**70 (32)**	**114 (44)**	**80 (18)**	**98 (16)**	**(102, 90)**
Ruderal Herbs						
Conyza canadensis	10 (6)	48 (36)	-	-	4 (4)	(6, 0)
Emilia fosbergii	6 (4)	3 (3)	-	13 (13)	-	-
Eupatorium spp.	29 (11)	13 (5)	17 (13)	19 (8)	29 (10)	(35, 16)
Euthamia caroliniana	10 (6)	-	-	6 (6)	2 (2)	(3, 0)
Gamochaeta purpurea	1623 (862)	-	33 (5)	-	104 (55)	(134, 45)
Houstonia procumbens	3 (3)	-	-	-	1 (1)	(0, 3)
Linaria floridana	54 (36)	293 (196)	43 (15)	13 (7)	92 (44)	(137, 3)
Oldenlandia corymbosa	3 (3)	-	1 (1)	3 (3)	2 (2)	(0, 5)
Oldenlandia spp.	6 (4)	57 (27)	-	-	2 (2)	(3, 0)
Oldenlandia uniflora	10 (10)	-	3 (2)	3 (3)	2 (2)	(3, 0)
Oxalis corniculata	67 (29)	-	-	-	17 (11)	(25, 0)
Phyllanthus tenellus	38 (38)	-	-	-	-	-
Physalis spp.	22 (11)	6 (6)	-	57 (22)	34 (31)	(51, 0)
Pilea microphylla	10 (6)	6 (4)	-	-	2 (2)	(3, 0)
Polypremum procumbens	-	-	5 (2)	-	6 (4)	(0, 19)
Richardia scabra	3 (3)	-	-	-	4 (4)	(6, 0)
Ruellia blechum	6 (4)	-	-	16 (10)	8 (3)	(13, 0)
Scoparia dulcis	-	-	4 (4)	-	4 (2)	(0, 11)
All ruderal herbs	**1900 (822)**	**427 (244)**	**106 (29)**	**131 (50)**	**314 (100)**	**(402, 101)**
Unknown						
Dicot - long hair, round cotyledons	140 (56)	73 (31)	-	45 (25)	38 (15)	(57, 0)
Solanaceae Family	10 (10)	-	-	-	2 (2)	(3, 0)
unidentified	162 (74)	535 (194)	145 (31)	350 (47)	248 (69)	(318, 106)
All unknowns	**312 (68)**	**608 (224)**	**145 (31)**	**395 (45)**	**288 (78)**	**(379, 106)**
Overall Total	**3333 (1101)**	**2330 (419)**	**1359 (172)**	**977 (116)**	**1430 (254)**	**(1795, 699)**

TSF = time-since-fire, LU = Long-unburned

Table 8. Mean species richness of replicates in each time-since-fire age class (± standard error) in summer and winter at three, six, ten, 24 and long-unburned (LU) time-since-fire.

	Time-Since-Fire				
Season	**3 yrs**	**6 yrs**	**10 yrs**	**24 yrs**	**LU**
Winter	16 (0.0)	15 (0.0)	14 (0.5)	13 (1.0)	17 (1.5)
Summer	25 (10.5)	12 (0.0)	11 (1.0)	9 (2.0)	15 (1.2)

Table 9. Results of negative binomial regression for seed density in response to time-since-fire. Table includes functional groups or species, best model, degrees of freedom, residual deviance (Res.Dev.), highest p-value for each parameter included in the model and Akaike Weights calculated from AIC_c (w_i).

Functional Groups	Best Model	DF	Res.Dev.	p	w_i
Graminoids	No association	-	-	-	-
Ruderal herbs	$TSF + TSF^2$	8	11.41	$\leq 7.0e\text{-}6$	0.687
Scrub herbs	No association	-	-	-	-
Shrubs	$TSF + TSF^2 + TSF^3$	7	12.28	≤ 0.0017	0.796
Subshrubs	$TSF + TSF^2$	8	13.24	<0.0046	0.440
Species					
Ceratiola ericoides	$TSF + TSF^2 + TSF^3$	7	12.37	≤ 0.0014	0.812
Cyperus spp.	No association	-	-	-	-
Eupatorium spp.	No association	-	-	-	-
Gamochaeta purpurea	No association	-	-	-	-
Hypericum cumulicola	No association	-	-	-	-
Lechea cernua	$TSF + TSF^2 + TSF^3$	7	13.10	≤ 0.0016	0.921
Linaria floridana	No association	-	-	-	-
Palafoxia feayi	No association	-	-	-	-
Paronychia chartacea	$TSF + TSF^2 + TSF^3$	7	11.31	≤ 0.0002	0.535
Phyllanthus tenellus	$TSF + TSF^2 + TSF^3$	7	12.04	≤ 0.0383	1.000
Poaceae	No association	-	-	-	-
Ruellia blechum	No association	-	-	-	-
Stipulicida setacea	No association	-	-	-	-

Table 10. Counts of seedling emergence during the first, second and third year of monitoring. Data is from all six months that samples were collected in trial I. Species in bold formed persistent seed banks. For species that occurred in controls (indicated with *) we present the percentage of seedlings emerging from the controls in relationship to the total number of seedlings found for that species. Seeds may have come from the substrate or seed rain.

	Origin	Span	# Seas.	Year 1	Year 2	Year 3
Scrub Herbs						
Balduina angustifolia	N	A/B/P	5/6	4	7	0
***Eryngium cuneifolium* (2.0%)**	**E, EN**	**B**	**6/6**	**21**	**27**	**0**
Helianthemum nashii	N	P	5/6	2	21	0
Hypericum cumulicola	**E, EN**	**B/P**	**6/6**	**56**	**39**	**2**
Lechea cernua	**E, EN**	**P**	**6/6**	**85**	**14**	**0**
Lechea spp.	**E, TH**	**P**	**6/6**	**81**	**15**	**1**
Paronychia chartacea	**E, EN**	**A**	**6/6**	**456**	**231**	**33**
Stipulicida setacea	**N**	**P**	**6/6**	**873**	**171**	**14**
Subshrubs						
Calamintha ashei	N, TH	P	5/6	14	6	0
Lechea deckertii	**N**	**P**	**6/6**	**59**	**31**	**0**
Palafoxia feayi	E	P	5/6	13	10	1
Polygonella robusta	E	P	5/6	14	17	0
Shrubs						
Ceratiola ericoides	**N**	**P**	**6/6**	**51**	**28**	**2**
Lyonia sp.	N	P	5/6	29	2	0
Spike Moss						
Selaginella arenicola	**N**	**P**	**6/6**	**2673**	**3713**	**364**
Graminoids						
Bulbostylis warei	N	P	3/6	4	6	0
***Cyperus spp.* (1.8%)**	**?**	**A/P**	**6/6**	**47**	**7**	**0**
Dichanthelium spp.	?	A/P	4/6	19	10	0
Panicum repens	IN	P	5/6	1	22	0
Paspalum notatum	EX	P	3/6	6	1	0
Paspalum setaceum	N	P	5/6	8	4	0
***Poaceae* (7.0%)**	**?**	**A/P**	**6/6**	**112**	**33**	**2**
Ruderal Herbs						
**Conyza canadensis* (1.8%)*	N	P	5/6	19	36	0
Emilia fosbergii	EX	A	2/6	0	7	0
Euthamia caroliniana	**N**	**P**	**6/6**	**5**	**11**	**1**

Ruderal Herbs	Origin	Span	# Seas.	Year 1	Year 2	Year 3
Eupatorium spp.	N	P	6/6	62	20	3
*Gamochaeta purpurea (1.4%)	N	A/B	6/6	657	161	0
*Linaria floridana (2.9%)	N	A	6/6	165	84	18
Oldenlandia corymbosa	EX	A/P	3/6	5	1	0
*Oldenlandia spp. (7.3%)	?	A/P	4/6	33	5	0
Oldenlandia uniflora	N	A	3/6	30	49	0
*Oxalis corniculata (8.3%)	N	A/P	6/6	69	74	0
Phyllanthus tenellus	EX	A	5/6	41	6	0
*Pilea microphylla (5.9%)	N	A/P	5/6	7	9	0
Physalis spp.	N	P	3/6	5	17	0
Richardia scabra	EX	A	4/6	11	3	0
Ruellia blechum	IN	A/P	4/6	11	8	0

Span = life span, # Seas. = numbers of season present in the seed bank,* = species that occurred in controls, N = native, E = endemic, EX= non-native, EN = endanger, TH = threatened, ? = unknown, A = annual, B=biennial, P = perennial.

CONCLUSION: MANAGEMENT IMPLICATIONS

Information regarding seed bank dynamics in native and degraded Florida rosemary scrub has important implications for management and restoration. Implementation of appropriate management strategies and restoring lost habitat will be important for the long-term conservation of threatened and endangered species endemic to the Lake Wales Ridge. Since changes in seed abundance with time-since-fire followed a similar pattern as aboveground vegetation, risk of local extinction of obligate seeders (reliant on the seed bank for recovery) is greater in long-unburned stands where species are no longer present aboveground. This study has broadened our understanding of which species form persistent soil seed banks and how seed densities change with time-since-fire.

Since scrub species were not found in the seed banks of the pasture sites, restoration will require reintroduction of either seeds or transplants. Soil transfer from rosemary scrub sites may be a useful technique for the introduction of scrub species abundant in the seed bank (e.g. *P. chartacea, S. setacea*, *H. cumulicola*). To optimize number of seeds collected, soil should be removed from areas in close vicinity to the target plant species or from litter patches. This technique will not only save time by alleviating the need to collect and sort seeds, but may also introduce soil microbes that promote germination of scrub endemics (Hawkes 2004). Fortunately, few species were found in the seed banks that will hinder the restoration effort. Since the three perennial grasses dominant in the pastures were not present in the seed bank, complete removal of their biomass (especially roots and rhizomes) should be sufficient to eliminate these species from the pastures. One suggestion for approaching the restoration of pastures is to remove the top layer of soil. This method will remove soil with elevated nutrient

levels and remove the roots and rhizomes of unwanted grasses. After soil removal the site should immediately be seeded with fast growing native species that will compete with non-native or undesired natives that will colonize the vacant soil. The subsequent stages of restoration would involve introduction of long-lived species that will take longer to establish.

