Spatial pattern and composition of the Florida scrub seed bank and vegetation along an anthropogenic disturbance gradient

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Abstract

Question: How does spatial pattern and composition of the seed bank and its relationship to above-ground cover vary across an anthropogenic disturbance gradient of intact Florida rosemary scrub, degraded scrub and improved pasture?

Location: Florida rosemary scrub, Lake Wales Ridge, Highlands County, FL, USA (27° 11′N, 81° 21′W).

Methods: In nine grid plots located in intact Florida rosemary scrub, degraded scrub and improved pasture, we assessed percentage vegetation cover and seed bank composition.

Results: The vegetation was dominated by long-lived perennials, while the seed bank was dominated by short-lived species. Shrubs were the dominant above-ground cover in rosemary scrub, sub-shrubs and the spike moss *Selaginella arenicola* in degraded scrub and non-native grasses in pastures. Scrub forbs were dominant in the seed bank of rosemary scrub, similar amounts of sedges, ruderal forbs and scrub forbs in degraded scrub, and ruderal species and sedges in pastures. Species absent from the vegetation were randomly distributed in the seed bank, while species present above-ground had an aggregated spatial distribution. In rosemary scrub, scrub forb seed banks were spatially aggregated and were positively associated with conspecific species above-ground and with litter cover. These patterns were not observed in degraded scrub, perhaps due to reduced shrub and increased bare ground.

Conclusion: Our results suggest that reduced shrub cover and increased bare ground in the degraded scrub may explain why there is less spatial aggregation of scrub forbs in the seed bank. Restoration of Florida rosemary scrub in pasture sites will require species reintroduction of appropriate scrub species; restoration of degraded scrub should emphasize increasing shrub cover to restore habitat spatial structure.

Introduction

Spatial structure has long been recognized as a major determinant of plant community dynamics (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 co-existence 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. Changes in spatial pattern can modify inter- and intra-specific species interactions, alter 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 degree 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 of disturbance will influence habitat spatial structure. This work evaluates how the structural relationship between the above-ground vegetation and seed bank varies along a disturbance gradient. Understanding how this relationship changes under diverse disturbance regimes may provide insight into community resilience to perturbations, mechanisms driving regeneration and steps necessary for restoration of community composition and structure (Hopfensperger 2007). Recovery from the soil seed bank has long been recognized as important to community processes since it plays a 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).

The spatial distributions of the vegetation and seed bank influence one another. The seed bank contributes to species distributions above-ground by affecting where recruitment will occur (Rusch 1992), and vegetation contributes to seed bank dispersal patterns as a source of seeds and by trapping seeds and preventing further movement (Aguiar & Sala 1997; Bullock & Moy 2004). Alteration of above- and below-ground spatial structure may therefore alter species' above-ground distributions or lead to population decline if seeds are dispersed away from areas suitable for germination.

To determine if structural changes above-ground alter the spatial pattern of the seed bank, we compared the above-ground vegetation and seed banks of two anthropogenically disturbed sites to intact Florida rosemary scrub. One disturbed community contained scrub degraded by mechanical disturbance, but with remnants of the original vegetation still present; the other was a former scrub site converted to pasture and dominated by non-native grasses. The sites differed in land-use history but shared the same topography and soil attributes typical of Florida rosemary scrub. Florida rosemary scrub is a sclerophyllous shrubland found on relic sand dunes throughout central and coastal Florida (Menges 1999). The largest and most ancient of these relic sand dunes, the Lake Wales Ridge, has one of the highest concentrations of endemic species in North America (Dobson et al. 1997), but unfortunately many of these species are threatened or endangered due to an 85% reduction of scrub habitat from commercial, agricultural and residential development (Weekley et al. 2008). In recent years, an economic shift away from agriculture in Florida has resulted in the abandonment of agricultural lands, thus providing an opportunity to restore areas now on private or publicly owned conservation land.

To derive steps that should be taken to restore species composition and habitat spatial structure in degraded scrub and pasture sites we addressed the following questions: (1) what is the species composition of the vegetation and seed bank and how does it differ among the three sites; (2) what is the spatial distribution (i.e. random, aggregated or uniform) of the seed bank and does it differ across the disturbance gradient; and (3) how does the spatial distribution of the seed bank relate to above-ground vegetation and microhabitat cover (bare ground, litter and shrub cover)? We predicted that increased anthropogenic disturbance would result in reduced spatial aggregation in the seed bank and loss of the structural association between the seed bank and above-ground cover.

