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Complete List of Authors:	Navarra, Jennifer; University Of Central Florida, Department of Biology Quintana-Ascencio, Pedro; University Of Central Florida, Department of Biology
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Species composition and spatial pattern of the vegetation and seed bank along a gradient of disturbance in Florida rosemary scrub

Navarra, Jennifer J.1,2 & Quintana-Ascencio, P.F.1,3

1 Department of Biology, University of Central Florida, 4000 Central Florida Blvd, Orlando, Florida USA ;

2 E-mail jnavarra@knights.ucf.edu, 3 E-mail pquintan@mail.ucf.edu

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Abstract

Question: How do species composition and spatial pattern of the vegetation and soil seed bank change along a disturbance gradient in Florida rosemary scrub? We hypothesized that changes in species composition will reflect contrasting abilities of species to cope with disturbance. We expected that increased anthropogenic disturbance would favor stress tolerant species and would reduce habitat spatial heterogeneity.

Location: Lake Wales Ridge, Highlands County, FL, USA.

Methods: During the summers and winters of 2007-2009, we assessed percent vegetation cover and soil seed bank species composition in nine grid plots located in three community types: native rosemary scrub, degraded scrub, and agriculturally improved pasture.

Results: 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 native and degraded scrub but species abundance and distribution differed. Shrubs comprised the dominant cover in native scrub and cover of subshrubs and *Selaginella arenicola* were dominant in degraded scrub. Vegetation cover was spatially aggregated across all sites and larger more homogenous patch sizes were observed in species with relatively higher abundances in the degraded scrub. Abundance of scrub herbs above- and belowground was highest in native scrub, lower in degraded scrub, and absent in 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.

Conclusions: While human activity disrupted the spatial structure in the degraded scrub, the more severe anthropogenic disturbance in pastures led to creation of a novel ecosystem unlikely to return to the native state.

Introduction

Disturbance is a main driver of community change (Pickett & White 1985). While disturbances at intermediate levels are presumed to maintain biotic diversity and spatiotemporal heterogeneity (Levin & Paine 1974), disturbances that are outside of the historic range can alter community composition and species spatial distribution (Zedler et al. 1983; Knapp 1996). 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). While the majority of studies demonstrating the influence of spatial pattern on ecological processes have been based on models (Tilman & 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 & Prati 2001; Tirado & Pugnaire 2003). The significance of spatial pattern raises questions of how anthropogenic disturbances, which frequently alter species composition and spatial distribution, will influence ecological processes in disturbed communities. It has been shown that 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 & Prati 2001; Tirado & Pugnaire 2003).

Although differences in disturbance history and intensity can alter the amount of spatial heterogeneity at various spatial scales (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 vegetation and seed bank along a disturbance gradient. The soil seed bank plays an important role in sustaining local plant populations after disturbance (Thompson & Grime 1979). 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 & 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). We compared species composition and spatial distribution among three community types: native rosemary scrub, degraded scrub, and agriculturally improved pasture. We hypothesized: (1) changes in composition of the seed bank and vegetation would reflect contrasting abilities of species to cope with disturbance, and (2) an increase in disturbance intensity would homogenize the spatial distribution of those species favored by the disturbance regime. In this study we evaluated how seed bank and vegetation varied along a disturbance gradient in terms of: (1) species composition, (2) spatial structure, and (3) the spatial and compositional relationship of the seed bank to standing vegetation.

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 Highlands County, central Florida (Township 38S, Range 30E, Sections 5-8, 18, 19, 29-32). 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). The Archbold Reserve, purchased by Archbold Biological Station in 2002, includes degraded scrub and agriculturally improved pasture. We 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 sites (plots 4-6) were subjected to natural fires and controlled burns (plots 4 and 6 = 10 years time-since-fire, plot 5 = long-unburned) and were found in areas with 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. geminata*) (Menges et al. 2008). After fire most shrub species resprout from rhizomes or roots (Menges & Kohfeldt 1995), and most obligate seeders (species killed by fire) such as *C. ericoides* and several herbaceous species recruit from the soil seed bank (Menges & Hawkes 1998).

Degraded scrub sites (plots 7-9) were cleared in the early 1970s (plot 8) and early 1980s (plots 7 and 9) and were mechanically disturbed (roller chopper). Vegetation structure (tall overgrown shrub patches) and reports from previous land owners indicated 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 communities.

Agriculturally improved pasture sites (plots 1-3) were cleared and planted with non-native forage grasses in the 1970s. These sites were heavily grazed and in the 12 year period from 1990-2002 the pastures were overstocked and overgrazed, often year round. Cattle were present on site until 2002. The pastures were dominated by three non-native grass species (*Paspalum notatum*, *Digitaria eriantha*, *Cynodon dactylon*), although some unpalatable shrub species still persist (*S. etonia*, *Sideroxylon tenax*, *Asimina obovata*).

We 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 (Menges 1999). Once all suitable sampling locations were identified, stratified random sampling was used to determine the final location of each plot.

Aboveground Cover Sampling

Between May and July 2007, we established nine 16 x 16 m macroplots, which provided three replicates per community type. We sub-divided each macroplot into 2 x 2 m subplots and each subplot into 40 x 40 cm quadrats. We sampled aboveground cover in a checkerboard pattern. We 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. Within each quadrat we made ocular estimates of percent cover in whole tenths of a percent (< 10% = trace amount). We assigned cover to the following categories: bare sand, litter, herbs, lichens, graminoids, subshrubs, shrubs, spike moss, and subcanopy (> 3 m). We also assessed percent cover for each species of vascular plant and ground lichen.

In February 2009, we resampled percent cover 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). During the resampling, we grouped dormant grasses into a single category because grasses died back in winter and individuals could not be identified at the species level.

Seed Bank Sampling

In August 2008 and January 2009 we collected soil samples from all nine macroplots using the same subset of subplots sampled for percent cover in February 2009. We 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 we collected the soil cores in a regular pattern within each quadrat.

Germination Monitoring

We used the seedling emergence method to determine species composition of the soil seed bank. We 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. We 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 we regularly changed the seedling flat locations to minimize micro-environmental effects. 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. The soil samples were monitored at monthly intervals for seedling emergence. We removed seedlings once they had been identified to the species level. For each sampling season, we monitored the soil samples for seedling emergence for eight to 12 months. During both seasons, germination rates plateaued before we discontinued germination monitoring.

Data Analysis

We used partial Mantel tests to evaluate the spatial relationship between vegetation and seed bank (controlling for spatial coordinates) (Legendre and Fortin 1989, McCune and Grace 2002). The significance of the correlation was tested with Monte Carlo randomization (10,000 permutations; conducted in R 2.9.1). We 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 & Oden 1979). 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 (Fortin & 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

(Legendre & Legendre 1998) with 10,000 permutations (conducted in R 2.9.1). Significance levels were corrected using progressive Bonferroni. We conducted the analyses at the species and functional group level. We divided the species into functional groups based upon growth habit and, for herbaceous species, habitat preference. We identified the following functional groups: (1) grasses (2) sedges (3) ruderal herbs (typical of disturbed habitats, generally not found growing aboveground in Florida scrub) (4) scrub herbs (Menges & Kohfeldt 1995) (5) other herbs (6) shrubs (7) subshrubs (8) lichens and (9) spike moss.

To assess similarity of species composition between the vegetation and seed bank we used the Sorensen similarity coefficient (S = 2a/(b+c), where **a** is the number of species common to both samples, **b** is the total number of species in the first sample, and **c** is the total number of species in the second sample) (Sorensen 1948). We used Non-metric Multidimensional Scaling (NMS) ordination with Sorensen distance to evaluate community level differences in percent vegetation cover and seed bank seed counts among the three communities. Rare species were removed (occurrence ≤ two sites) from the analysis (McCune & Grace 2002). We 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 a NMS scree plot (using PC-ORD 5.0).

Results

Species Composition

Vegetation

Overall the vegetation included 76 species (69 at reduced sample, 71 without lichens) in summer 2007 and 57 (53 without lichens) in winter 2009. 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 S1). Seasonal decline in species richness largely resulted from absence of seasonally dormant and annual herbaceous species during the winter months.

The vegetation was dominated by long-lived perennials across all communities; however, the dominant functional groups varied (Figure 1). Shrubs were the dominant vegetation in rosemary scrub during both seasons. Approximately half of the vegetation cover in the degraded scrub plots was comprised of two subshrub species (*Licania michauxii* and *Polygonella robusta*) and a spike 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. 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). The NMS ordination of vegetation percent cover showed that the three communities 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 2).

<u>Seed Bank</u>

A total of 10,636 seedlings belonging to 52 species were found in the seed bank across all three communities and two seasons of sampling. Rosemary scrub had 30 species (2,271 seedlings), degraded scrub 36 (2,257 seedlings), and pasture 42 (6,108 seedlings) (Table S2). The seed banks in all three communities were dominated by short-lived herbaceous species; however, the dominant functional group varied among the communities (Figure 1). Across all communities 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 community, scrub herb densities were lower than in rosemary scrub. Pastures were dominated by ruderal herbs which comprised ~50-70% of the emerging seedlings (Figure 1). Across all sites, seed densities were higher during winter than in summer. Seed bank size was generally equivalent among the three communities; however, 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 when compared to the two scrub communities. NMS ordination of seed bank data showed that the three communities 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 2).