Restoration of the disturbed scrub should stress reinstatement of native spatial structure, distribution, and abundance of scrub species. The results from this study suggest that a decline in scrub herb density above- and belowground may be a result of fire suppression and degraded scrub may benefit from controlled burning. A change from an aggregated seed bank distribution in rosemary scrub to a random distribution in disturbed scrub could result in a more homogeneous aboveground spatial distribution of scrub herbs post-fire. Whether a change in spatial distribution of scrub herbs will have a negative or positive impact on these species is unknown. The disturbance history in the degraded scrub is thought to favor scrub herbs since it has increased bare sand cover. While restoration of spatial structure in degraded scrub may not be essential for the conservation of threatened and endangered plant species, changes in vegetation structure can make habitats unsuitable for animal species. In particular suitable habitat for the endangered Florida scrub jay must have certain percentages of open space and oak shrub cover (Breininger et al. 1998). Restoring native spatial structure and species abundances in degraded scrub will be challenging and might require better comprehension of what biotic and abiotic variables maintain the structure in native rosemary scrub.

APPENDIX – SUPPLEMENTARY MATERIAL

Lichens
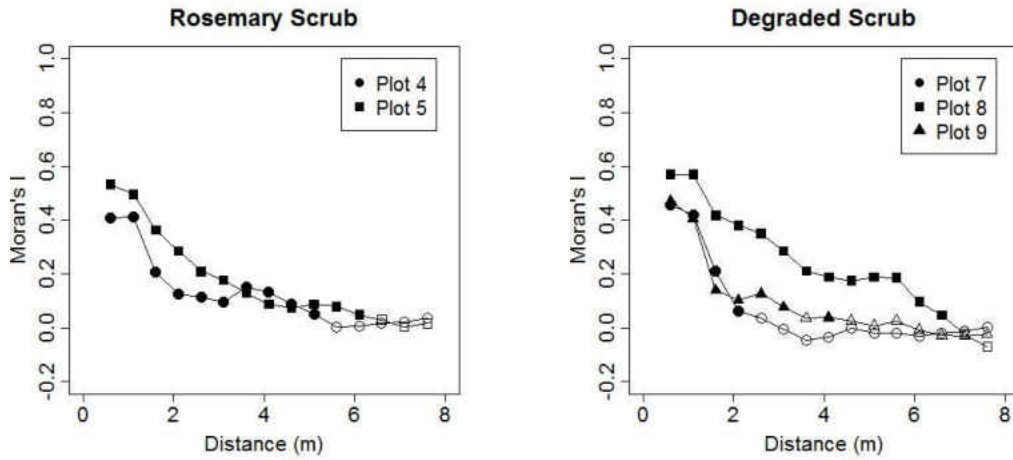
Selaginella arenicola
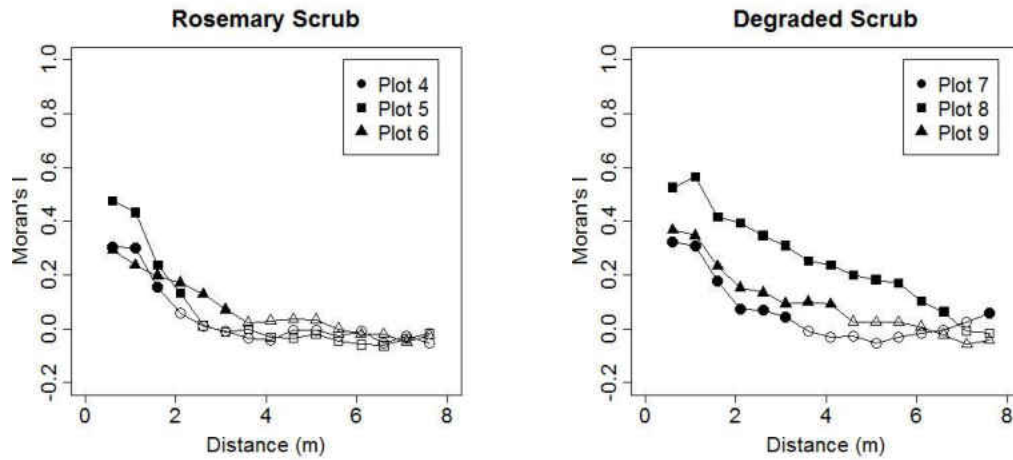
Ceratiola ericoides
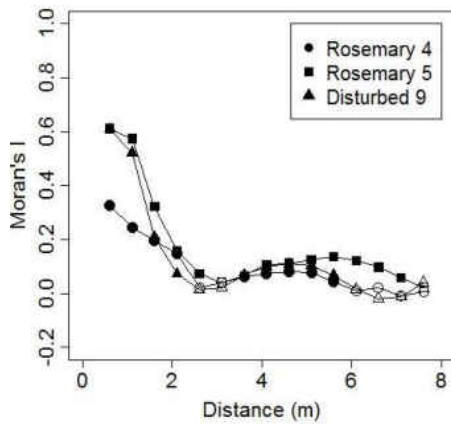
Figure S17. Lichen (top), *S. arenicola* (middle), and *C. ericoides* (bottom) - Moran's *I* correlograms of vegetation in rosemary scrub and degraded scrub. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.

Subshrub
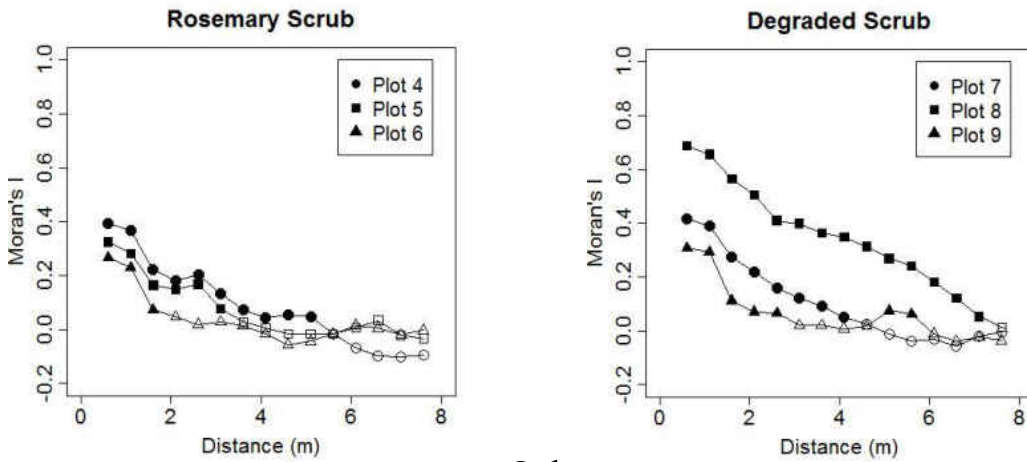
Oaks
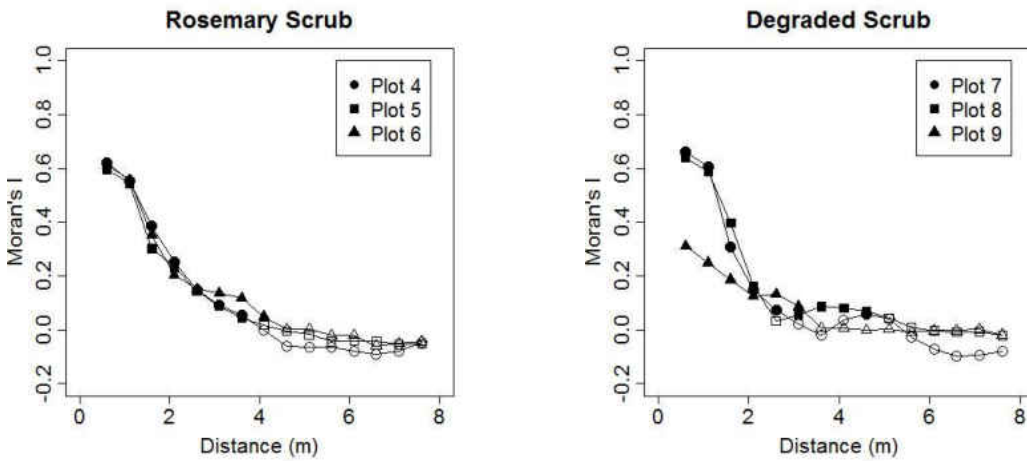
Palmettos
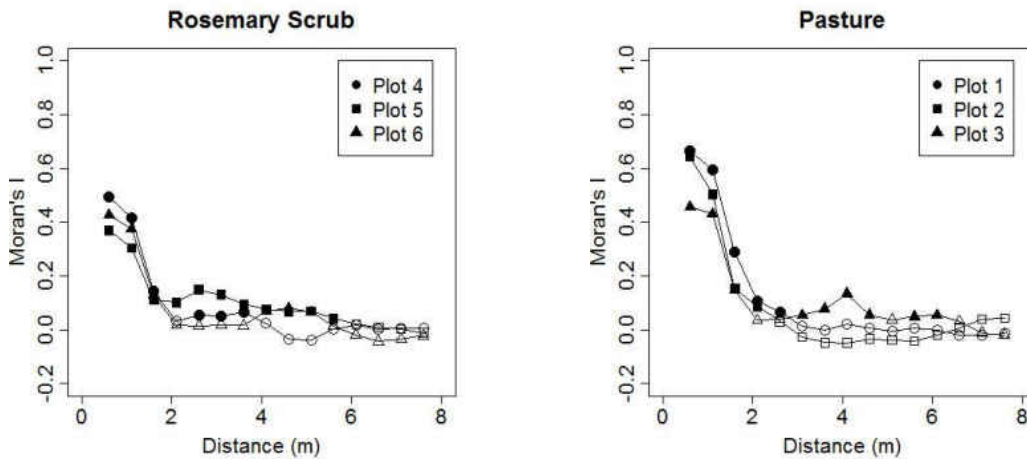
Figure S18. Subshrub (top), palmettos (*Sabal etonia*, *Serenoa repens*) (middle), and oaks (*Quercus chapmanii*, *Quercus geminata*, *Quercus inopina*) (bottom) - Moran's *I* correlograms of vegetation in rosemary scrub, degraded scrub and pasture. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.