Methods

Study site

This research was conducted at Archbold Biological Station (ABS) and the adjacent Archbold Reserve (Reserve). ABS is located near the southern end of the Lake Wales Ridge in Highlands County, central Florida (27° 11′N, 81° 21′ W). The region experiences temperatures ranging from a mean of 8.33 °C in the winter to 34.05 °C in the summer, and receives an average annual rainfall of 1364 mm (ABS weather data, 1932–2009). ABS comprises a matrix of xeric uplands (southern ridge sandhills, sand pine scrub, rosemary scrub, scrubby flatwoods), mesic flatwoods and seasonal wetlands (Abrahamson et al. 1984). The Archbold Reserve, purchased by ABS in 2002, includes degraded scrub and agriculturally improved pasture. One of the management objectives of ABS is to restore scrub habitat in degraded areas of the Reserve.

Intact Florida rosemary scrub sites (plots 4–6) were subjected to natural fires and controlled burns (plots 4 and 6 = 10 yr since fire, plot 5 = long-unburned) and are 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 (Hunter & Menges 2002), but also includes patches of shrub species such as palmettos (*Serenoa repens*, *Sabal etonia*) and clonal oaks (*Quercus chapmanii*, *Quercus inopina*, *Quercus geminata*) (Menges et al. 2008). Florida rosemary scrub is a fire-maintained ecosystem with a fire return interval of 15–25 yr (Menges 2007). After fire, most shrub species resprout from rhizomes or roots (Menges & Kohfeldt 1995). Florida rosemary (*C. ericoides*) and many herbaceous species recruit from the soil seed bank (Menges & Hawkes 1998). Many forbs endemic to rosemary scrub are 'gap specialists' (e.g. *Hypericum cumulicola*, *Paronychia chartacea* ssp. *chartacea*) and have the greatest abundance, survival and seed production in the years immediately following fire (Hawkes & Menges 1996;

Menges & Kimmich 1996; Menges 1999). As time-since-fire increases, herbaceous species abundance declines as gaps close, with increased shrub, litter and lichen cover (Menges & Hawkes 1998).

Degraded scrub sites (plots 7–9) were mechanically cleared in the early 1970s (plot 8) and early 1980s (plots 7 and 9) and were disturbed via roller chopper. Vegetation structure (tall overgrown shrub patches) and reports from previous landowners indicated that these sites were long-unburned. These areas were also lightly grazed with cattle present onsite until 2002. Species composition of degraded and rosemary scrub are similar; however, relative species abundance and distribution of some species differ between the two sites. Bare ground cover is higher in the degraded scrub, while shrub cover is reduced and average shrub height is greater than intact scrub (Menges & Rickey 2005).

Improved pasture sites (plots 1–3) were cleared and seeded with non-native forage grasses in the 1970s. These sites were heavily grazed in the 12-yr period from 1990 to 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 persist (*S. etonia*, *Sideroxylon tenax*, *Asimina obovata*).

Site selection

We evaluated the vegetation and seed bank in replicated sites ($n = 3$, total nine sites) of three areas that differed in disturbance history but shared similar topography and soil attributes typical of rosemary scrub. We selected degraded scrub and pasture sampling locations based on soil and elevation attributes. Rosemary scrub patches occur on 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.

Above-ground cover sampling

Between May and Jul 2007, we established nine 16 m × 16 m macroplots, i.e. three replicates of each community. We sub-divided each macroplot into 2 m × 2 m subplots and each subplot into 40 cm × 40 cm quadrats. We sampled above-ground cover in a checkerboard pattern, collecting data from every other 2 m × 2 m subplot (32 per macroplot) and every other 40 cm × 40 cm quadrat (13 per subplot, 416 sample units per macroplot) within each of the selected subplots. Within each quadrat, we made ocular estimations of percentage cover to the nearest 10% (<10% = trace amount). We assigned cover to the

following structural components: ground cover (bare ground, litter, lichens), herb layer (ruderal forbs, scrub forbs, graminoids, spike moss), subshrub layer (woody species < 0.5 m), shrub layer (woody species 0.5—3.0 m) and subcanopy (>3 m). We also assessed percentage cover for each species of vascular plant and ground lichen.