Spatial Structure

<u>Ground cover</u>

Across all communities non-vegetative ground cover (bare sand, litter, and lichens) exhibited an aggregated distribution (Figure S1 and S2). Native and degraded scrub communities showed a more heterogeneous spatial distribution of bare sand and litter than the pastures. Spatial pattern of bare sand, litter and lichen cover showed no distinct differences between native and degraded scrub (Figure S1).

The vegetation exhibited an aggregated distribution; however, the degree of aggregation and shape of the correlograms differed among some species and communities. Moran's *I* correlograms revealed differences among communities for grasses, scrub herbs, shrubs, and palmettos. For grasses, patch size was larger in degraded scrub than native scrub (Figure S3). Grasses in pastures generally had intense clumping indicated by higher Moran's *I* values which declined rapidly. Most native and degraded scrub sites had a grass distribution that was more spread out and sparse than in pastures. Spatial pattern for shrubs was similar between degraded scrub and pastures which showed a stronger pattern of spatial aggregation than native scrub (Figure S3). Scrub herbs in degraded scrub had slightly larger patch sizes than in native scrub (Figure 3). Palmettos typically showed a stronger pattern of aggregation in pastures than in native scrub (Figure S4).

At the species level, *Aristida gyrans*, *P. chartacea*, and *L. michauxii* showed differences in spatial distribution among communities. *A. gyrans* and *P. chartacea* exhibited a larger more homogenous spatial distribution in the degraded scrub and smaller patch size in rosemary scrub (Figure 3 and Figure S5). *L. michauxii* showed a small patchy spatial distribution in rosemary scrub and a larger homogenous distribution in the degraded scrub (Figure 3).

<ins>Seed Bank</ins>

Spatial autocorrelation was less common in the seed bank compared to the vegetation, especially among species that were absent from aboveground vegetation. Seeds of sedges generally showed a random distribution or were aggregated in small patches (Figure S6). Seeds of ruderal herbs had random distributions, but did show aggregation if the species was present aboveground (Figure S6). Seeds of scrub herbs generally showed a stronger pattern of aggregation in rosemary than degraded scrub (Figure S7).

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 4). A random distribution was observed across all plots and communities for wind dispersed ruderal herbs that were never recorded aboveground (*Eupatorium capillifolium, Gamochaeta purpurea*, and *Scoparia dulcis*) (Figure S7, S8, and S9). Seeds of *Linaria floridana*, *O. corymbosa*, and *Richardia brasiliensis* exhibited an aggregated distribution at sites where they were present aboveground (Figure S8 and S9).

Relationship Above- and Belowground

Species composition above and belowground was dissimilar across all sites. While Sorensen values across community type 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 1). In terms of structural association above and belowground, plots with high shrub cover (rosemary 5 and pasture 1) exhibited a slight correlation between the vegetation and seed bank. A positive relationship between percent shrub cover and mantel r values suggests shrub cover as an important determinant of structural association above and belowground ($p = 0.014$, adj $R^2 = 0.5$, F-stat = 10.5) (Figure 5).

The seed banks of some species and functional groups were correlated with aboveground microhabitats (bare sand, litter, and shrub cover) and with the occurrence of the same species aboveground (Table 2; for full list see Table S3). The seed banks of scrub herbs 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 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 (Table S3). At the species level, there was a greater tendency for the seed banks of scrub herb species (*H. cumulicola, P. chartacea, S. setacea*) to be positively associated with occurrence of conspecific species aboveground and litter cover in rosemary scrub than in degraded. Seed banks of ruderal species (*L. floridana* and *O. corymbosa*) showed positive correlation with shrub cover in the degraded scrub and pasture (Table 2).

Discussion

Differences in disturbance history influenced community composition, species relative abundance, and species spatial distribution. 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). Human disturbance altered species abundances and seed dispersal patterns in the degraded scrub but did not lead to a loss of scrub species from the community. In the pastures loss of the majority of native scrub species and introduction of non-native grasses resulted in the creation of a novel ecosystem unlikely to return to its native state (Hobbs et al. 2006). Change in disturbance type and intensity can result in alteration of species composition, select for plant morphological characteristics tolerant of the disturbance regime, and alter suitable microhabitat availability (Diaz et al. 1992; Jimenez & Armesto 1992; 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).

Our data indicated mechanisms explaining changes in community composition. In the pastures the only native species that persisted were those with structural or chemical defenses that deterred herbivory. In the degraded scrub vegetation, an increase in abundance of species growing close to the ground may have resulted from roller chopping which possibly favored short statured species able to resprout. Short statured species may have also benefited from reduced competition with shrubs. Reduced abundance of scrub herbs in the seed banks of the degraded scrub is likely due to fire suppression. Scrub herbs are known to decline as time-since-fire increases due to a reduction in bare sand gap availability with increased shrubs, litter and lichen cover (Hawkes & Menges 1996; Schafer et al. 2010). While aboveground bare sand cover may have been marginally 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).

Although changes in species abundances and dominant growth forms were observed across the disturbance gradient, we found species characteristics such as life span and primary reproductive method were not; long-lived perennial species reliant upon vegetative/clonal 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 of long-lived species aboveground and short-lived species in the seed bank is frequently reported in the literature (Figueroa et al. 2004; Shaukat & Siddiqui 2004). In this study, dominance of vegetatively reproducing species aboveground likely explains the lack of correspondence of species composition above- and belowground. Lack of correspondence of both compositional (Thompson & Grime 1979; Tekle & Bekele 2000) and structural attributes (Arroyo et al. 1999) between the vegetation and seed bank have been found in other plant communities.

Spatial aggregation was ubiquitous throughout the vegetation but was less frequent in the seed bank. While differences in species abundances across the disturbance gradient were apparent, aboveground differences in spatial pattern among the communities were less conclusive. Spatial pattern differences were found among sites, but in most cases dissimilarity among the communities 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 differed. 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 & Kohfeldt 1995).

Differences in spatial pattern were observed for species and functional groups with altered aboveground abundances in the degraded scrub when compared to rosemary scrub. 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). 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 open space 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 communities 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*) across all sites.

The greatest differences in seed bank spatial structure were observed for scrub herbs in rosemary versus degraded scrub. Our results indicated a greater tendency for the seed banks of scrub herbs in rosemary scrub to have an aggregated distribution and to be associated 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. 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 (Aguiar & Sala 1997; Bullock & 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. Reduced shrub cover in the degraded scrub may explain the lack of association of the scrub herb seed banks with aboveground microhabitats.

The pasture plot with a 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 have been facilitated by the presence of shrubs in the pastures which excluded grasses from growing directly beneath them. In scrub the interaction between shrubs and herbs is different; herbaceous species are negatively impacted by shrubs, which is evident from their decline in abundance as shrub cover increases (Menges & Hawkes 1998).

Understanding how differences in disturbance history will alter community composition, abundance, and spatial distribution allows for better prediction of how communities may change under diverse disturbance regimes. Anthropogenically disturbed communities may not follow predictable recovery sequences due to drastic changes imposed on the biotic and abiotic environment (Stylinski & Allen 1999). 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, increasing disturbance intensity led to a loss of species sensitive to the disturbance regimes and resulted in greater abundance of species with favorable morphological characteristics. Alteration of species abundances led to changes in the spatial structure of the anthropogencally disturbed communities by increasing the patch sizes of favored species. Restoration of rosemary scrub habitat will require reintroduction of scrub species to the pastures.

Restoration in the degraded scrub should focus on reinstating native spatial structure and species abundances. 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 abundances in degraded habitats.

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References

Abrahamson, W.G., Jonhnson, J.N., Layne, J.N. & Peroni, P.A. 1984. Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales Ridge. *Florida Scientist* 47: 209-250.

Adler, P., Raff, D. & Lauenroth, W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465-479.

Aguiar, M.R. & Sala, O.E. 1997. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78: 93-100.

Arroyo, M.T.K., Cavieres, L.A., Castor, C. & Humana, A.M. 1999. Persistent soil seed bank and standing vegetation at a high alpine site in the central Chilean Andes. *Oecologia* 119: 126-132.

Bergelson, J. 1990. Spatial patterning in plants: Opposing effects of herbivory and competition. *Journal of Ecology* 78: 937-948.

Bergelson, J., Newman, J.A. & Floresroux, E.M. 1993. Rates of weed spread in spatially heterogeneous environments. *Ecology* 74: 999-1011.

Bullock, J.M. & Moy, I.L. 2004. Plants as seed traps: inter-specific interference with dispersal. *Acta Oecologica* 25: 35-41.

Caballero, I., Olano, J., Escudero, A. & Loidi, J. 2008. Seed bank spatial structure in semi-arid environments: Beyond the patch-bare area dichotomy. *Plant Ecology* 195: 215-223.

Collins, B., Wein, G. & Philippi, T. 2001. Effects of disturbance intensity and frequency on early old-field succession. *Journal of Vegetation Science* 12: 721-728.

Diaz, S., Acosta, A. & Cabido, M. 1992. Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science* 3: 689-696.