Sedges   Ruderal Herbs
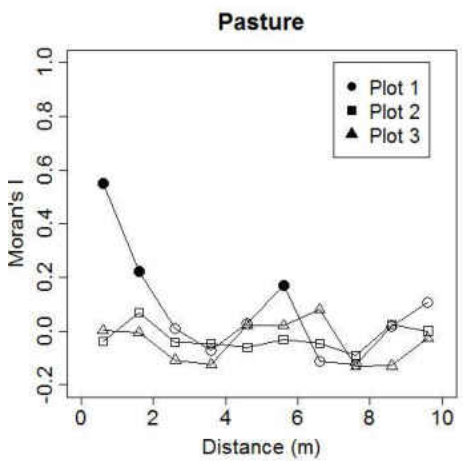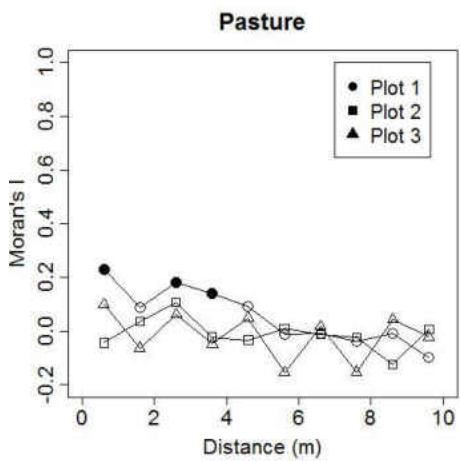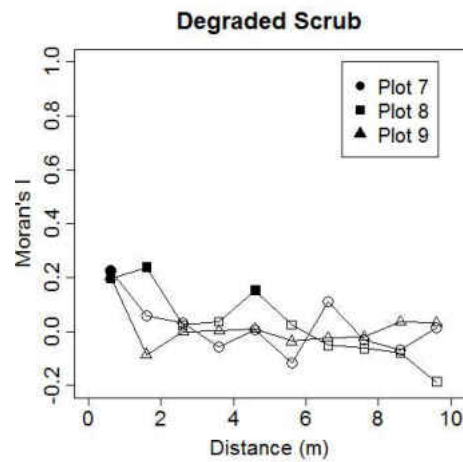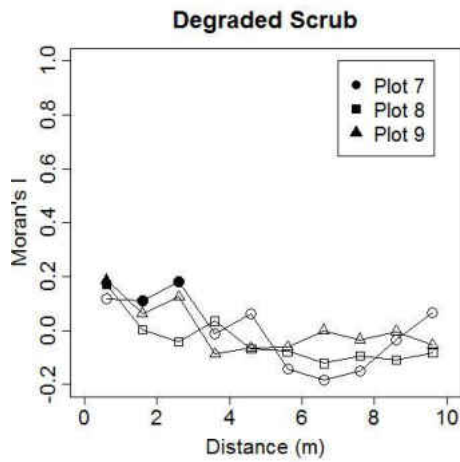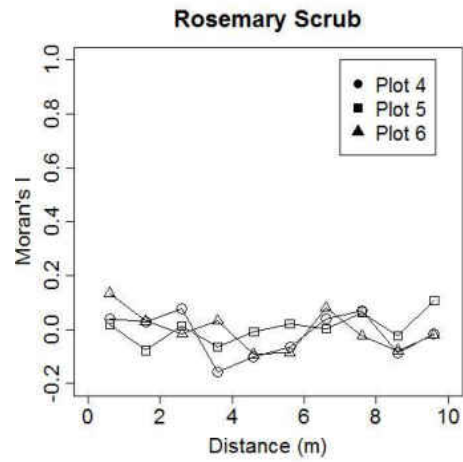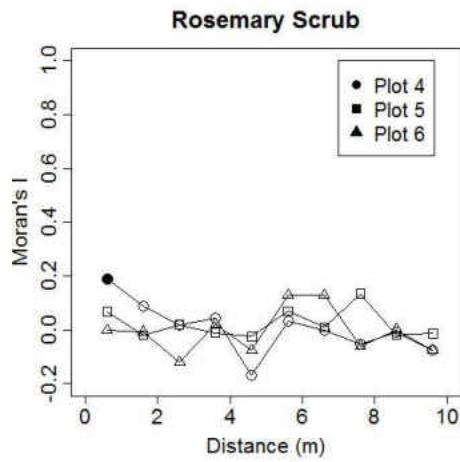
Figure S19. Sedges (left) and ruderal herbs (right) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p \leq 0.05$; open symbols = $p \geq 0.05$.

83
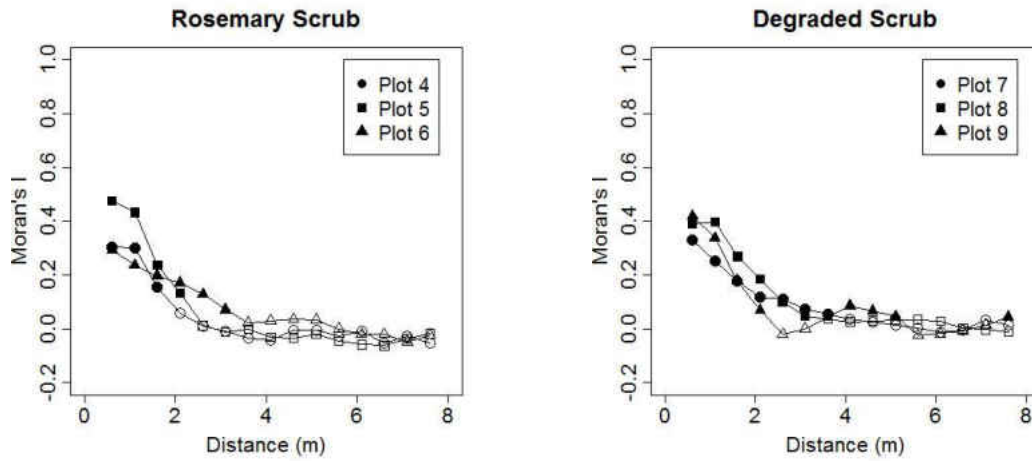
Scrub Herbs

Paronychia chartacea
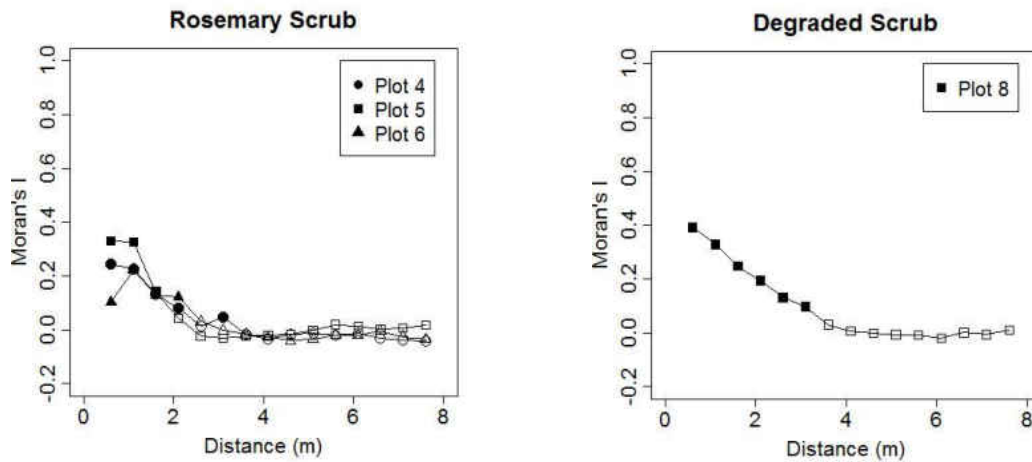
Stipulicida setacea
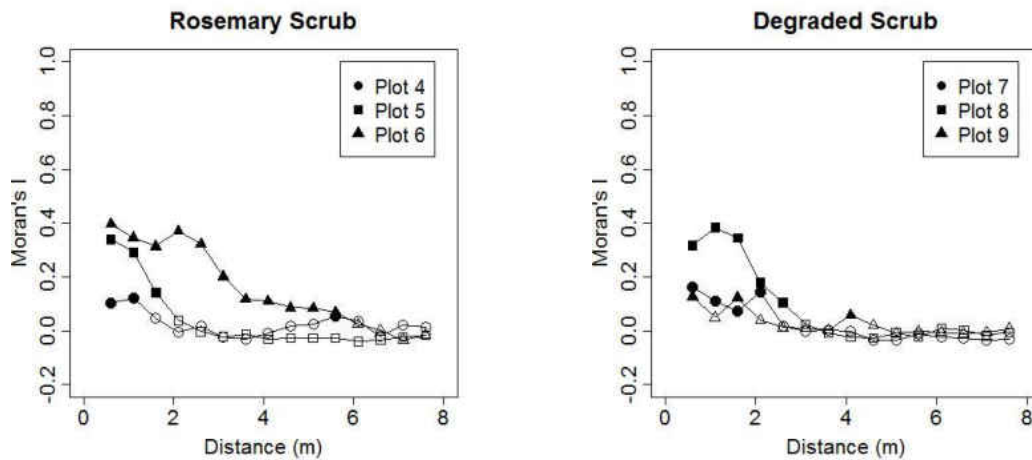
Figure S20. Scrub herbs (top), *P. chartacea* (middle), and *S. setacea* (bottom) - Moran's *I* correlograms of vegetation in rosemary scrub and degraded scrub. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.
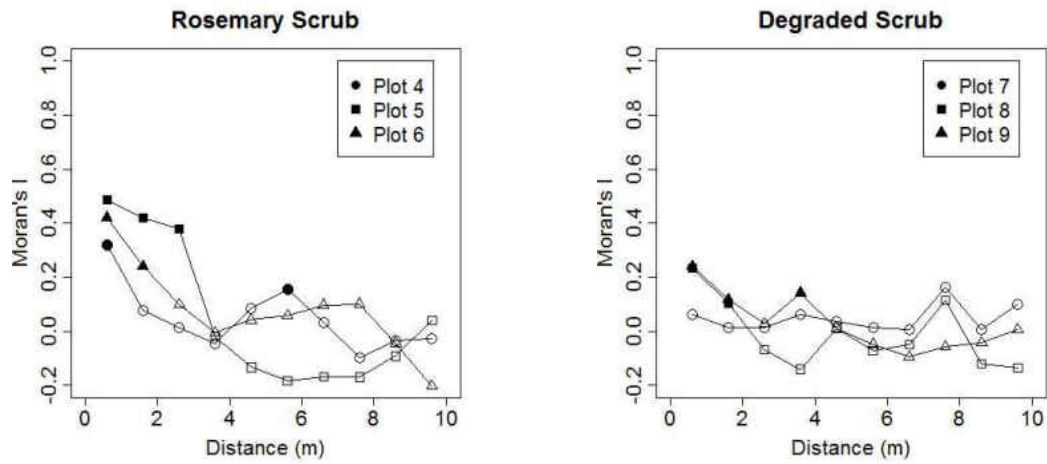
Scrub Herbs