Seed bank sampling

In Jan 2009 we collected soil samples from the nine macroplots; randomly selecting a subset of ten subplots within each macroplot previously sampled for above-ground cover. We collected and aggregated five 1.92-cm diameter by 3-cm deep soil cores from each quadrat (130 subsamples per macroplot; 1170 samples in total). We collected the soil cores in a regular pattern within each quadrat.

We used the seedling emergence method to determine species composition of the soil seed bank (Roberts 1981). We sieved each soil sample to break up soil structure and large litter and potted the soil (including litter, ~0.5 cm in depth) on top of a white sand substrate collected from fire lanes at ABS. All sand used as substrate was heated to 85 °C for a minimum of 8 h to kill any seeds that may have been present. We placed the potted soil samples into shade houses (covered on all sides to reduce contamination by exogenous seeds) located on the University of Central Florida campus (120 miles NE of the study site) 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 ensure all seeds in the substrate 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 were identified to species level. We monitored the soil samples for seedling emergence for 9 mo. Germination rates reached a plateau before we discontinued germination monitoring. For the analysis, we identified the following functional groups based upon growth habit and habitat preference: (1) sedges (2) ruderal forbs (typical of disturbed habitats, generally not found growing above-ground in Florida scrub) and (3) scrub forbs (Menges & Kohfeldt 1995).

Data analysis

We used permutational multivariate analysis of variance (Permanova) to test for differences in species composition of the vegetation and seed bank among the three sites. Significance was assessed using F-tests developed from sequential sum of squares permutations (10,000

permutations) of the raw data (Anderson 2001). The significance level was adjusted to $\alpha \leq 0.017$ after Bonferroni correction (Roberts 1981). All analyses were conducted in R 2.9.1 (R Development Core Team 2009, Vienna, Austria).

We used Moran's I spatial autocorrelation to evaluate spatial pattern within the soil seed bank. When neighbours at different focal distances are more similar or dissimilar than would be expected at random, the spatial pattern is autocorrelated (Sokal & Oden 1979). The value for the Moran's I index ranges between -1 and 1, where a value near 0 indicates a random spatial pattern, a positive value indicates aggregated distribution, and a negative value indicates over-dispersion. We assessed the significance of the Moran's I value at each distance class (60–1060 cm, 11 classes, increasing by 100 cm) on $\log + 1$ transformed data (Fortin & Dale 2005) using a Monte Carlo randomization test (Legendre & Legendre 1998) with 10,000 permutations. Significance levels were corrected using progressive Bonferroni (Legendre & Legendre 1998). We conducted the analyses at the species and functional group level. Controlling for spatial co-ordinates, we used partial Mantel tests to evaluate the spatial relationship of the seed bank with conspecific above-ground plants and microhabitat cover (bare ground, litter, shrub cover) (Legendre & Fortin 1989; McCune & Grace 2002). The significance of the correlation was assessed with Monte Carlo randomization tests (10,000 permutations).

Results
Species composition

Vegetation and ground cover

Overall, the vegetation included 66 vascular plants and five terrestrial lichens (Appendix S1). The pastures had 35 species, degraded scrub 56 and rosemary scrub 49. The vegetation was dominated by long-lived perennials across all sites; however, the dominant functional groups varied by community (Fig. 1). Between the rosemary and degraded scrub, species identity was roughly equivalent; however, species abundances were substantially altered. Shrubs were the dominant vegetation cover in rosemary scrub, and low-growing subshrubs (*Licania michauxii* and *Polygonella robusta*) and a spike moss (*Selaginella arenicola*) were the dominant cover in the degraded scrub. Mean bare ground cover was higher and mean litter cover lower in the degraded scrub than the rosemary scrub. In the pastures, non-native forage grasses (*Cynodon dactylon*, *Digitaria eriantha*, *Paspalum notatum*) were the dominant cover, and only a few native scrub species persisted in the vegetation (*Opuntia humifusa*, *Sabal etonia*, *Sideroxylon tenax*, *Smilax arenicola*), likely due to their ability to evade herbivory. Bare ground cover was considerably lower in the pastures than degraded and rosemary scrub (Fig. 1). Permanova
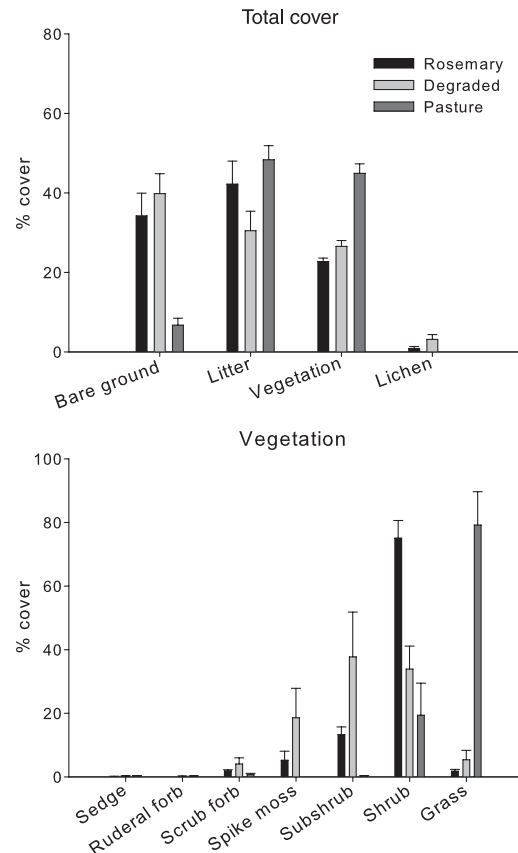