Figueroa, J.A., Teillier, S. & Jaksic, F.M. 2004. Composition, size and dynamics of the seed bank in a Mediterranean shrubland of Chile. *Austral Ecology* 29: 574-584.

Fortin, M.J. & Dale, M. 2005. *Spatial analysis: A guide for ecologists*. Cambridge Univ. Press, Cambrige.

Hawkes, C.V. & Menges, E.S. 1996. The relationship between open space and fire for species in a xeric Florida shrubland. *Bulletin of Torrey Botanical Club* 123: 81-92.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. & Zobel, M. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1-7.

Hopfensperger, K.N. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116: 1438-1448.

Jimenez, H.E. & Armesto, J.J. 1992. Importance of the soil seed bank of disturbed sites in Chilean Matorral in early secondary succession. *Journal of Vegetation Science* 3: 579-586.

Knapp, P.A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: History, persistence, and influences to human activities. *Global Environmental Change* 6: 37-52.

Legendre, P. & Legendre, L. 1998. *Numerical Ecology*. 2nd. Elsevier, Amsterdam.

Levin, S.A. & Paine, R.T. 1974. Disturbance, patch formation, and community structure. *Proceeding of the National Academy Science* 71: 2744-2747.

McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Glenden Beach, OR.

Menges, E.S. 1999. Ecology and conservation of Florida scrub In: Anderson, R.C., Fralish, J.S. & M., B.J. (eds.) *Savannas, barrens and outcrop plant communities of North America*, Cambridge Univ. Press, Cambridge.

Menges, E.S., Craddock, A., Salo, J., Zinthefer, R. & Weekley, C.W. 2008. Gap ecology in Florida scrub: Species occurrence, diversity and gap properties. *Journal of Vegetation Science* 19: 503-514.

Menges, E.S. & Hawkes, C.V. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecological Applications* 8: 935-946.

Menges, E.S. & Kohfeldt, N. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bulletin of Torrey Botanical Club* 122: 282-297.

Mladenoff, D.J., White, M.A., Pastor, J. & Crow, T.R. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3: 294-306.

Noble, I.R. & Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.

Olano, J.M., Caballero, I., Laskurain, N.A., Loidi, J. & Escudero, A. 2002. Seed bank spatial pattern in a temperate secondary forest. *Journal of Vegetation Science* 13: 775-784.

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, INC., Orlando.

Quintana-Ascencio, P., Caballero, I., Olano, J., Escudero, A. & Albert, M. 2009. Does habitat structure matter? Spatially explicit population modelling of an Iberian gypsum endemic. *Population Ecology* 51: 317-328.

Rusch, G. 1992. Spatial pattern of seedling recruitment at two different scales in a limestone grassland. *Oikos* 65: 433-442.

Schafer, J.L., Menges, E.S., Quintana-Ascencio, P.F. & Weekley, C.W. 2010. Effects of time-since-fire and microhabitat on the occurrence and density of the endemic Paronychia chartacea ssp. chartacea in Florida scrub and along roadsides. *American Midland Naturalist* 163: 294-310.

Shaukat, S.S. & Siddiqui, I.A. 2004. Spatial pattern analysis of seeds of an arable soil seed bank and its relationship with above-ground vegetation in an arid region. *Journal of Arid Environments* 57: 311-327.

Sokal, R.R. & Oden, N.L. 1979. Spatial autocorrelation in biology 1. Methodology. *Biological Journal of the Linnean Society* 10: 199-228.

Sorensen, T.A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter* 5: 1-34.

Stoll, P. & Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82: 319-327.

Stylinski, C.D. & Allen, E.B. 1999. Lack of native species recovery following severe exotic disturbance in Southern Californian shrublands. *Journal of Applied Ecology* 36: 544-554.

Tekle, K. & Bekele, T. 2000. The role of soil seed banks in the rehabilitation of degraded hillslopes in Southern Wello, Ethiopia. *Biotropica* 32: 23-32.

Thompson, K. & Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67: 893-921.

Tilman, D. & Kareiva, P. 1997. *Spatial ecology. The role of space in population dynamics and interspecific interactions.* Princeton Univ. Press, Princeton, N.J.

Tirado, R. & Pugnaire, F.I. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136: 296-301.

Turner, M.G. 1989. Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171-197.

Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1-22.

Zedler, P.H., Clayton, R.G. & McMaster, G.S. 1983. Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64: 809-818.

Table 1. Sorensen similarity coefficients for species composition between the vegetation and seed bank. Analysis was conducted using summer 2007 vegetation data and winter 2009 seed bank data.

Vegetation vs. Seed Bank		
Habitat	**ID**	**Sorensen**
Rosemary	4	0.226
Rosemary	5	0.178
Rosemary	6	0.140
Degraded	7	0.226
Degraded	8	0.408
Degraded	9	0.293
Pasture	1	0.194
Pasture	2	0.059
Pasture	3	0.063

Table 2. Partial mantel test results of correlation of the aboveground microhabitats versus the seed bank of various species and functional groups. Analyses were 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 (**Error! Reference source not found.**3).

		Mantel r							
Habitat	**ID**	**Veg**	**p**	**BS**	**p**	**Litter**	**p**	**Shrub**	**p**
Scrub Herbs									
Rosemary	4	0.004	0.224	-0.013	0.995	-0.004	0.585	0.008	0.164
Rosemary	5	0.364	1.0e-4*	-0.025	0.746	0.261	1.0e-4*	0.088	0.007*
Rosemary	6	0.121	0.003*	-0.008	0.572	0.267	1.0e-4*	-0.006	0.533
Degraded	7	0.020	0.143	0.012	0.323	-0.021	0.764	0.006	0.345
Degraded	8	0.048	0.078	-0.009	0.570	0.048	0.086	-0.025	0.722
Degraded	9	0.015	0.287	-0.039	0.870	-0.030	0.966	0.016	0.272
Hypericum cumulicola									
Rosemary	5	0.335	0.003*	-0.054	0.887	0.371	1.0e-4*	0.114	0.006*
Degraded	9	0.147	0.110	-0.073	0.904	-0.033	0.860	0.005	0.424
Linaria floridana									
Rosemary	6	0.034	0.999	-0.024	0.729	0.153	0.024*	0.020	0.278
Degraded	8	0.052	0.172	0.071	0.018*	-0.070	1.000	0.251	1.0e-4*
Pasture	1	0.425	0.032	0.001	0.400	0.010	0.298	0.089	0.014*
Oldenlandia corymbos									

Pasture	1	0.023	0.003*	-0.008	0.801	-0.007	0.825	0.176	1.0e-4*
Paronychia chartacea									
Rosemary	4	0.142	0.004*	0.012	0.330	0.047	0.062	-0.017	0.862
Rosemary	5	0.146	0.021*	-0.055	0.918	0.175	0.001*	0.078	0.023*
Rosemary	6	0.071	0.199	-0.030	0.788	0.356	1.0e-4*	-0.051	0.960
Degraded	7	-	-	-0.026	0.625	-0.043	0.739	0.094	0.090
Degraded	8	0.066	0.065	-0.022	0.673	0.023	0.291	-0.042	0.807
Degraded	9	0.108	0.081	-0.035	0.678	-0.037	0.879	0.049	0.157
Stipulicida setacea									
Rosemary	4	0.137	0.002*	-0.041	0.966	-0.004	0.493	-0.021	0.994
Rosemary	5	0.143	0.059	-0.024	0.663	0.021	0.308	-0.009	0.555
Rosemary	6	0.259	0.001*	-0.047	0.974	0.147	0.006*	-0.008	0.564
Degraded	7	0.216	0.003*	0.018	0.344	-0.028	0.712	-0.011	0.587
Degraded	8	0.037	0.450	0.007	0.410	-0.018	0.608	-0.045	0.753
Degraded	9	0.043	0.473	-0.025	0.527	-0.030	0.787	0.044	0.224