Eupatorium capillifolium
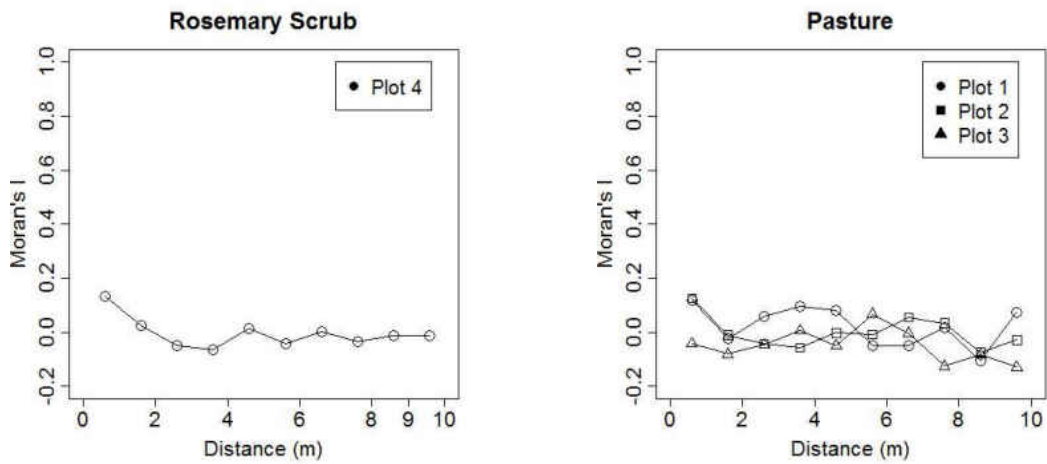
Figure S21. Scrub herbs (top) and *E. capillifolium* (bottom) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.

Gamochaeta purpurea
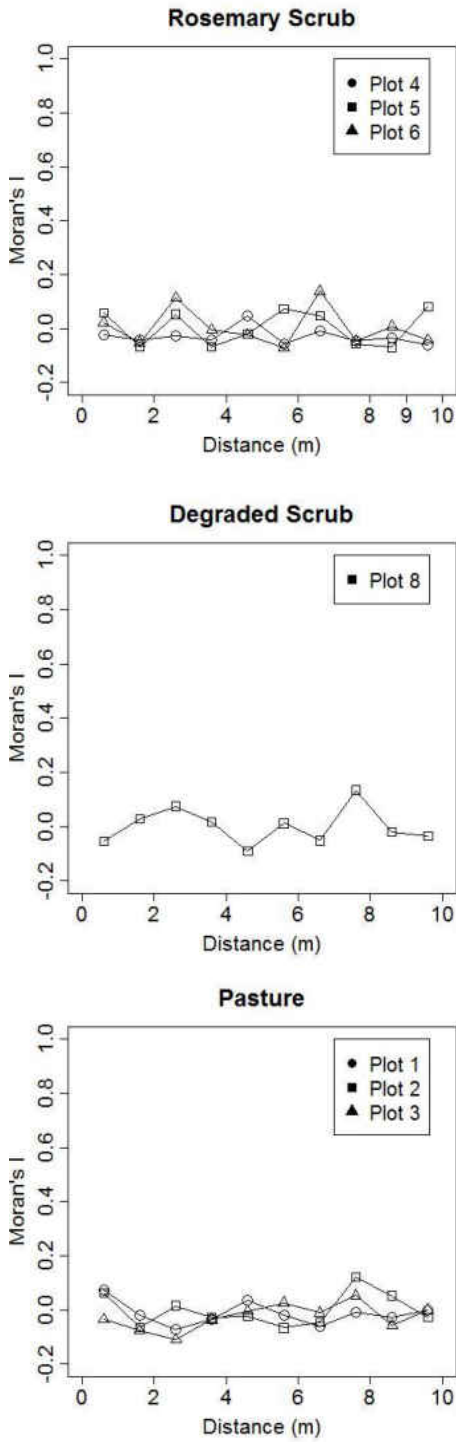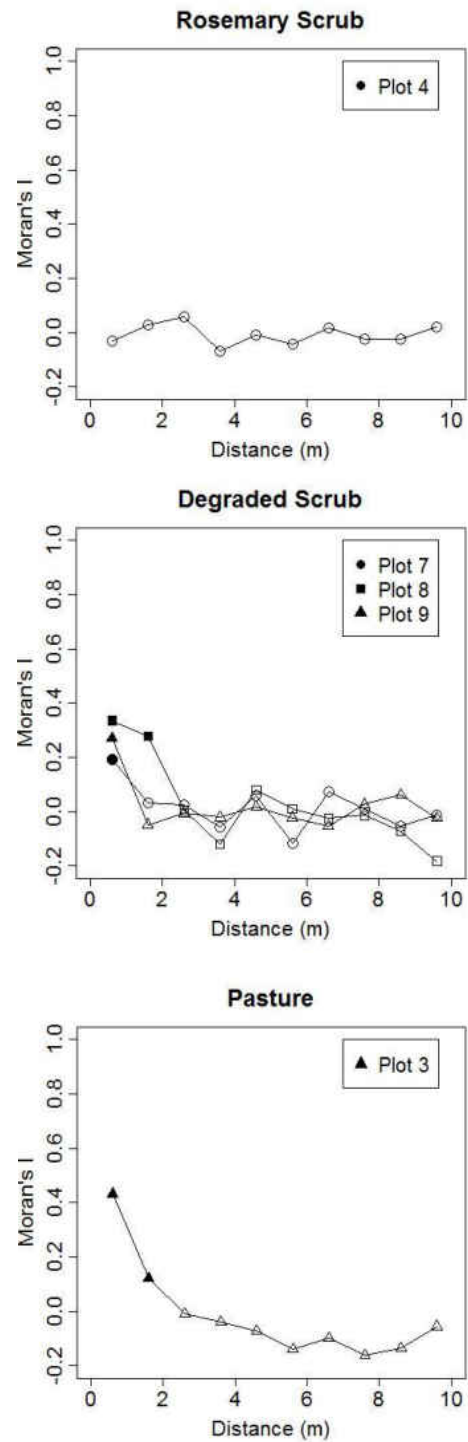
Linaria floridana