Fig. 1. Mean percentage total ground cover (± standard error) of litter, bare ground, lichens and vegetation (top), and percentage of the vegetation cover comprised by each functional group (bottom). Estimated from samples collected from Archbold Biological Station and the Archbold Reserve in 2007.

results revealed significantly different species composition among all three sites and for all pair-wise comparisons (Table 1a).

Table 1. Permanova results for the comparison of species composition of the vegetation and seed bank among intact rosemary scrub, degraded scrub and agriculturally improved pasture. Samples were collected at Archbold Biological Station and the Archbold Reserve in 2007 (vegetation) and 2009 (seed bank).

	P	df	F-ratio
a. Vegetation			
Rosemary, degraded & pasture	0.002*	2	3.37
Rosemary vs degraded	0.001*	1	1.77
Rosemary vs pasture	0.001*	1	4.37
Degraded vs pasture	0.001*	1	3.96
b. Seed bank			
Rosemary, degraded & pasture	0.002*	2	4.57
Rosemary vs degraded	0.0001*	1	3.60
Rosemary vs pasture	0.0001*	1	5.77
Degraded vs pasture	0.064	1	3.78

*$P \leq 0.017$.

Seed bank

Germination trials of seed bank soil samples yielded 3424 seedlings belonging to 46 plant species (Appendix S1). Rosemary scrub had 27 species (720 seedlings, 21%), degraded scrub 26 (801 seedlings, 23%), and pasture 38 (1903 seedlings, 56%). The seed banks in all three sites were dominated by short-lived herbaceous species; while long-lived species such as shrubs were absent and sub-shrub and grass species exhibited low species richness and seed density. Rosemary scrub was largely dominated by scrub forbs, which comprised ~70% of the emerging seedlings (Fig. 2). Two scrub forbs, *Paronychia chartacea* ssp. *chartacea* (25%) and *Stipulicida setacea* (38%), were almost exclusively responsible for this pattern; however, *Hypericum cumulicola* had equivalent representation in sites where it was present above-ground. Degraded scrub had more or less equal percentages of scrub forbs (32%), ruderal forbs (24%) and sedges (26%) (Fig. 2). At these sites, scrub forb densities in the seed bank were lower than in rosemary scrub. Pastures were dominated by ruderal forbs and sedges, which comprised ~66% of the emerging seedlings (Fig. 2). Seedling emergence (used to approximate seed bank size) was generally equivalent among the sites; however, a prolific seeding forb in one pasture plot (*Oldenlandia corymbosa* in plot 1) led to a near doubling of average seed density of the pastures when compared to the two scrub communities. Permanova results revealed significantly different species composition among the three communities (Table 1b). Pair-wise comparisons of rosemary scrub with degraded scrub and pasture were significantly different, but comparison of degraded scrub and pasture sites were not significantly different (Table 1b).
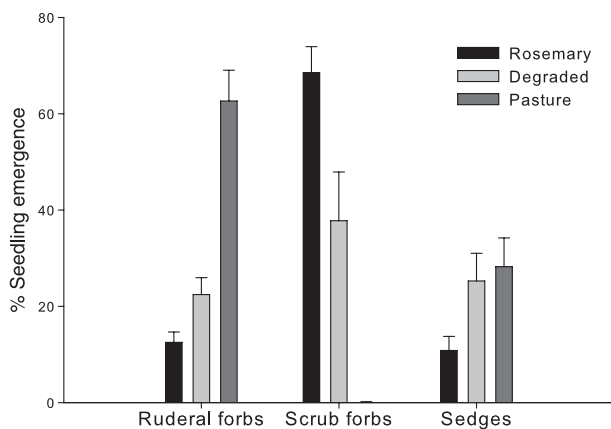

Fig. 2. Mean percentage seedling emergence (± standard error) organized by functional group. Values were estimated from samples collected from Archbold Biological Station and the Archbold Reserve in 2009.