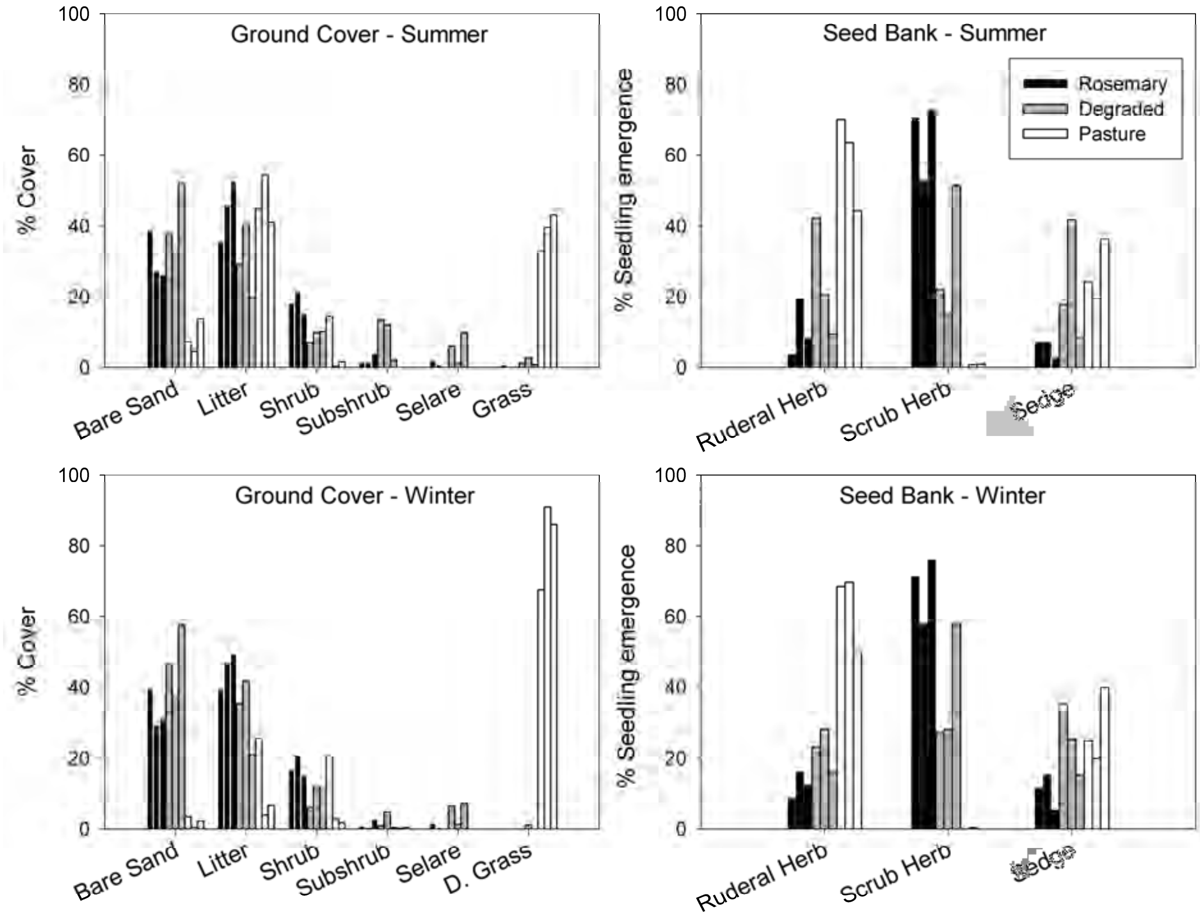

Figure 1. Percent ground cover in summer 2007 (top left) and winter 2009 (bottom left) and percent seedling emergence from the seed bank of ruderal herbs, scrub herbs, and sedges in summer 2008 (top right) and winter 2009 (bottom right). Selare = *S. arenicola*, D. Grass = dormant grass.

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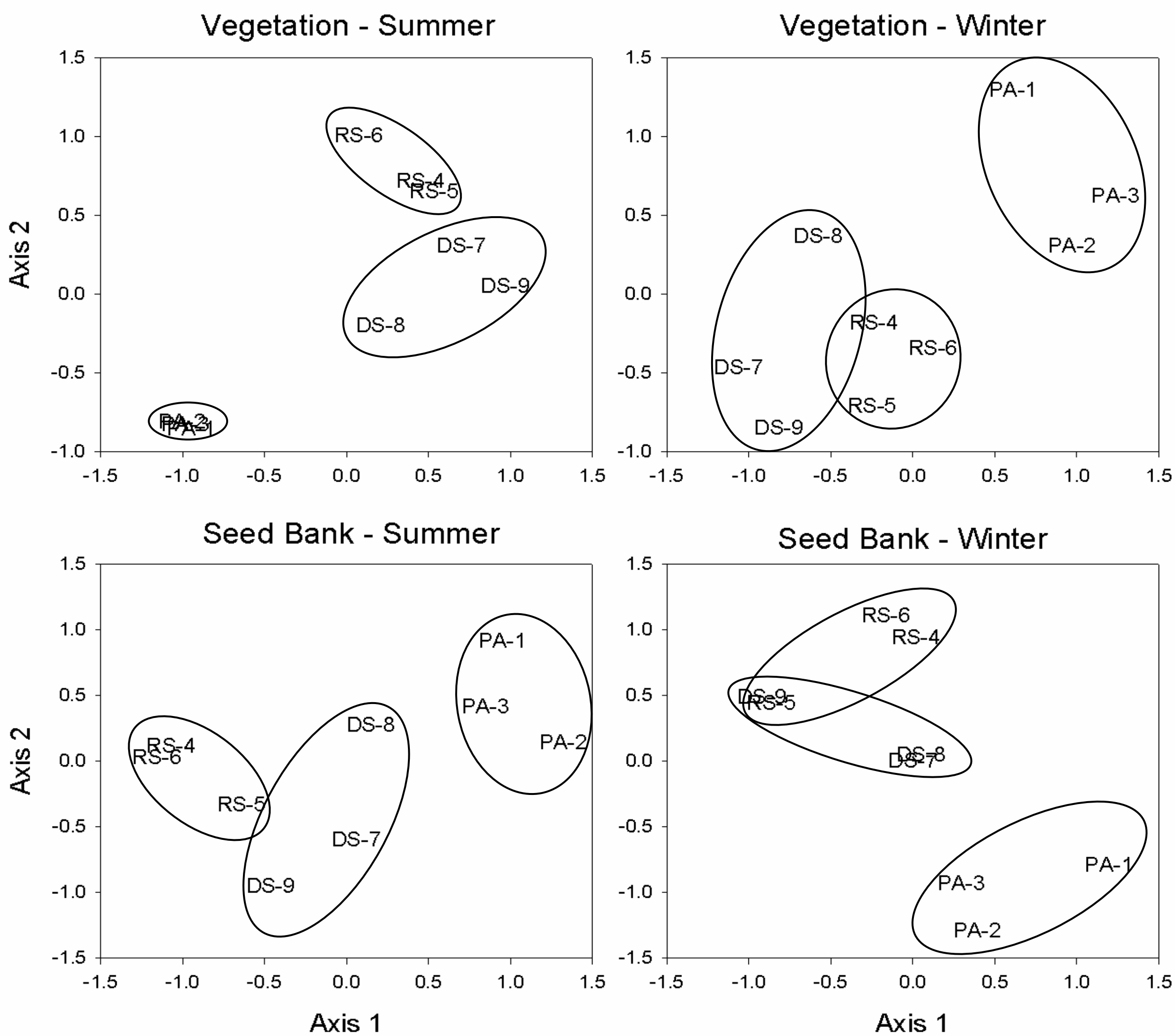

Figure 2. NMS ordination plots of the vegetation and seed bank in summer and winter. RS = rosemary scrub, DS = degraded scrub, PA = pasture, number denotes site ID.