Figure S22. *G. purpurea* (left) and *L. floridana* (right) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.
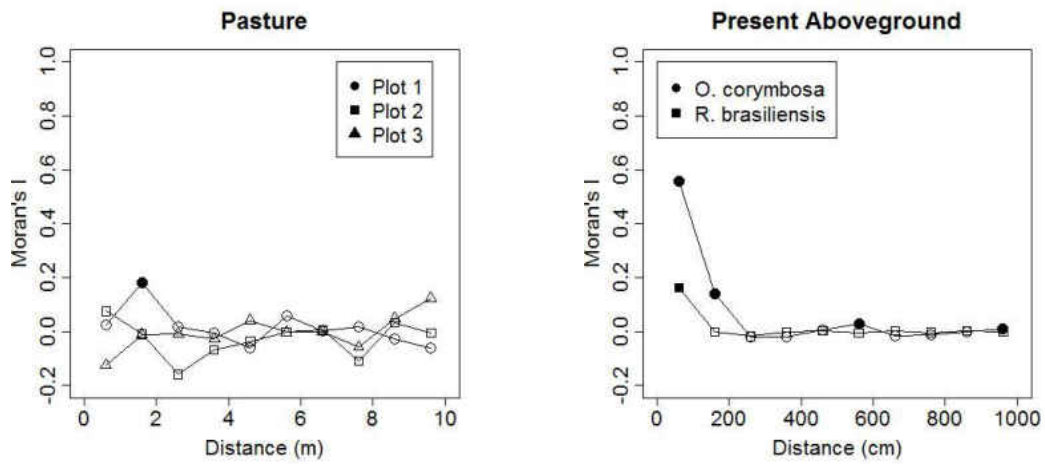
Figure S23. *Scoparia dulcis* (left), *O. corymbosa* and *R. brasiliensis* (right) - Moran's *I* correlograms of seed bank in pasture. Solid symbols = p ≤ 0.05; open symbols = p ≥ 0.05.
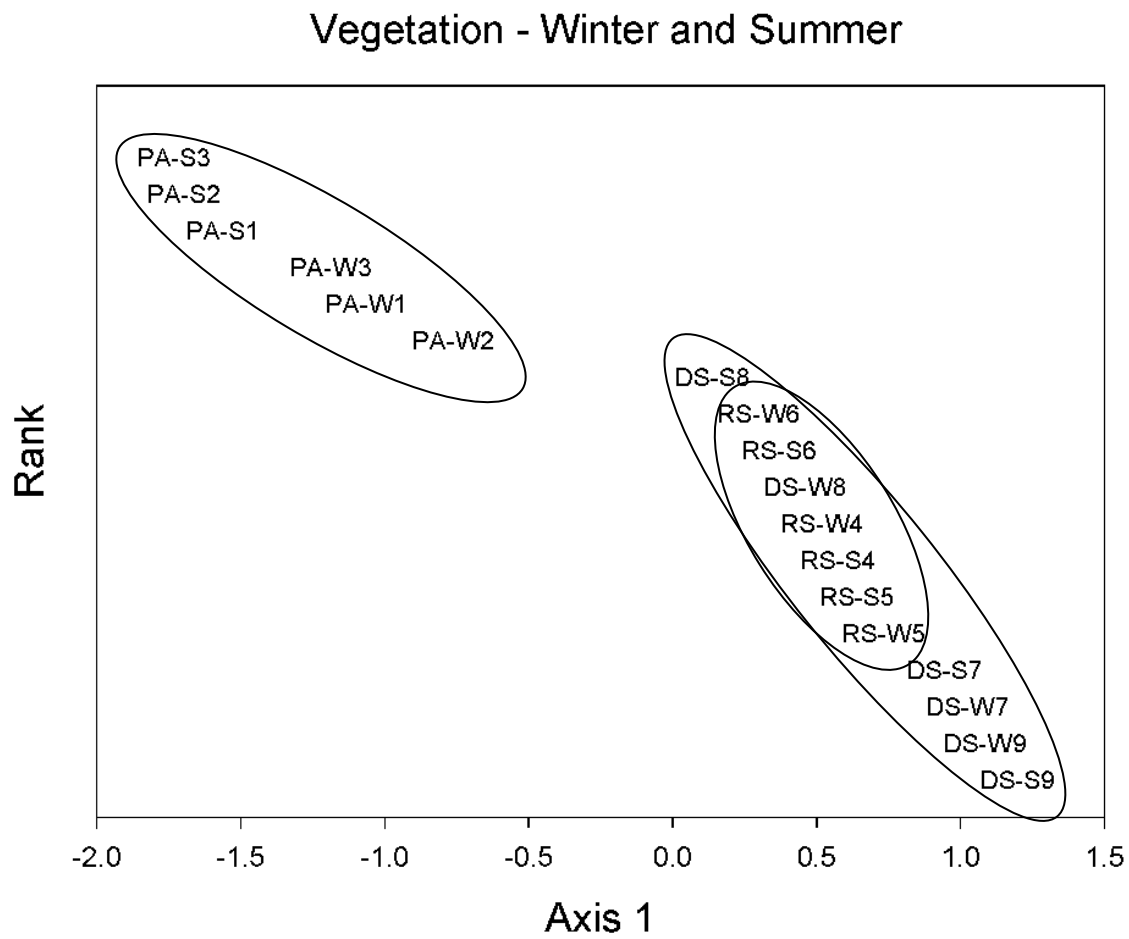
Figure S24. NMS ordination plot of vegetation percent cover during summer and winter. RS = rosemary scrub, DS = degraded scrub, PA = pasture, W = winter, S= summer, number denotes the plot ID number.
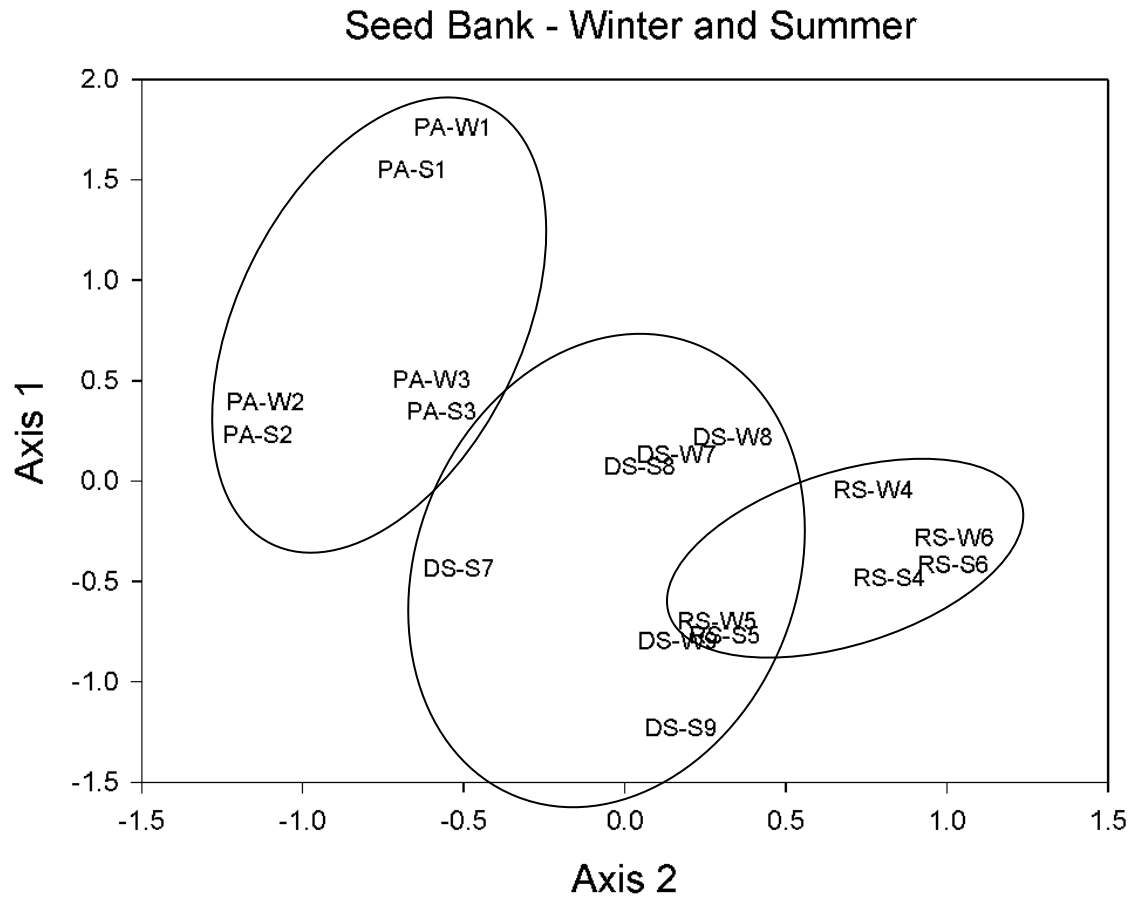
Figure S25. NMS ordination plot of seed bank seed counts during summer and winter. RS = rosemary scrub, DS = degraded scrub, PA = pasture, W = winter, S= summer, number denotes the plot ID number.

Rosemary Scrub

Degraded Scrub
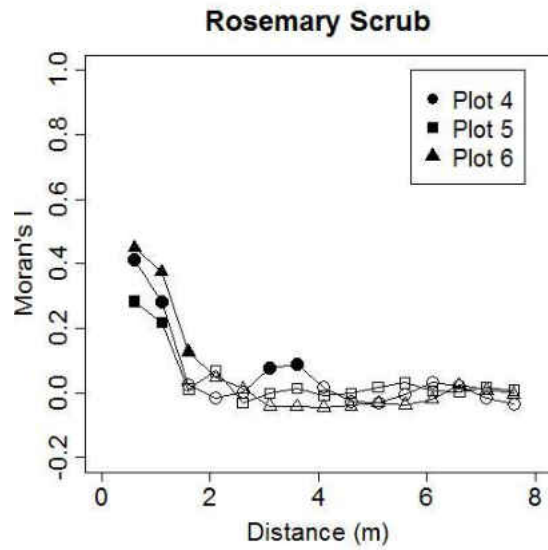
Pasture

Figure S26. Rare shrubs (*Asimina obovata*, *Lyonia fruticosa*, *Persea humilis*, *Sideroxylon tenax*, *Ximenia Americana*) - Moran's *I* correlogram of vegetation in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p \leq 0.05$; open symbols = $p \geq 0.05$.
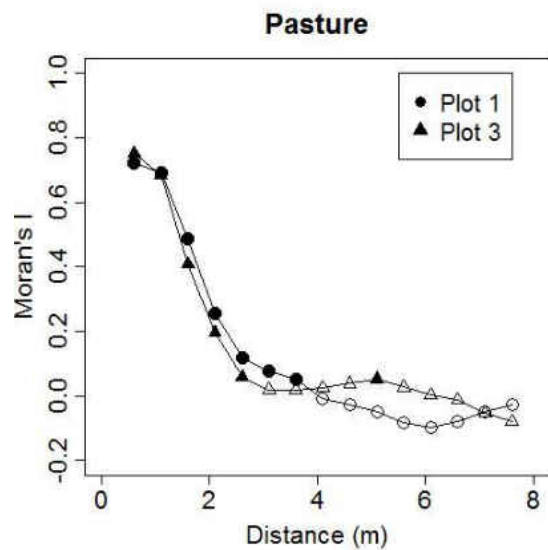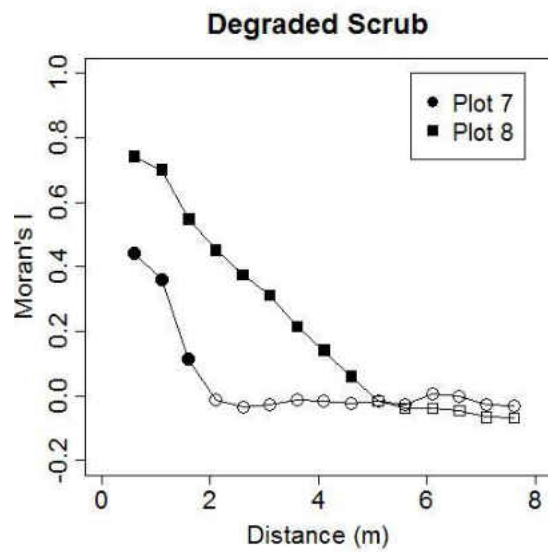
Table S11. Mean percent cover ± (standard error) of vegetation across the three vegetation types in summer 2007 and winter 2009.