Spatial structure within seed bank

In general, seeds of species absent from the above-ground vegetation showed a random spatial distribution within the seed bank soil samples, while seeds of species present above-ground tended to be spatially aggregated. Seeds of sedges generally showed a random distribution or were aggregated in small patches. Seeds of ruderal forbs had random distributions, but showed aggregation if the species were present above-ground (Fig. 3). Seeds of scrub forbs generally showed a stronger pattern of aggregation in rosemary than in degraded scrub (occurrence was not high enough to analyse spatial structure in pastures) (Fig. 4).

At the species level, seeds of *P. chartacea* ssp. *chartacea*, *S. setacea* and *H. cumulicola* (all scrub forbs) were generally aggregated in small patches in rosemary scrub and randomly distributed in degraded scrub (Fig. 5). We found a random distribution across all plots for wind-dispersed ruderal forbs never recorded above-ground (*Eupatorium capillifolium, Gamochaeta purpurea* and *Scoparia dulcis*). Most other species lacked seed structures that promote wind dispersal and are likely dispersed by gravity and/or animals. Seeds of *Linaria floridana, O. corymbosa* and *Richardia brasiliensis* exhibited an aggregated distribution at sites where they were present above-ground.

Spatial relationship above- and below-ground

When considering all species present above-ground and in the seed bank, plots with high shrub cover (rosemary plot 5 and pasture plot 1) exhibited a slight but significant positive spatial correlation between the vegetation and the seed bank. A positive relationship between percentage shrub cover and Mantel *r*-values suggests shrub cover may be an important determinant of structural association above- and below-ground ($P = 0.014$, adj $R^2 = 0.5$, *F*-stat = 10.5; Fig. 6).

The seed banks of some species and functional groups were correlated with above-ground microhabitats (bare ground, litter and shrub cover) and with the occurrence of the same species above-ground (Table 2). The seed banks of scrub forbs were positively associated with above-ground 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 above-ground microhabitats. Ruderal forbs typically had the highest amount of correlation with microhabitats in degraded scrub, and associations were found with conspecific above-ground plants, bare ground and shrub cover (Table 2). At the species level, there was a greater tendency for the seed banks of scrub forb
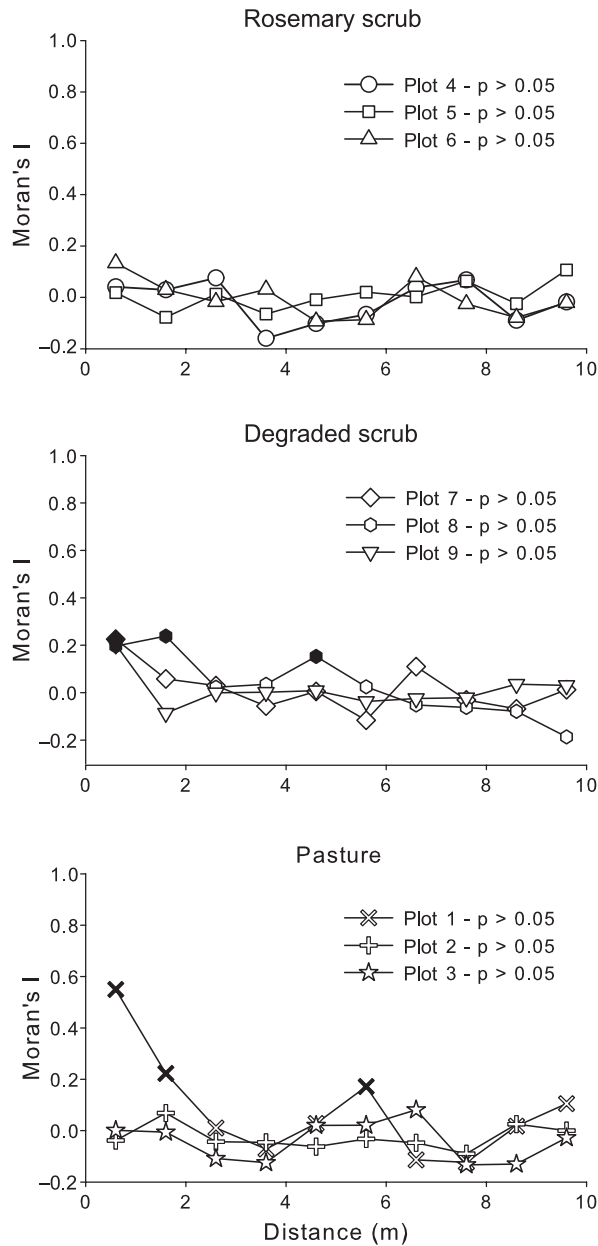
Fig. 3. Moran's *I* correlograms of ruderal forb seed banks in rosemary and degraded scrub calculated from samples collected from Archbold Biological Station and the Archbold Reserve in 2009. Significant Moran *I* values (solid symbols) between 0 and 1 indicate an aggregated spatial pattern; non-significant values (open symbols) indicate a random spatial pattern.