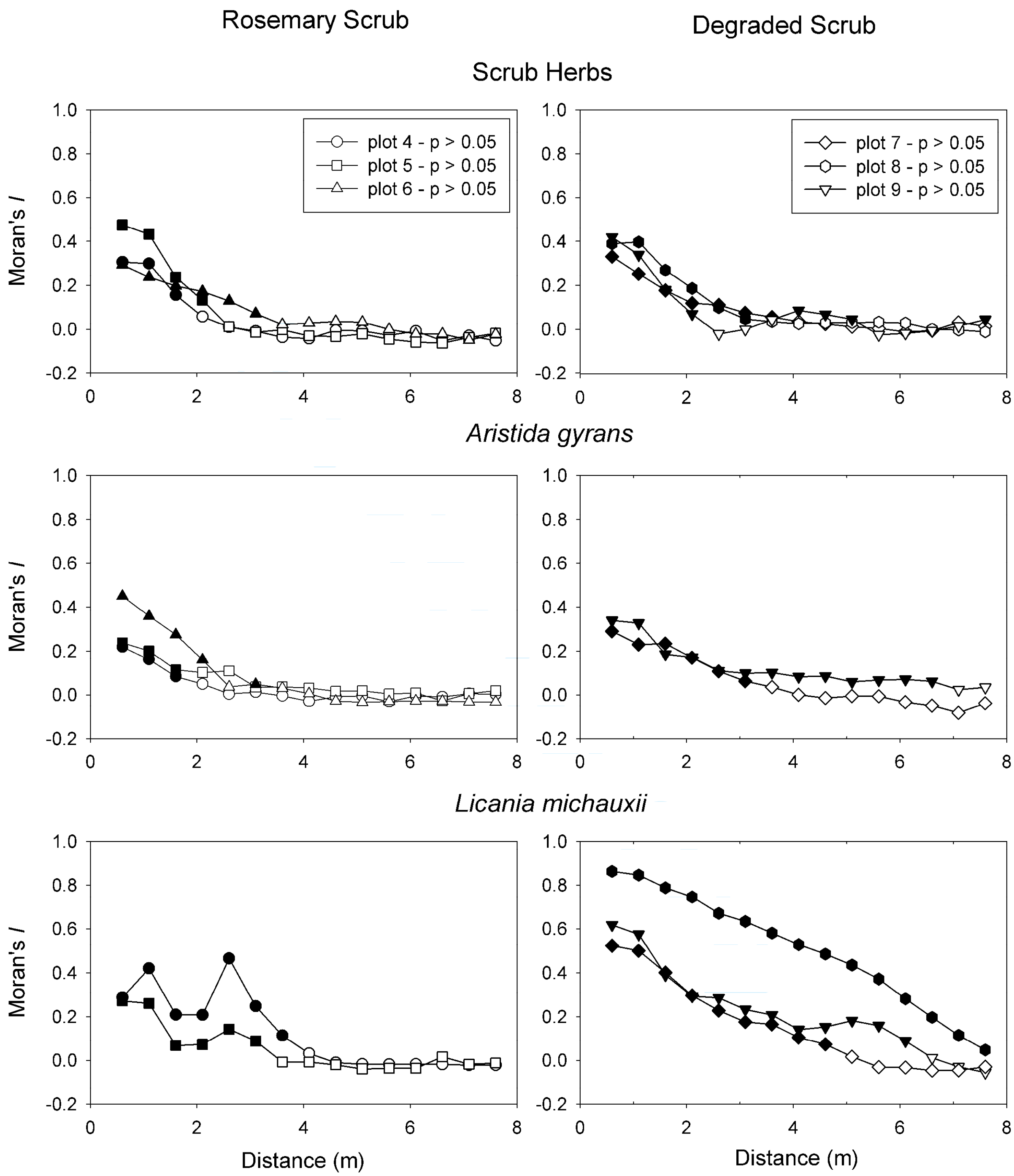

Figure 3. Moran's *I* correlograms of scrub herbs (top), *A. gyrans* (middle), *L. michauxii* (bottom) between the rosemary and degraded scrub vegetation.

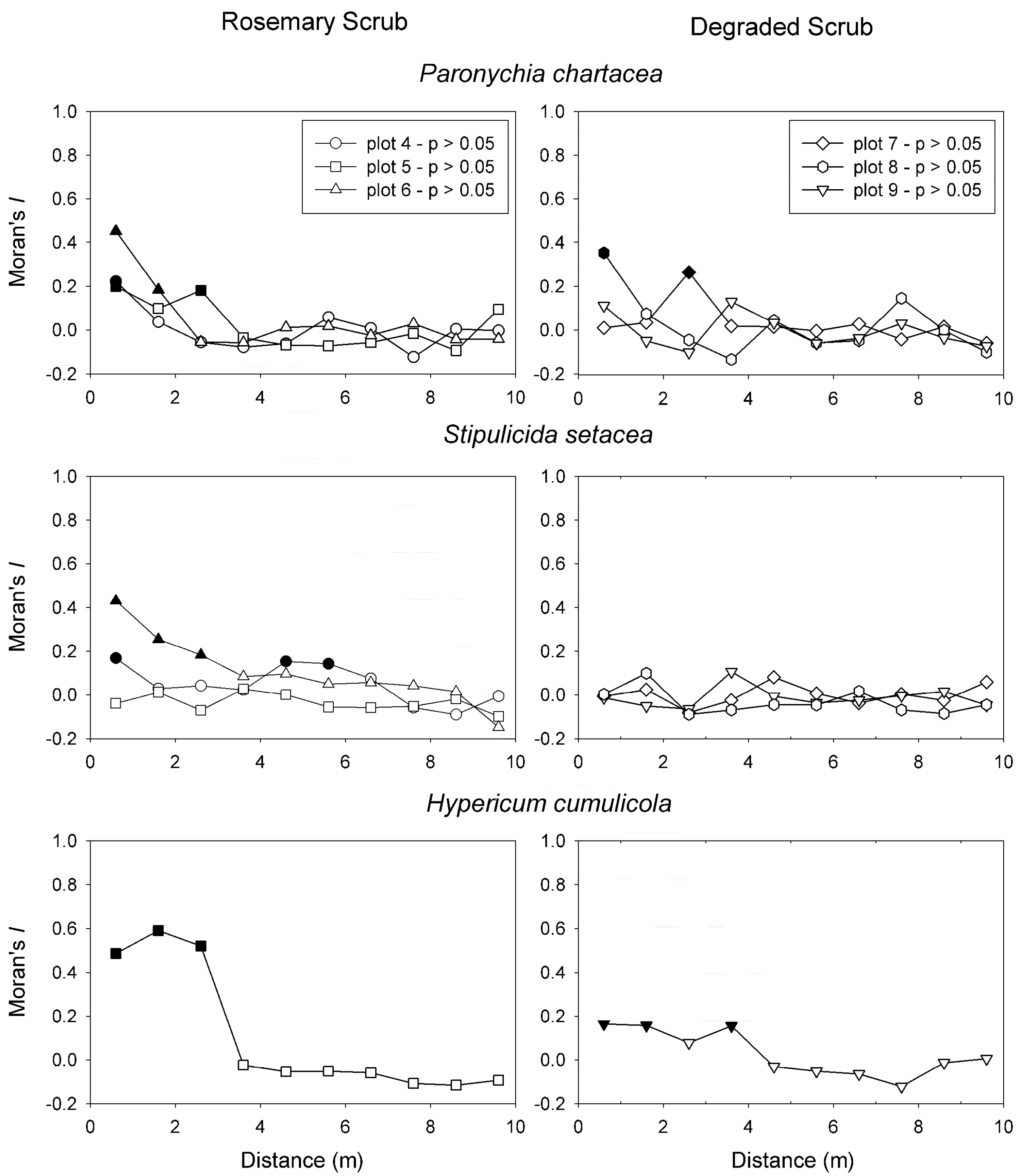

Figure 4. *P. chartacea* (top) and *S. setacea* (middle), *H. cumulicola* (bottom) - Moran's I correlograms of seed bank in rosemary scrub and degraded scrub.

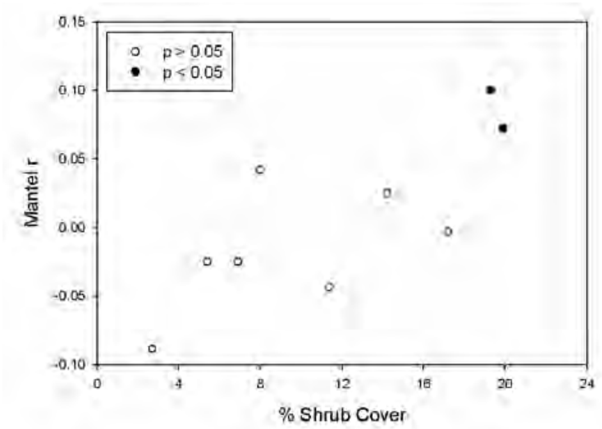

Figure 5. Partial mantel r values for the comparison of vegetation versus the seed bank plotted against percent shrub cover of each plot.

APPENDIX – SUPPLEMENTARY MATERIAL

Table S1. 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 gyrans	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	-	-	0.01 (0.01)	-	-	-

Ambrosioides						
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)	-
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)	-
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 S2. 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 sp.	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)
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 Seed density	**2141 (320)**	**2345 (357)**	**4694 (2033)**	**2520 (670)**	**2776 (792)**	**6734 (3488)**

Table S3. Partial 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	0.123	0.089	0.036*	-0.049	0.939	-0.006	0.563
Rosemary	5	-	-	-0.001	0.471	-0.010	0.529	-0.033	0.835
Rosemary	6	-0.022	0.570	0.013	0.315	0.035	0.239	0.052	0.061
Degraded	7	0.028	0.234	0.092	0.020*	0.002	0.452	0.032	0.191
Degraded	8	0.064	0.013*	0.088	0.001*	-0.007	0.576	0.156	1.0e-4*
Degraded	9	-0.026	0.356	0.045	0.228	-0.033	0.820	-0.011	0.506
Pasture	1	-0.106	0.991	0.019	0.110	-0.001	0.467	-0.009	0.561
Pasture	2	-	-	-0.008	0.764	0.031	0.139	-0.004	0.540
Pasture	3	0.014	0.109	0.007	0.200	0.020	0.054	0.035	0.012*
Sedges									
Rosemary	4	0.193	0.003*	0.160	0.002*	-0.033	0.824	-0.020	0.852
Rosemary	5	-	-	-0.046	0.848	-0.029	0.679	0.000	0.452
Rosemary	6	-0.026	1.000	-0.005	0.532	-0.005	0.488	0.009	0.356
Degraded	7	-0.019	0.858	-0.011	0.758	-0.012	0.835	0.004	0.260
Degraded	8	-0.004	0.599	0.021	0.084	-0.007	0.622	0.027	0.052

Degraded	9	-	-	0.039	0.251	-0.045	0.931	-0.044	0.804
Pasture	1	0.029	0.210	0.011	0.222	-0.029	0.679	-0.055	0.998
Pasture	2	-	-	-0.015	0.986	-0.027	0.725	-0.012	0.483
Pasture	3	-0.009	0.842	0.015	0.087	0.008	0.180	0.032	0.007*
Grasses									
Rosemary	4	-0.012	0.675	0.035	0.226	-0.023	0.506	-0.016	0.692
Rosemary	5	-0.035	0.249	0.027	0.295	-0.038	0.673	0.017	0.257
Rosemary	6	-0.034	1.000	-0.037	0.919	-0.038	0.816	0.025	0.255
Degraded	7	0.048	0.127	-0.066	0.904	0.020	0.244	-0.006	0.403
Degraded	8	-0.032	0.539	0.216	0.001*	-0.076	0.906	0.102	0.106
Degraded	9	0.048	0.125	-0.066	0.905	0.020	0.246	-0.006	0.403
Pasture	1	0.126	0.017*	0.020	0.105	-0.038	0.807	0.016	0.243
Pasture	2	0.018	0.235	0.005	0.335	0.013	0.354	0.033	0.202
Pasture	3	-0.048	0.806	0.073	0.101	-0.028	0.639	0.061	0.382

