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Dispersal Ecology of Desert Mosses Along Gradients of Elevation, Wildfire Disturbance and Local Niche

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DISPERSAL ECOLOGY OF DESERT MOSSES ALONG GRADIENTS OF ELEVATION, WILDFIRE DISTURBANCE AND LOCAL NICHE

by

Robert Joseph Smith

Bachelor of Science in Botany and Plant Pathology
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A thesis submitted in partial fulfillment
of the requirements for the

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Robert Joseph Smith

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ABSTRACT

Dispersal Ecology of Desert Mosses Along Gradients of Elevation, Wildfire Disturbance and Local Niche

by

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Much of the variation in plant communities can be explained by the dispersal of individuals across landscapes, an ecological process that contributes to clinal variation, post-disturbance recovery and habitat occupancy. The role of dispersal is of particular concern for Mojave Desert plant communities that may not be able to tolerate recent departures from historical fire regimes. The aim of this thesis was to infer how dispersal is reflected by patterns of diversity in disturbed and undisturbed bryophyte communities in the Spring Mountains of southern Nevada. Chapter 2 presents an examination of sub-surface bryophyte communities (propagule "soil-banks") along a 1400 m elevational gradient spanning three major vegetation zones. Compositional changes and three measures of diversity were positively associated with elevation and climatic moisture, a pattern consistent with increasing spore deposition in proximity to fecund, high-elevation source populations. Chapter 3 is an assessment of the roles of dispersal in time and in space as bryophyte communities recover from wildfires at Red Rock Canyon. Sub-surface soil-banks harbored greater diversity than either the spore rain or existing surface communities, although the reduced diversity associated with recent and severe wildfires implied that recovery could be negatively impacted if changing fire regimes inhibit soil-bank replenishment. Finally, Chapter 4 considers habitat limitation versus dispersal limitation as possible constraints on local-scale bryophyte diversity in a single undisturbed community at Red Rock Canyon. Variation in species composition was a nearly equal balance of purely spatial influences (dispersal) and of spatially structured habitats afforded by the arrangement of perennial shrubs. Collectively, this thesis demonstrates that the movement of individuals across landscapes promotes variation in non-vascular plant communities along ecological gradients in the Mojave Desert. Appreciation of the mechanisms that structure diversity can be a starting point for conscientious land use policies and practices, including those that impact both individual disturbances and entire disturbance regimes.

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No work is conducted in a vacuum without the advice and support of friends. Among them, I thank Mandy Slate for her devotion to all things bryo and for help collecting soils along the elevation gradient. Anna James gave perspective not only to ecological matters, but more broadly to their place in the real world. I am grateful to Rick McNeill, who got me seriously started on the path to botany in the first place. Most especially, I thank Sarah Jacobs for her continuous support, for deep and meaningful conversations, and for going to grab the .45 when the cougar yowled in the Rubies. The support of this community of colleagues and friends was a tremendous asset.

PREFACE

> *The ethics of reverence for life makes no distinction between higher and lower, more precious and less precious lives. It has good reasons for this omission.*
>
> – Albert Schweitzer (1965)

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CHAPTER 1

INTRODUCTION

Plant communities contain a wealth of complex information conveyed by the species compositions, abundances and spatial distributions of individuals at given localities. Even in communities that possess very few species, diversity is a rich expression of taxonomic, phylogenetic, functional and spatial complexity. Such complexity is the joint result of historical arrivals from regional species pools and the capacity of individuals to tolerate local conditions once they arrive. Thus, information about diversity has the capacity to explain not only how communities were formed in the past, but also how they persist in their current configurations.

Topography, climate and disturbances provide a mosaic of environments over which plant communities continually shift and reorganize (Tansley 1939), and nowhere is this illustrated more clearly than in the Mojave Desert of the southwestern United States. Arguably the most important components of desert plant communities are bryophytes, non-vascular plants including mosses and liverworts. Perhaps no other form of plant life is as elegantly suited to live in the Mojave Desert as are bryophytes. World-record tolerance of heat stress (Stark et al. 2009) and the capacity to withstand the complete lack of all intracellular water (Proctor et al. 2007) are features by which bryophytes actively metabolize and reproduce when conditions are favorable, permitting them to successfully endure the demanding abiotic conditions of the Mojave Desert. Bryophytes are highly desirable constituents of biotic soil crusts because they provide a host of ecosystem functions, which are generally not redundant: as individual bryophyte species are lost, desert soils become increasingly prone to altered nutrient regimes, higher soil temperatures, lower soil moisture and the negative effects of weathering and erosion (Bowker et al. 2010). These small plants also colonize barren sites which are uninhabitable for even the most robust vascular plants (Fig. 1.1), and they frequently influence germination and succession (Cornelissen et al. 2007). Serious attention to the mechanisms that structure bryophyte diversity and functioning will be crucial for conserving the wealth of ecosystem functions provided by biotic soil crust plants in the Mojave Desert.