|	SUMMER 2007			WINTER 2009		
	Rosemary	**Degraded**	**Pasture**	**Rosemary**	**Degraded**	**Pasture**
Grasses						
Andropogon sp.	0.54 (0.28)	-	0.03 (0.03)	0.02 (0.02)	-	-
Aristida spp.	1.16 (0.31)	1.37 (0.70)	-	1.15 (0.22)	3.95 (2.83)	-
Axonnpus furcatus	-	-	0.11 (0.09)	-	-	-
Cenchrus spinifex	-	0.25 (0.25)	-	-	-	-
Cynodon dactylon	-	0.02 (0.02)	5.63 (0.78)	-	-	0.32 (0.16)
Desmodium incanum	-	-	0.06 (0.05)	-	-	-
Dichanthelium sp.	0.03 (0.02)	-	-	0.01 (0.01)	-	-
Digitaria eriantha	-	2.72 (2.72)	67.9 (14.1)	-	-	36.9 (17.6)
Paspalum notatum	-	-	4.94 (2.67)	-	-	1.88 (1.20)
Melinis repens	-	0.63 (0.59)	0.18 (0.12)	-	0.47 (0.38)	-
Setaria parviflora	-	-	0.04 (0.04)	-	-	-
Sporobolus indicus var. indicus	-	-	0.16 (0.16)	-	-	-
All Grasses	**1.73 (0.57)**	**5.02 (2.91)**	**79.2 (10.5)**	**1.19 (0.24)**	**4.43 (2.63)**	**39.3 (16.3)**
Sedges						
Bulbostylis ciliatifolia	-	0.02 (0.02)	-	-	0.08 (0.05)	-
Cyperus spp.	0.11 (0.08)	0.16 (0.14)	0.28 (0.13)	0.13 (0.13)	0.26 (0.26)	0.03 (0.03)
Rhynchospora megalocarpa	0.03 (0.03)	-	-	0.78 (0.55)	0.03 (0.03)	-
All Sedges	**0.14 (0.07)**	**0.19 (0.16)**	**0.28 (0.13)**	**0.91 (0.53)**	**0.36 (0.29)**	**0.03 (0.03)**
Ruderal Herbs						
Chenopodium ambrosioides	-	-	0.01 (0.01)	-	-	-
Emilia sonchifolia	-	-	0.005 (0.005)	-	-	0.04 (0.04)
Linaria floridana	-	0.02 (0.02)	-	0.01 (0.01)	0.19 (0.19)	0.01 (0.01)
Oldenlandia corymbosa	-	-	0.01 (0.01)	-	-	0.03 (0.03)
Phytolacca americana	-	-	0.01 (0.01)	-	-	-
Physalis walteri	-	0.12 (0.12)	0.04 (0.04)	-	0.13 (0.13)	0.04 (0.04)
Richardia brasiliensis			0.09 (0.09)		0.41 (0.41)	0.05 (0.05)
All Ruderal Herbs	**-**	**0.14 (0.12)**	**0.18 (0.18)**	**0.01 (0.01)**	**0.73 (0.55)**	**0.18 (0.18)**
Scrub Herbs						
Asclepias sp.	0.02 (0.01)	0.01 (0)	-	-	-	-
Balduina angustifolia	0.04 (0.04)	0.01 (0.01)	-	0.11 (0.11)	0.03 (0.03)	-
Chamaecrista fasciculata	0.01 (0.01)	0.05 (0.02)	-	0.02 (0.02)	0.03 (0.03)	-
Chapmannia floridana	0.20 (0.11)	2.57 (1.67)	0.45 (0.41)	0.11 (0.09)	0.70 (0.48)	0.02 (0.02)
Cnidoscolus stimulosus	0.09 (0.05)	0.07 (0.05)	-	0.09 (0.06)	0.20 (0.16)	-

91

Scrub Herbs	Rosemary	Degraded	Pasture	Rosemary	Degraded	Pasture
Euphorbia rosescens	-	0.13 (0.13)	-	-	0.04 (0.04)	-
Helianthemum nashii	-	0.03 (0.02)	-	-	0.13 (0.13)	-
Hypericum cumulicola	0.07 (0.07)	0.01 (0.01)	-	0.13 (0.13)	0.04 (0.04)	-
Lechea cernua	0.05 (0.03)	0.16 (0.08)	-	0.09 (0.04)	0.29 (0.17)	-
Lechea deckertii	-	0.05 (0.05)	-	-	-	-
Liatris ohlingerae	0.01 (0)	-	-	-	-	-
Paronychia chartacea	0.35 (0.12)	0.14 (0.08)	-	0.29 (0.02)	0.17 (0.09)	-
Pityopsis graminifolia	-	0.07 (0.07)	-	-	0.22 (0.22)	-
Polygonella basiramia	0.20 (0.20)	0.02 (0.02)	-	0.26 (0.26)	0.07 (0.07)	-
Polygonella polygama	0.01 (0.01)	-	-	-	-	-
Polanisia tenuifolia	-	-	-	-	-	-
Stipulicida setacea	0.51 (0.19)	0.17 (0.03)	-	0.28 (0.13)	0.18 (0.14)	-
Stylisma abdita	0.13 (0.12)	0.03 (0.03)	-	0.02 (0.02)	-	-
All Scrub Herbs	**1.69 (0.39)**	**3.52 (1.74)**	**0.45 (0.41)**	**1.40 (0.33)**	**2.11 (0.65)**	**0.02 (0.02)**
Other Herbs						
Commelina erecta	-	0.01 (0)	0.14 (0.10)	-	0.01 (0.01)	-
Tradescantia roseolens	0.10 (0.06)	0.07 (0.07)	0.07 (0.07)	-	0.23 (0.23)	0.05 (0.05)
Tillandsia recurvata	-	0.06 (0.06)	0.03 (0.03)	0.11 (0.07)	0.09 (0.09)	0.03 (0.03)
All Other Herbs	**0.10 (0.06)**	**0.14 (0.06)**	**0.25 (0.16)**	**0.11 (0.07)**	**0.33 (0.19)**	**0.08 (0.04)**
Shrubs						
Asimina obovata	0.19 (0.19)	0.47 (0.47)	-	0.58 (0.58)	0.05 (0.05)	-
Ceratiola ericoides	11.7 (8.68)	10.2 (10.2)	-	20.6 (16.2)	14.4 (14.4)	-
Lyonia fruticosa	0.98 (0.98)	-	-	0.46 (0.46)	-	-
Palmetto seedling	0.32 (0.20)	0.03 (0.02)	-	0.77 (0.29)	0.07 (0.02)	0.01 (0.01)
Persea humilis	1.28 (1.04)	2.34 (1.23)	-	0.01 (0.01)	4.30 (2.51)	-
Quercus chapmanii	7.77 (2.42)	3.56 (2.63)	-	10.4 (6.63)	2.26 (1.24)	-
Quercus geminata	0.82 (0.47)	2.33 (1.52)	0.03 (0.03)	1.94 (1.31)	12.8 (10.7)	0.15 (0.15)
Quercus inopina	26.6 (9.32)	4.58 (2.50)	-	14.4 (3.69)	6.68 (5.25)	-
Sabal etonia	4.82 (0.47)	0.82 (0.33)	10.9 (8.39)	7.10 (1.99)	1.55 (0.92)	45.6 (19.7)
Serenoa repens	14.3 (6.53)	2.17 (1.09)	1.80 (0.93)	21.5 (10.8)	4.88 (3.37)	-
Sideroxylon tenax	0.41 (0.29)	3.12 (2.46)	6.64 (2.91)	0.26 (0.06)	0.72 (0.39)	11.74 (4.35)
Ximenia americana	3.34 (0.80)	0.05 (0.05)	-	4.34 (1.91)	0.01 (0.01)	-
All Shrubs	**72.5 (5.36)**	**29.7 (4.84)**	**19.4 (10.1)**	**82.3 (3.37)**	**47.8 (7.68)**	**57.5 (16.0)**
Subshrubs						
Calamintha ashei	0.08 (0.08)	0.16 (0.16)	-	0.09 (0.09)	0.27 (0.27)	-
Galactia regularis	0.04 (0.04)	0.02 (0.01)	-	-	-	-
Licania michauxii	2.36 (0.94)	26.2 (12.3)	0.04 (0.02)	0.08 (0.08)	0.71 (0.56)	-

Subshrubs	Rosemary	Degraded	Pasture	Rosemary	Degraded	Pasture
Macroptilium atropupureum	-	-	0.03 (0.03)	-	-	-
Opuntia humifusa	5.21 (3.21)	1.57 (0.72)	0.06 (0.03)	5.85 (4.04)	1.30 (1.06)	2.78 (2.46)
Palafoxia feayi	0.05 (0.01)	0.18 (0.12)	-	0.06 (0.03)	0.22 (0.17)	0.05 (0.05)
Polygonella robusta	-	4.84 (2.33)	-	0.02 (0.02)	7.38 (6.59)	-
Smilax sp.	2.22 (1.07)	1.84 (0.96)	0.14 (0.09)	1.35 (0.76)	2.21 (0.67)	0.22 (0.22)
Vaccinium myrsinites	1.56 (1.03)	0.03 (0.02)	-	0.54 (0.36)	-	-
Vitis rotundifolia	1.41 (1.41)	-	0.01 (0.01)	-	-	-
All Subshrubs	**13.0 (2.54)**	**34.9 (13.9)**	**0.29 (0.08)**	**7.98 (4.51)**	**12.1 (6.11)**	**3.04 (2.34)**
Pine Tree						
Pinus clausa	2.50 (1.65)	-	-	0.29 (0.16)	-	-
Lichens						
Cladonia evansii	0.42 (0.42)	0.03 (0.02)	-	0.74 (0.74)	0.12 (0.06)	-
Cladonia leporina	1.50 (0.79)	9.37 (4.24)	-	0.88 (0.41)	6.29 (1.47)	-
Cladonia prostrata	1.39 (0.73)	1.04 (0.62)	-	0.76 (0.46)	0.84 (0.25)	-
Cladonia substratum	0.03 (0.03)	-	-	-	-	-
Cladonia subtenuis	0.06 (0.04)	0.15 (0.12)	-	0.07 (0.07)	0.04 (0.04)	-
All Lichens	**3.39 (1.93)**	**10.6 (4.25)**	**-**	**2.45 (1.63)**	**7.29 (1.79)**	**-**
Spike Moss						
Selaginella arenicola	5.00 (2.75)	15.9 (7.35)	-	3.38 (2.36)	24.9 (9.29)	-
Total Veg. Cover	**23.6 (1.38)**	**29.7 (0.77)**	**45.0 (2.38)**	**21.2 (1.25)**	**20.1 (0.91)**	**45.0 (4.28)**

Table S12. Mean seed bank density (m^{-2}) ± (standard error) across the three vegetation types in summer 2008 and winter 2009.