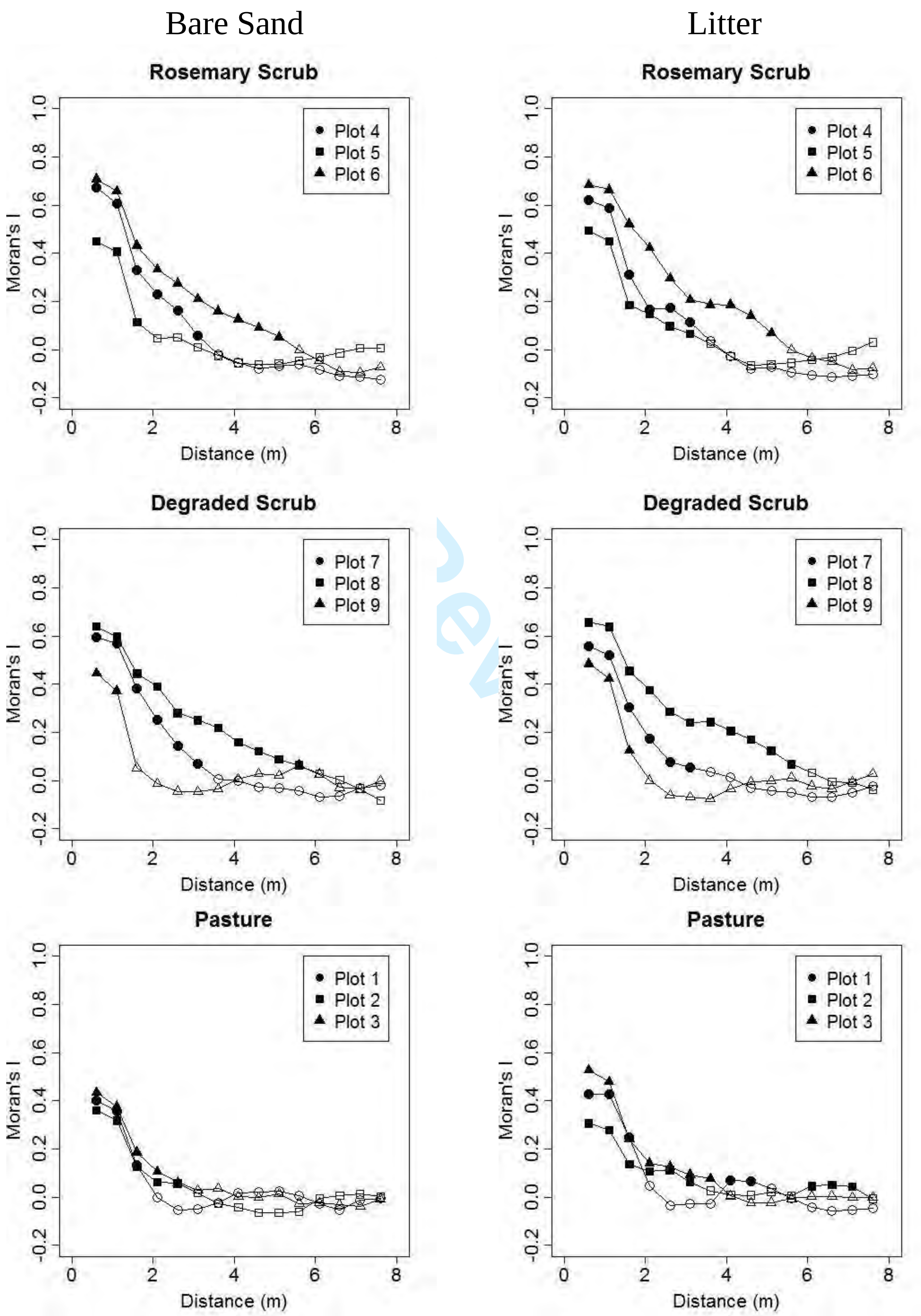

Figure S1. Bare sand (right) and litter (left) - Moran's *I* correlograms of ground cover in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

Lichens

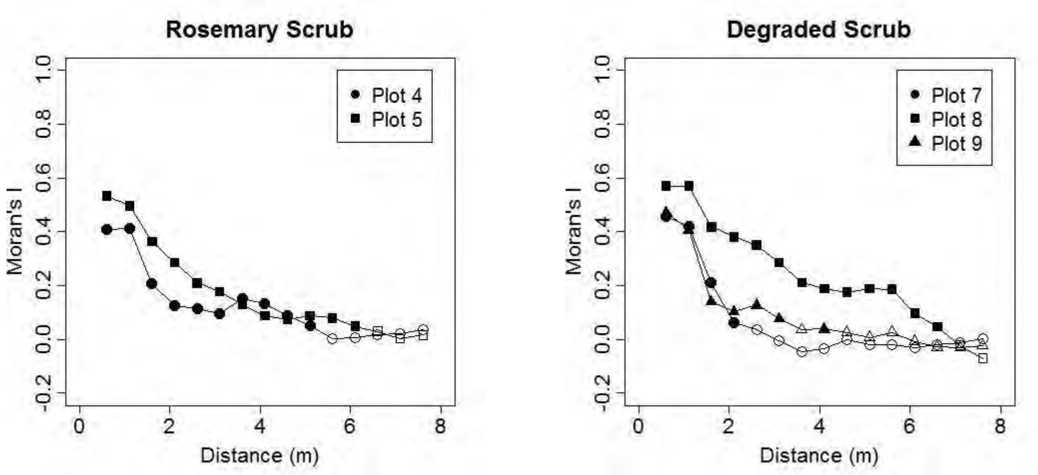

Figure S2. Lichen - Moran's *I* correlograms of vegetation in rosemary scrub and degraded scrub. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

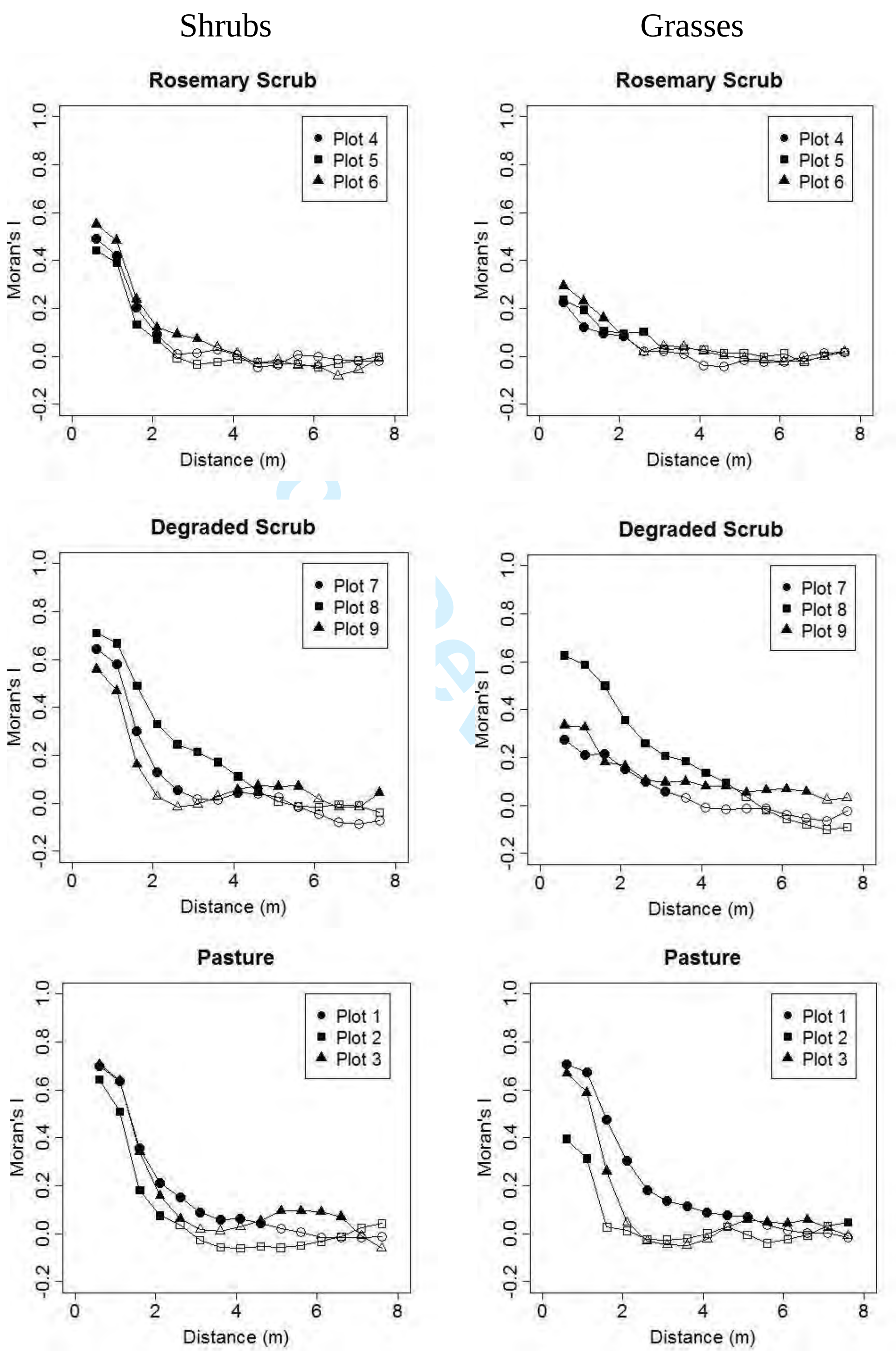

Figure S3. Moran's *I* correlograms of shrubs (left) and grasses (right) between the rosemary and degraded scrub vegetation. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