Fig. 4. Moran's *I* correlograms of scrub forb seed banks in the rosemary and degraded scrub calculated from samples collected from Archbold Biological Station and the Archbold Reserve in 2009 (occurrence was not high enough to analyse spatial structure in pastures). Significant Moran *I* values (solid symbols) between 0 and 1 indicate an aggregated spatial pattern; non-significant values (open symbols) indicate a random spatial pattern.

Discussion

The spatial distribution of the seed bank and its association with above-ground cover varied across the disturbance gradient. Spatial pattern 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 above-ground. The greatest differences in seed bank spatial structure were observed for scrub forbs in rosemary vs degraded scrub. Our results indicated a greater tendency for the seed banks of scrub forbs in rosemary scrub to exhibit higher seed densities, have an aggregated distribution, and to be associated with above-ground vegetation/microhabitat cover (presence of species above-ground, litter cover and shrub cover). Canopy structure, above-ground species composition and distribution, and microhabitat cover are known to influence seed bank spatial pattern (Olano et al. 2002). In rosemary scrub forbs, seeds tended to cluster around mother plants but were also dispersed away from plants and were potentially trapped in litter

species (*H. cumulicola, P. chartacea, S. setacea*) to be positively associated with occurrence of conspecific species above-ground and litter cover in rosemary scrub than in degraded scrub. Seed banks of ruderal species (*L. floridana* and *O. corymbosa*) showed a positive correlation with shrub cover in the degraded scrub and pasture (Table 2).
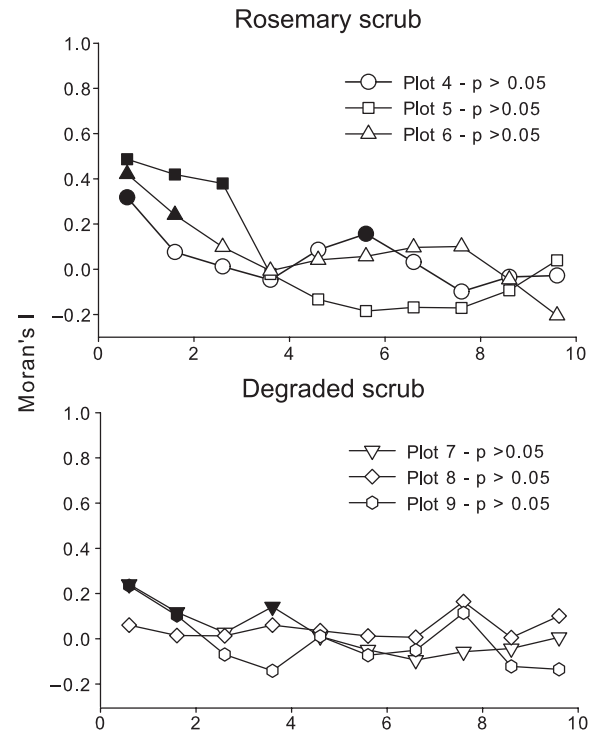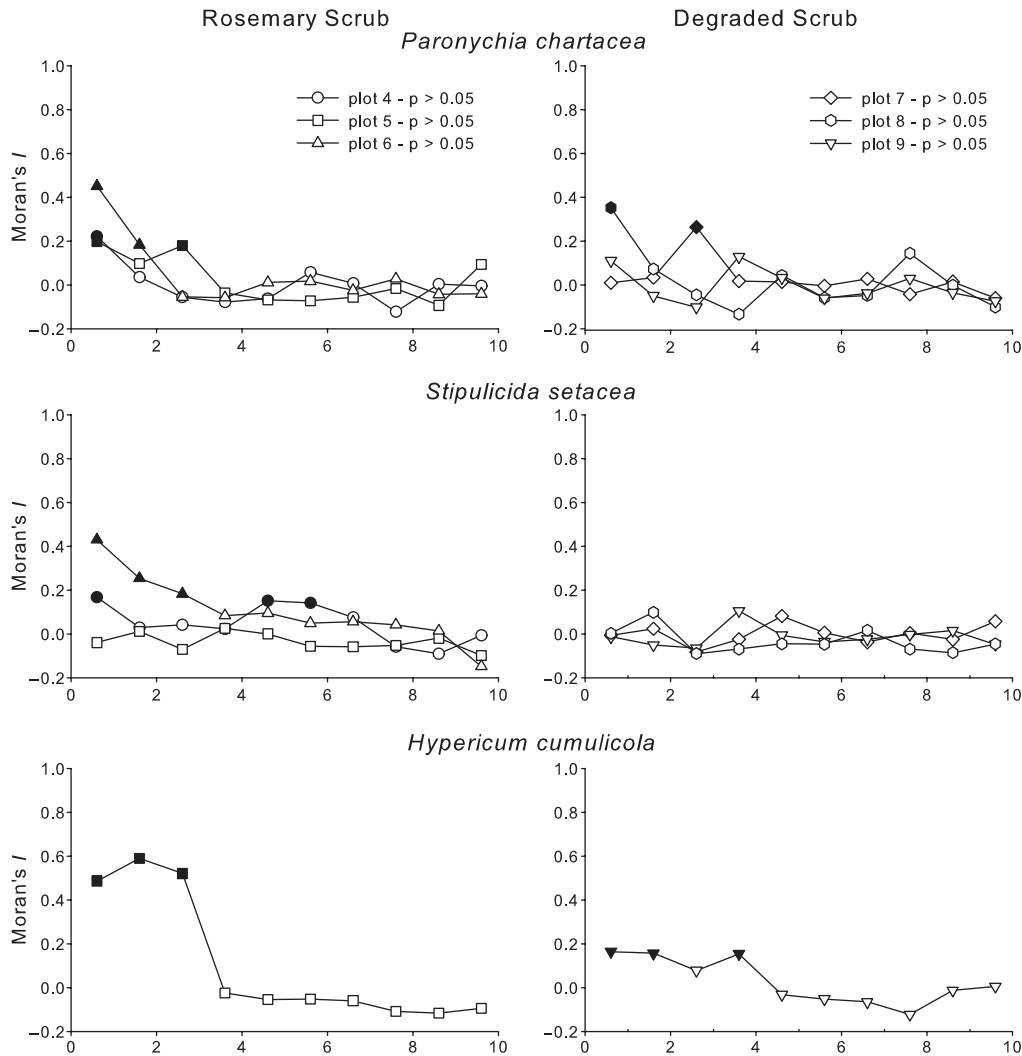
Fig. 5. Moran's *I* correlograms of *Paronychia chartacea* (top), *Stipulicida setacea* (middle) and *Hypericum cumulicola* (bottom) seed banks in rosemary (left) and degraded scrub (right) calculated from samples collected from Archbold Biological Station and the Archbold Reserve in 2009. Significant Moran *I* values (solid symbols) between 0 and 1 indicate an aggregated spatial pattern; non-significant values (open symbols) indicate a random spatial pattern.

patches. In similar arid systems with high bare ground cover and patchy vegetation distribution, seeds aggregate beneath shrub and litter patches due to their restriction of lateral seed movement and due to the contrasting inability of bare ground to retain seeds (Aguiar & Sala 1997; Bullock & Moy 2004; Caballero et al. 2008). Reduced shrub cover and increased bare ground in the degraded scrub may explain why there is less spatial aggregation of scrub forbs in the seed bank. Larger gap sizes with uniform spatial distribution are known to increase dispersal distances (Bergelson et al. 1993).