	SUMMER 2008			WINTER 2009		
	Rosemary	**Degraded**	**Pasture**	**Rosemary**	**Degraded**	**Pasture**
Grasses						
Axonopus furcatus	-	4 (2)	4 (2)	-	-	21 (16)
Cenchrus spinifex	-	2 (2)	-	-	-	-
Digitaria sp.	-	-	4 (4)	7 (7)	-	30 (30)
Eustachys petraea	-	4 (2)	2 (2)	-	-	-
Juncus sp.	9 (2)	5 (3)	4 (2)	5 (5)	5 (0)	14 (5)
Panicum spp.???	2 (2)	4 (4)	9 (2)	2 (2)	-	2 (2)
Poaceae family	14 (5)	14 (8)	19 (8)	5 (3)	9 (4)	14 (6)
Melinis repens	-	-	-	-	5 (5)	32 (32)
Setaria parviflora	-	-	-	-	-	4 (4)
Unknown gram#20	-	-	-	4 (2)	5 (3)	11 (5)
All Grasses	**25 (5)**	**32 (9)**	**41 (13)**	**23 (13)**	**25 (4)**	**128 (88)**
Sedges						
Bulbostylis ciliatifolia	-	28 (21)	-	-	27 (13)	4 (4)
Cyperaceae Family (sum)	60 (19)	237 (127)	588 (251)	131 (60)	342 (121)	873 (444)
Cyperus compressus	-	-	-	-	-	2 (2)
Cyperus croceus	4 (4)	9 (5)	39 (19)	5 (0)	4 (4)	108 (76)
Cyperus polystachyos	2 (2)	-	14 (2)	-	-	12 (4)
Cyperus retrorsus	-	9 (6)	25 (10)	12 (5)	12 (8)	41 (17)
Cyperus surinamensis	-	-	28 (11)	21 (11)	-	66 (22)
Fimbristylis autumnalis	-	-	-	-	-	5 (3)
Fimbristylis dichotoma	-	-	7 (5)	-	-	5 (3)
Kyllinga brevifolia	-	-	11 (8)	-	-	30 (25)
All Sedge	**60 (19)**	**266 (147)**	**588 (234)**	**131 (46)**	**368 (132)**	**877 (418)**
Ruderal Herbs						
Conyza canadensis	2 (2)	-	4 (2)	-	-	62 (46)
Eupatorium capillifolium	4 (4)	7 (4)	87 (31)	30 (12)	9 (6)	193 (60)
Fabaceae sp.	5 (0)	2 (2)	4 (4)	2 (2)	-	2 (2)
Gamochaeta purpurea	30 (5)	12 (6)	41 (12)	50 (4)	39 (23)	67 (11)
Houstonia procumbens	-	-	-	2 (2)	2 (2)	14 (9)
Linaria floridana	18 (15)	99 (65)	23 (16)	41 (22)	271 (109)	57 (36)
Ludwigia maritime	-	-	4 (2)	-	2 (2)	14 (4)
Ludwigia sp.	-	-	-	-	-	4 (4)
Micromeria brownie	-	-	-	-	-	4 (2)

Ruderal Herbs	Rosemary	Degraded	Pasture	Rosemary	Degraded	Pasture
Oldenlandia corymbosa	21 (16)	2 (2)	919 (885)	5 (3)	4 (4)	1332 (1282)
Oldenlandia uniflora	2 (2)	5 (3)	122 (64)	2 (2)	4 (4)	74 (27)
Phyla nodiflora	-	-	4 (2)	-	-	2 (2)
Pluchea odorata	-	-	4 (4)	-	-	2 (2)
Polypremum procumbens	11 (6)	11 (8)	89 (26)	9 (4)	5 (3)	58 (18)
Richardia brasiliensis	-	-	7 (7)	-	-	32 (29)
Scoparia dulcis	4 (4)	128 (125)	207 (114)	4 (4)	2 (2)	310 (177)
All Ruderal Herbs	**96 (28)**	**266 (118)**	**1513 (786)**	**143 (14)**	**337 (139)**	**2226 (1243)**
Scrub Herbs						
Chamaecrista fasciculata	5 (0)	2 (2)	2 (2)	-	5 (5)	-
Hypericum cumulicola	43 (37)	37 (37)	-	57 (57)	64 (61)	-
Lechea cernua	19 (2)	34 (2)	4 (2)	11 (3)	30 (5)	2 (2)
Paronychia chartacea	260 (86)	71 (25)	2 (2)	317 (195)	182 (93)	-
Polygonella basiramia	2 (2)	-	-	2 (2)	-	-
Polanisia tenuifolia	-	7 (7)	-	5 (3)	19 (12)	-
Stipulicida setacea	379 (152)	105 (44)	-	494 (210)	151 (58)	-
All Scrub Herbs	**708 (162)**	**255 (34)**	**7 (4)**	**886 (265)**	**452 (70)**	**2 (2)**
Spike Moss (sporophyte)						
Selaginella arenicola	37 (17)	319 (141)	-	2 (2)	27 (21)	-
Subshrubs						
Opuntia humifusa	2 (2)	-	-	-	-	-
Palafoxia feayi	2 (2)	4 (2)	-	5 (3)	7 (7)	-
Polygonella robusta	-	48 (29)	-	-	97 (81)	-
All Subshrubs	**4 (4)**	**51 (30)**	**-**	**5 (3)**	**105 (89)**	**-**
Unidentified						
Dicot	149 (29)	112 (9)	182 (23)	60 (11)	80 (29)	131 (13)
Monocot	5 (3)	11 (3)	5 (3)	2 (2)	5 (3)	-
Unknown	5 (3)	21 (3)	11 (5)	9 (5)	4 (4)	4 (2)
All Unidentified	**159 (30)**	**143 (8)**	**198 (20)**	**71 (12)**	**89 (34)**	**135 (12)**
Total	**2141 (320)**	**2345 (357)**	**4694 (2033)**	**2520 (670)**	**2776 (792)**	**6734 (3488)**

Table S13. Mantel test results of the correlation of the vegetation/seed bank with spatial coordinates.

Habitat	ID	Vegetation		Seed Bank	
		Mantel r	p	Mantel r	p
Rosemary	4	0.096	0.0002*	0.024	0.131
Rosemary	5	0.115	0.0003*	0.050	0.047*
Rosemary	6	0.167	0.0001*	0.094	0.003*
Degraded	7	-0.002	0.508	0.049	0.015*
Degraded	8	0.073	0.0007*	-0.002	0.539
Degraded	9	-0.020	0.708	0.079	0.007*
Pasture	1	-0.031	0.870	0.013	0.307
Pasture	2	-0.042	0.950	0.008	0.322
Pasture	3	0.071	0.004*	-0.008	0.645

Table S14. Mantel test results of correlation of the aboveground microhabitats versus the seed bank of three functional groups. Analyses were conducted using summer 2007 vegetation data and winter 2009 seed bank data. Veg = occurrence of plants aboveground, BS = bare sand.

					Mantel r				
Habitat	**ID**	**Veg**	**p**	**BS**	**p**	**Litter**	**p**	**Shrub**	**p**
Ruderal Herbs									
Rosemary	4	0.124	0.212	0.087	0.037*	-0.049	0.942	-0.007	0.587
Rosemary	5	-	-	0.000	0.459	-0.008	0.521	-0.030	0.804
Rosemary	6	0.022	0.755	0.016	0.279	-0.008	0.521	0.059	0.042*
Degraded	7	0.028	0.265	0.090	0.024*	0.001	0.461	0.031	0.237
Degraded	8	0.065	0.018*	0.090	0.0005*	-0.002	0.464	0.159	0.0001*
Degraded	9	0.027	1.000	0.046	0.225	-0.032	0.817	-0.012	0.506
Pasture	1	0.110	1.000	0.017	0.124	-0.001	0.469	-0.009	0.575
Pasture	2	-	-	-0.008	0.755	0.031	0.142	-0.004	0.572
Pasture	3	0.014	0.146	0.007	0.203	0.019	0.061	0.034	0.026*
Sedges									
Rosemary	4	0.193	0.004*	0.157	0.002*	-0.033	0.825	-0.021	0.877
Rosemary	5	-	-	-0.048	0.861	-0.031	0.693	-0.004	0.511
Rosemary	6	0.024	1.000	-0.005	0.518	-0.004	0.483	0.011	0.348
Degraded	7	0.021	1.000	-0.013	0.822	-0.013	0.855	0.002	0.334
Degraded	8	0.004	0.597	0.021	0.078	-0.007	0.640	0.027	0.058
Degraded	9	-	-	0.040	0.248	-0.044	0.913	-0.045	0.825
Pasture	1	0.027	0.279	0.014	0.162	-0.028	0.689	-0.055	0.999
Pasture	2	-	-	-0.015	0.985	-0.027	0.732	-0.012	0.496
Pasture	3	0.008	0.803	0.015	0.087	0.008	0.176	0.031	0.007*
Grasses									
Rosemary	4	0.012	0.627	0.034	0.249	-0.023	0.519	-0.016	0.709
Rosemary	5	0.041	0.998	0.024	0.350	-0.042	0.791	0.011	0.368
Rosemary	6	0.033	1.000	-0.036	0.918	-0.038	0.814	0.026	0.259
Degraded	7	0.069	1.000	0.053	0.247	0.000	0.394	-0.070	1.000
Degraded	8	0.032	0.547	0.216	0.0008*	-0.075	0.903	0.102	0.102
Degraded	9	0.046	0.196	-0.066	0.909	0.020	0.254	-0.006	0.422
Pasture	1	0.126	0.017*	0.018	0.121	-0.039	0.804	0.016	0.244
Pasture	2	0.017	0.230	0.005	0.327	0.013	0.359	0.033	0.248
Pasture	3	0.048	0.813	0.075	0.093	-0.020	0.575	0.065	0.389

Appendix S1. Script used to perform the Mantel test between the seed bank and vegetation, seed bank and spatial coordinates, and vegetation and spatial coordinates.