Palmettos

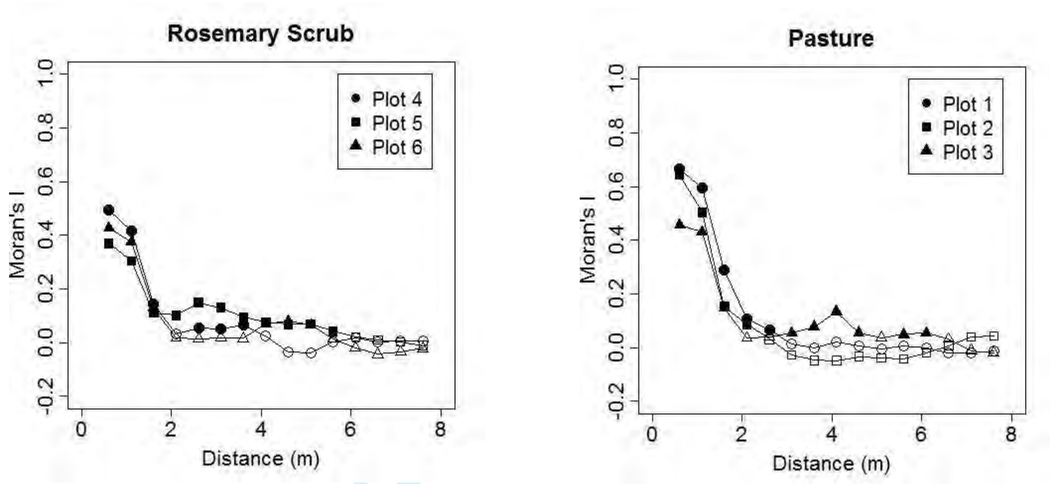

Figure S4. Palmettos (*Sabal etonia*, *Serenoa repens*) - Moran's *I* correlograms of vegetation in rosemary scrub, degraded scrub and pasture. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

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Paronychia chartacea

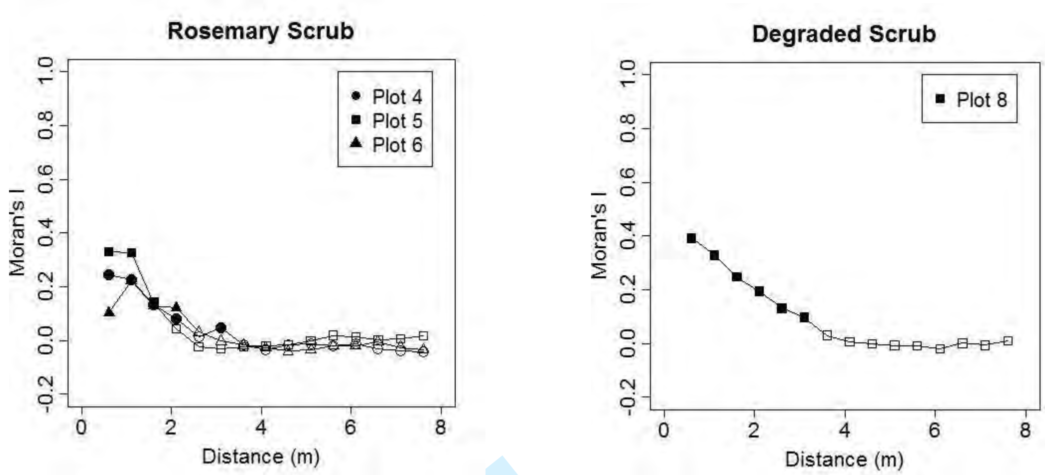


Figure S5. *P. chartacea* - Moran's *I* correlograms of vegetation in rosemary scrub and degraded scrub. Solid symbols = $p < 0.05$; open symbols = $p < 0.05$.

17 Sedges Ruderal Herbs

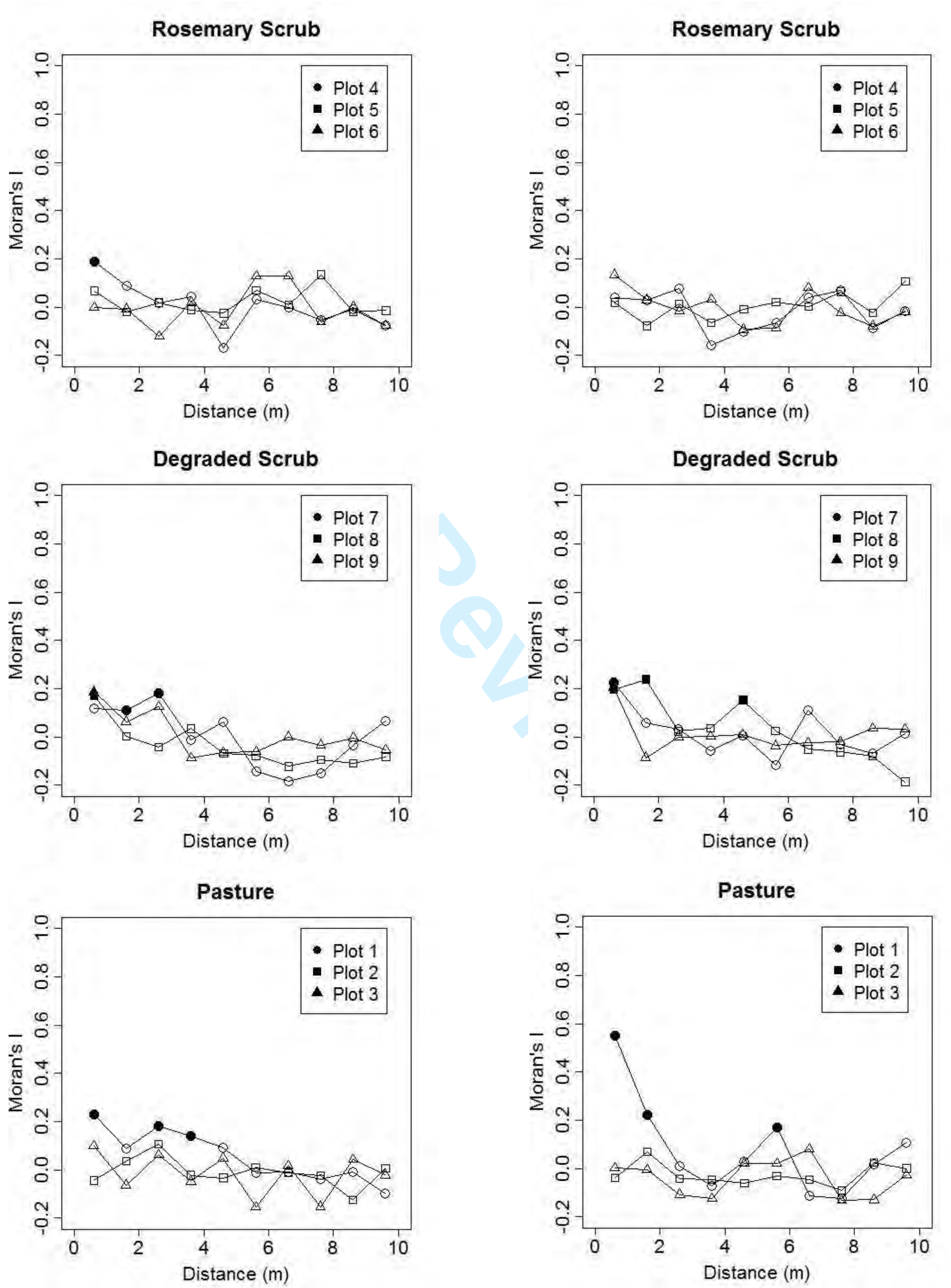
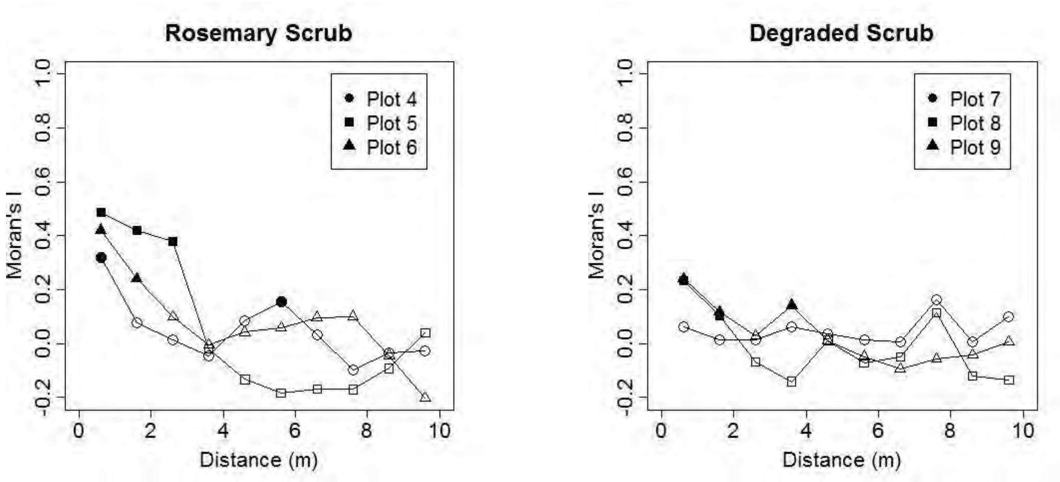