A change from an aggregated to a random spatial distribution of the seed banks for scrub forbs that inhabit open sand gaps in rosemary scrub may have ecological consequences. 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. A change from an aggregated to a homogeneous distribution may influence the genetic structure of the population, modify seed and pollen distributions, alter plant interactions with pollinators, or change inter- and intra-specific species interactions (Levin & Kerester 1975; Hassell & Wilson 1997; Lehman & Tilman 1997; Menges 2007).

The two main predictors of seed bank spatial structure in our study were presence of the species above-ground and amount of shrub cover. Species absent from the above-ground vegetation, such as wind-dispersed ruderal species, showed a random distribution (e.g. *Eupatorium capillifolium*, *Gamochaeta purpurea*, *Scoparia dulcis*) across all
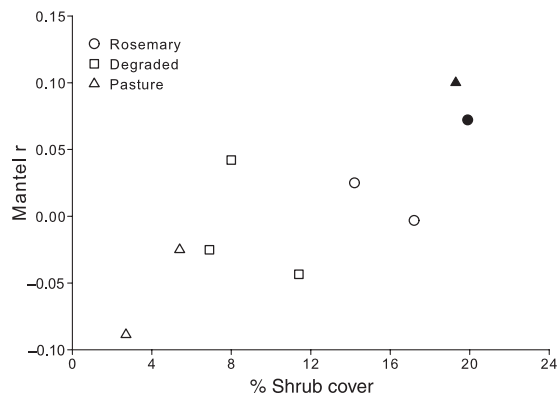
Fig. 6. Partial Mantel *r*-values for the comparison of vegetation vs the seed bank plotted against percentage shrub cover of each plot. Calculations were made from samples collected from Archbold Biological Station in 2007 (vegetation) and 2009 (seed bank). Solid symbols indicate $P \leq 0.05$.

sites, and species present above-ground were spatially aggregated at short distances. Amount of shrub cover may be an important factor influencing structural correlation between the vegetation and seed bank since the two sites with the highest shrub cover, one rosemary and a pasture site, were the only sites with a positive spatial correlation between above- and below-ground. While shrub cover may be driving this spatial correlation, the interaction between shrubs and herbs was different between the two sites. In the pasture seed banks, species present above-ground (e.g. *Linaria floridana*, *Oldenlandia corymbosa*) were correlated with above-ground plants and shrub cover. For-bs and sedges were generally only found growing beneath shrubs; thus these species appear to be facilitated by the presence of shrubs in the pastures, possibly because shrubs excluded grasses from growing directly beneath them. The competitive advantage of shrubs over grasses has been found in other systems (McPherson & Wright 1990; Köchy

Table 2. Partial Mantel test results of correlation of above-ground microhabitats vs the seed bank of various species and functional groups. Samples were collected at Archbold Biological Station and the Archbold Reserve in 2007 (vegetation) and 2009 (seed bank).

| Mantel *r* | | | | | | | | | |
Habitat	Plot	Veg	*P*	BS	*P*	Litter	*P*	Shrub	*P*
Scrub forbs									
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

Veg = occurrence of same species above-ground; BS = bare ground.

*$P \leq 0.05$.

& Wilson 2000; Lett & Knapp 2003). In scrub, the interaction between shrubs and forbs is competitive; herbaceous species decline in abundance as shrub cover increases (Menges & Hawkes 1998).

The results of this study highlight the need to take spatial structure into account when restoring anthropogenically disturbed systems. In addition to reintroducing species absent from the disturbed community, a greater challenge is presented in determining how to restore native spatial structure and species abundances in degraded habitats. Similar to other systems with high bare ground cover and patchy vegetation distributions, shrub cover appears to influence dispersal patterns of rosemary scrub species present in the seed bank. Restoration of rosemary scrub habitat in the pasture sites will require reintroduction of scrub species, since the majority of these species were absent from the vegetation and seed bank. Restoration in the degraded scrub should focus on reinstating native spatial structure and species abundances; this may be achieved by increasing shrub cover. At both sites care should be taken to restore the patchy spatial dynamics found in rosemary scrub.

Acknowledgements

References

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Mean vegetation percent cover (±standard error) and mean seed bank density (m^{-2}) in rosemary scrub, degraded scrub, and pasture. Estimates were made from samples collected from Archbold Biological Station in 2007 (vegetation) and 2009 (seed bank).

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