##Mantel test comparisons between summer 2007 vegetation and winter 2009 seed bank data –

#analyzed as functional groups

Mantel test comparing vegetation, seed bank data, and spatial coordinates

Open vegetation and seed bank data matrix

data <- read.table("Mantel.1_Veg.s_vsSB.w.txt", header=T)

Separate out vegetation and seed bank data matrices and create a pseudo-species (1 entered in

#this column if species are absent, 0 if species are present)

Winter 2009 seed bank data

sb_w <- data[1:130,]

sb_sub <- sb_w[,5:43]

sum_sb <- as.vector(rowSums(sb_sub))

sb_pseudo <- ifelse(sb_sub >0, 0, 1)

sb <- cbind(sum_sb, sb_pseudo)   #merges pseudo species with seed bank data

Summer 2007 vegetation data

veg_s <- data[131:260,]

veg_sub <- veg_s[,5:43]

sum_veg <- as.vector(rowSums(veg_sub))

veg_pseudo <- ifelse(veg_sub>0, 0, 1)

veg <- cbind(sum_veg, veg_pseudo) #merges pseudo species with vegetation data

Create dissimilarity matrices for vegetation, seed bank, and spatial coordinates

##Create dissimilarity matrix of spatial coordinates with Euclidian distance measure

xy_dist <- dist(veg_s[,1:2])

##Create dissimilarity matrix of vegetation using Bray-Curtis distance measure

veg_dist <- distance(veg, "bray-curtis")

library(vegan) #Open vegan library because horn distance measure is not available in ecodist

##Create dissimilarity matrix of seed bank using horn distance measure

sb_dist <- vegdist(sb, method="horn")

detach(package:vegan)   # Close vegan library

Perform simple Mantel test crossing each matrix

veg_sb <- mantel(veg_dist ~ sb_dist, nperm=10000) # Cross vegetation and seed bank matrices

veg_xy <- mantel(veg_dist~ xy_dist, nperm=10000) #Cross vegetation and spatial coordinates

sb_xy <- mantel (sb_dist ~ xy_dist, nperm=10000)   #Cross seed bank and spatial coordinates

Appendix S2. Script used to perform the Mantel test between winter vs. summer vegetation data.

library(ecodist)

##Mantel test comparisons between summer 2007 and winter 2009 vegetation data

#analyzed as individual species

Open vegetation data files

data <- read.table("Mantel.5_Veg.s_vsSB.w.txt", header=T)

Separate out summer and winter vegetation data matrices and create a pseudo-species

#(1 entered in this column if species are absent, 0 if species are present)

Summer 2007 vegetation data

veg_s <- data[1:130,]

```
veg_s_sub <- veg_s[,12:40]

sum_s <- as.vector(rowSums(veg_s_sub))

veg_s_pseudo <- ifelse(sum_s>0, 0, 1)

veg_s_fin <- cbind(veg_s_sub, veg_s_pseudo) #merges pseudo species with vegetation data


## Winter 2009 vegetation data

veg_w <- data[131:260,]

veg_w_sub <- veg_w[,12:40]

sum_w <- as.vector(rowSums(veg_w_sub))

veg_w_pseudo <- ifelse(sum_w>0, 0, 1)

veg_w_fin <- cbind(veg_w_sub, veg_w_pseudo) #merges pseudo species with seed bank data


## Create dissimilarity matrices for vegetation and spatial coordinates

##Create dissimilarity matrix of spatial coordinates with Euclidian distance measure

xy_dist <- dist(veg_w[,2:3])

##Create dissimilarity matrix of vegetation using Bray-Curtis distance measure

veg_dist_w <- distance(veg_w_fin, "bray-curtis")

veg_dist_s <- distance(veg_s_fin, "bray-curtis")


## Perform simple mantel test crossing the two matrices

vegW_vegS <- mantel(veg_dist_w ~ veg_dist_s, nperm=10000) # Crosses vegetation matrices
```

Appendix S3. Script used to perform the Mantel test between winter vs. summer seed bank data

library(ecodist)

##Mantel test comparisons between summer 2008 and winter 2009 seed bank data

#analyzed as individual species

Open seed bank data file

data <- read.table("Mantel.SB9_sum08.vs.win09.txt", header=T)

Separate out summer and winter seed bank data matrices and create a pseudo-species

#(1 entered in this column if species are absent, 0 if species are present)

Summer 2008 seed bank data

sb_s <- data[1:130,]

sb_s_sub <- sb_s[,17:22]

sum_s <- as.vector(rowSums(sb_s_sub))

sb_s_pseudo <- ifelse(sum_s>0, 0, 1)

sb_s_fin <- cbind(sb_s_sub, sb_s_pseudo)   #merges pseudo species with seed bank data

Winter 2009 seed bank data

sb_w <- data[131:260,]

sb_w_sub <- sb_w[,17:22]

sum_w <- as.vector(rowSums(sb_w_sub))

sb_w_pseudo <- ifelse(sum_w>0, 0, 1)

sb_w_fin <- cbind(sb_w_sub, sb_w_pseudo) #merges pseudo species with seed bank data

Create dissimilarity matrices for seed bank and spatial coordinates

##Create dissimilarity matrix of spatial coordinates with Euclidian distance measure

xy_dist <- dist(veg_w[,2:3])

##Create dissimilarity matrix of seed bank using Horn distance measure

Need to open and close vegan package in order to use a distance measure not included in

ecodist library(vegan)

sb_dist_s <- vegdist(sb_s_fin, method="horn")

sb_dist_w <- vegdist(sb_w_fin, method="horn")

detach(package:vegan)   # Close vegan library

Perform simple mantel test crossing the two matrices

sb.w_sb.s <- mantel(sb_dist_w ~ sb_dist_s, nperm=10000) # Crosses two seed bank matrices

Appendix S4. Script used to perform the Moran's *I* calculation for species in the seed bank and vegetation.

library(spdep)

Open file for either seed bank or vegetation data and attach column names

data <- read.table("Moran.Veg9_sum07.txt", header=T)

names(data)

Log + 1 transform each species/column of data and combine results with XY coordinates

log_trans <- log(data[,3:length(data)] + 1)

plot <- cbind(data[,1:2], log_trans[,1:length(log_trans)])

Set up some variables that will be used later in the script

col_names <- names(plot)[3:length(plot)]   # list of the column names

```
col_indices <- seq(3,length(plot))

output_list <- as.vector(length(col_indices), mode="list") # will produce the output list

coords <- coordinates(plot[,1:2])                          # defines the XY coordinates

vec_length <- 15

x_vec <- rep(0, vec_length)


## For loop that will iteratively run Moran's I for each column of data

for (col in 1:length(col_indices)) {

        results <- matrix(data = NA, nrow = 3, ncol = vec_length) # creates a table for results

        coeff_vec <- rep(0, vec_length)  # gives the Morn's I values

        bins_vec <- rep(0, vec_length)   # gives the sample size

        prob_vec <- rep(0, vec_length)   # gives the probability

        r1 <- 0                                  # Defines lower distance bound

        r2 <- 60                                 # Defines upper distance bound

for (i in 1:vec_length) {

        nb_1 <- dnearneigh(coords,r1,r2) # identifies neighbors of regional points by Euclidean
        #distance
        ## Conducts the Moran's I calculation with 10,000 permutations to test for significance
        moran1 <- moran.mc(plot[,col_indices[col]], nb2listw(nb_1, zero.policy=T), nsim=1,
        #zero.policy=T)
        ## Used to create table of results calculated by the "morn.mc" function
        coeff_vec[i] <- moran1$statistic
        bins_vec[i] <- moran1$parameter
```

```r
        prob_vec[i] <- moran1$p.value

        x_vec[i] <- r2

        r1 <- r1 + 50          # distance added with each lag to the lower bound,

        r2 <- r2 + 50          # distance added with each lag to the upper bound

                               # 50 cm used for vegetation data, 100 cm for seed bank data


        ## organizes results into a single table

        results[1,] <- coeff_vec

        results[2,] <- bins_vec

        results[3,] <- prob_vec

        output_list[[col]] <- results  # gives the output list of results

}

for (i in 1:length(col_names)) {

        # Writes a text file for each species containing the results calculated above

        sp_data <- output_list[[i]]

        sp_name <- col_names[i]

        write.table     (sp_data, file=sprintf("%s.txt", sp_name), quote=FALSE)

}
```

Appendix S5. Script used to calculate the Morisita Index for the seed bank.

library(vegan)

Open seed bank data file

plot <- read.table("SB4_summer.txt", header=T)

Organize data for the analysis

spp.m <- plot[,5:length(plot)]

Performs Morisita index calculation with α=0.05

morisita <- dispindmorisita(spp.m, unique.rm = T, crit = 0.05)

Appendix S6. Script used to calculate regression models and weighted AIC$_c$ values for seed bank density data.

library(MASS)

Open data table and attach row header names

sb <- read.table ("Reg_density_nojan93.txt", header=T)

attach(sb)

Center each predictor variable by subtracting the mean

cTSF <- TSF-mean(TSF)

Save response variable (species) being analyzed to a vector name

spp <- round(phyten)

Setting up variables for summary table for the response variable

model   <- NULL

rows   <- NULL

```r
model.df <- NULL

k       <- NULL

sumlogL  <- NULL

sumaic   <- NULL

ms       <- c(           # Model specification vector, maintains a string description of models to run

        "spp ~ 1",

        "spp ~ cTSF" ,

        "spp ~ cTSF + I(cTSF^2)",

        "spp ~ cTSF + I(cTSF^2) + I(cTSF^3)"

        )

# Iteratively Fit Models

for (i in 1:length(ms)) {

    fm       <- glm.nb(as.formula(ms[i]))

    model    <- append(model, as.character(formula(fm)[3]))

    rows     <- append(rows, nrow(sb))

    model.df <- append(model.df, df.residual(fm))

    k        <- append(k, nrow(sb) - df.residual(fm))

    sumlogL  <- append(sumlogL, logLik(fm))

    sumaic   <- append(sumaic, AIC(fm))

    summary(fm)

}
```

Gives a summary table of models and AIC values

sumtable = data.frame(model, rows, model.df, k, sumlogL, sumaic) # Recombine all data

#collected into its own data frame

sumtable[order(sumtable[["sumaic"]]),]

Run regression models – cubic, quadratic and linear

model1c <- glm.nb(spp ~ cTSF + I(cTSF^2) + I(cTSF^3))

summary(model1c)

model2c <- glm.nb(spp ~ cTSF + I(cTSF^2))

summary(model2c)

model3c <- glm.nb(spp ~ cTSF)

summary(model3c)

Calculate the AIC_c value for each model

AICc_C3 <- sumaic + 2*k*(k+1)/(rows-k-1)

Calculate the numerator and denominator variables needed to calculate the weight

delti_C3 <- AICc_C3-min(AICc_C3)

L_modeli_C3 <- exp(-0.5*delti_C3)

Calculate the weight of each model

wi_C3 <- L_modeli_C3/sum(L_modeli_C3)

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