Figure S6. Sedges (left) and ruderal herbs (right) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

Scrub Herbs



Eupatorium capillifolium

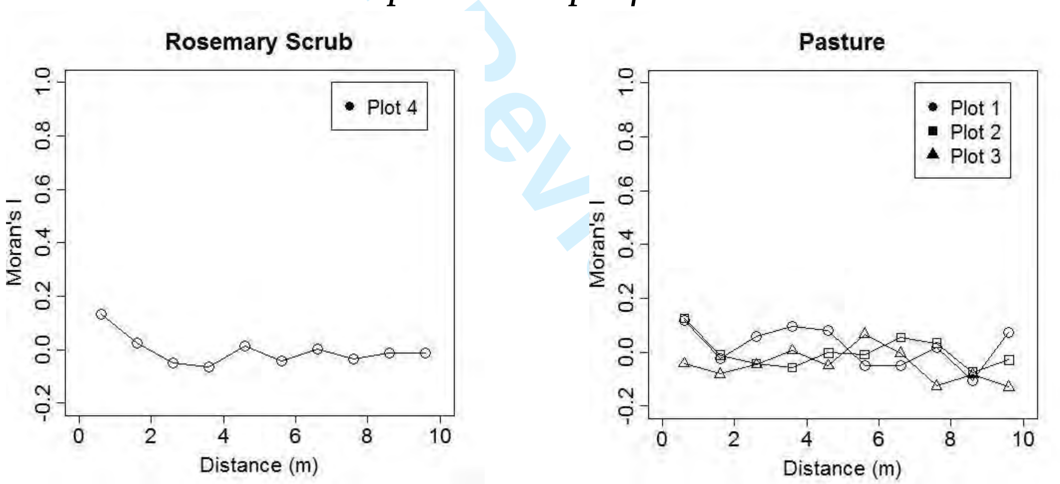


Figure S7. Scrub herbs (top) and *E. capillifolium* (bottom) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

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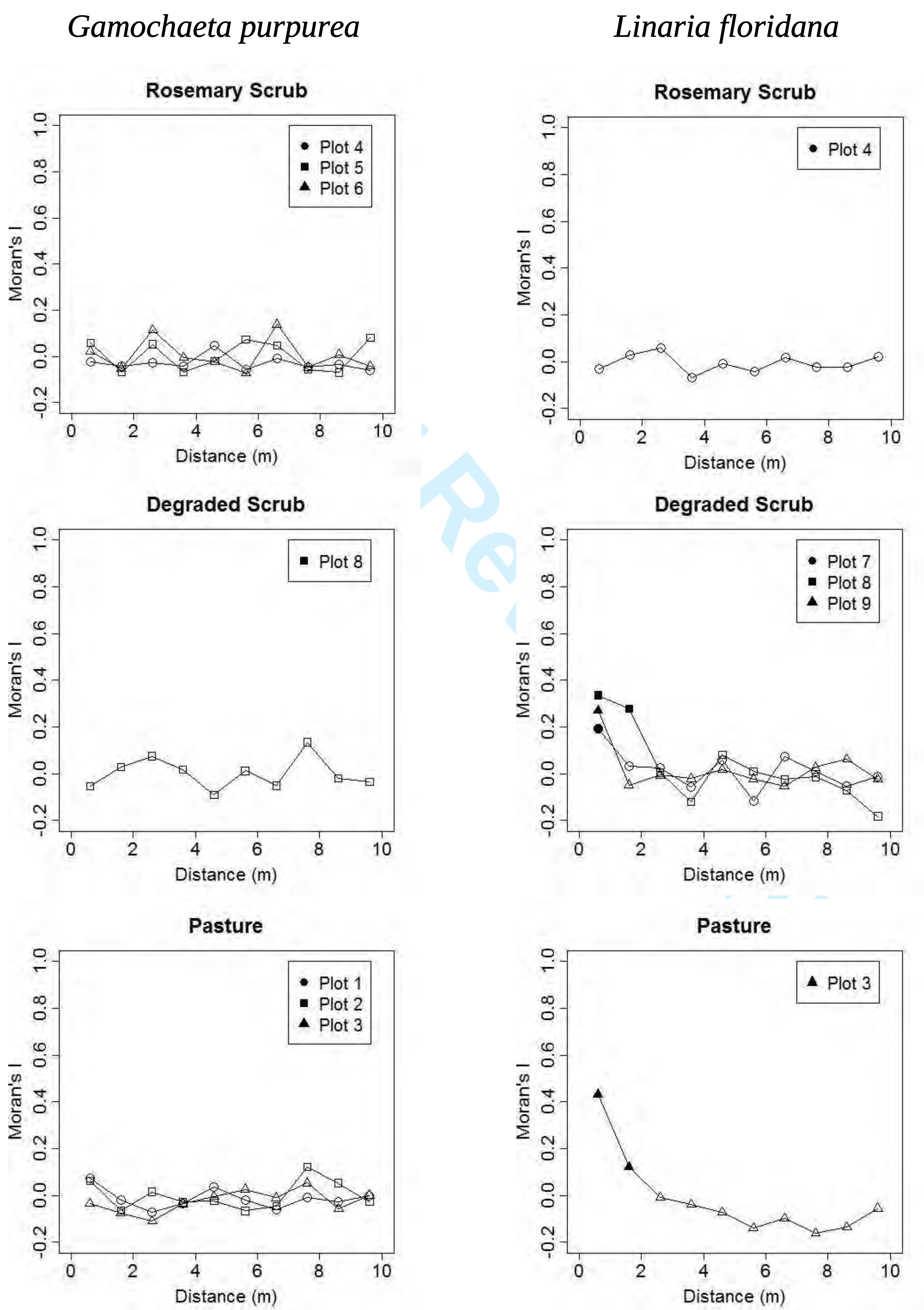

Figure S8. *G. purpurea* (left) and *L. floridana* (right) - Moran's *I* correlograms of seed bank in rosemary scrub, degraded scrub, and pasture. Solid symbols = $p < 0.05$; open symbols = $p > 0.05$.

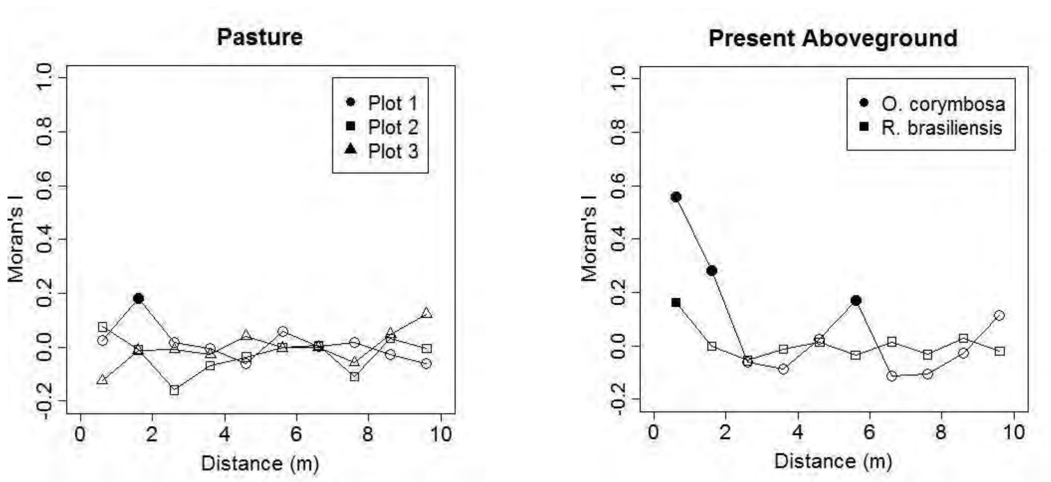

Figure S9. *Scoparia dulcis* (left), *O. corymbosa* and *R. brasiliensis* (right) - Moran's *I* correlograms of seed bank in pasture. Solid symbols = $p < 0.05$; open symbols = $p < 0.05$.