Simple and classical biogeographical concepts related to source-sink dynamics and dispersal among insular populations (MacArthur and Wilson 1967) can explain much of the variation among plant communities arrayed across Mojave Desert landscapes. For example, the “sky islands” archetype proposed by Heald (1967) is consistent with patterns of community differentiation among desert mountain ranges, as well as the vertical zonation of vegetation observed along elevational gradients within ranges. Patterns of vertical zonation and positive diversity–elevation trends are particularly evident among desert bryophytes as the result of differential reproduction along elevational gradients (Stark and Castetter 1987). Following successful reproduction (Fig. 1.2), some propagules immediately germinate, but many others are lofted into the air as part of the aerial “spore rain”, while still others are incorporated into soil propagule banks (hereafter “soil-banks”). Dormant propagules (and vegetative tissues) accumulated in soils are a form of “dispersal in time” similar to that observed for many vascular plants in the southwestern U.S. (Venable and Lawlor 1980). Despite our knowledge of bryophyte dispersal in time, it is currently unknown whether elevational trends observed in surface communities are also evident in corresponding soil-banks. Determining how soil-bank diversity covaries with elevation is the objective of the second section of this thesis entitled “Cryptic Diversity in Bryophyte Soil-banks Along a Desert Elevational Gradient”.

The movement of individuals across landscapes provides linkages among local communities that promote colonization after disturbance events like wildfires. Bryophytes are among the first plants to colonize fire-disturbed areas in dry regions (Hilty et al. 2004), presumably as a consequence of allochthonous spore rain (Southorn 1976), although propagules and vegetative plant parts may also survive fires in soil-banks (Puche and Gimeno 2000) or in small-scale refugia above ground (Hylander and Johnson 2010). Despite the possibility that individuals occasionally escape disturbances, entire communities may not be quite as tolerant of major changes to historical fire regimes. Intensifying human activities in southwestern U.S. deserts are currently promoting fire regimes unlike any in recorded history. Fires are rapidly increasing in frequency, extent and severity (Abella 2010), and are linked to declining bryophyte abundances in the region (Johansen 2001). This is particularly worrisome given that post-fire recovery of desert bryophytes takes much longer than that of other soil organisms (Johansen et al. 1984). Because fires can completely sterilize upper soil layers (Schimmel and Granström 1996) where most bryophyte propagules reside (Lewis-Smith 1993), intensifying fire regimes could also impair post-fire recovery from soil-banks if rates of attrition exceed corresponding inputs to the soil. Understanding how bryophyte dispersal (in time and in space) interacts with the age and severity of wildfires is the objective of the third section of this thesis entitled "Post-Fire Recovery of Desert Mosses: Effects of Fires and Dispersal in Time and Space".

In the face of changing disturbance regimes which threaten bryophytes, resource managers require knowledge of how bryophytes are limited at the local level, both by the availability of suitable habitat (habitat limitation) and by the ability of individuals to disperse among localities (dispersal limitation). Understanding these ecological filters reveals much about the processes that generate realized communities (Keddy 1992) and can help guide management efforts. Prior to conservation work, managers must accurately determine the degree to which habitat or dispersal limitations influence communities and they must also infer which potential communities could colonize an area (Bowker 2007). Bryophyte communities in landscapes beyond the Mojave Desert are chiefly influenced by environmental factors related to habitat, probably because dispersal limitations are overcome by abundant, lightweight and easily dispersed propagules (Hájek et al. 2011). Despite this knowledge, the relative influences of habitat vs. dispersal remain unclear at highly localized spatial scales and in very arid systems. Quantifying the relative contributions of habitat and dispersal limitations is the objective of the fourth and final section of this thesis entitled "Local Habitat or Dispersal: Constraints on Non-Vascular Plant Diversity in the Mojave Desert".

Figure 1.1. Bryophytes (foreground, dark patches) inhabiting rocky microsites with low productivity, Red Rock Canyon, Mojave Desert.

Figure 1.2. *Tortula inermis* (Brid.) Mont., a bryophyte commonly found in the reproductive stage at Red Rock Canyon. Viable spores (produced in the brown, vertical sporophytes) may either germinate immediately, disperse by aerial spore rain or remain dormant in soil-banks.

CHAPTER 2

CRYPTIC DIVERSITY IN BRYOPHYTE SOIL-BANKS ALONG A DESERT ELEVATIONAL GRADIENT

Abstract

Propagule soil-banks are important for colonization and for the maintenance of regional diversity among bryophytes of temperate regions, yet they have not previously been reported from hot desert ecosystems and little is known about the relationship between soil-bank diversity and elevation. I used emergence germination methods to explore patterns of species composition and richness in bryophyte soil-banks along a 1400 m elevational gradient spanning three major vegetation zones in the Mojave Desert of the southwestern United States. Climate variables related to water availability (mean annual precipitation, relative humidity and soil moisture) were significantly and positively correlated with elevation. A total of 17 bryophyte taxa were present in soils collected at twelve sites. Community compositions shifted with increasing elevation, suggesting that soil-banks along the gradient are an important “cryptic” component of the regional species pool. Bayesian linear regressions revealed that three measures of community diversity were positively associated with elevation: species richness, Shannon entropy and phylogenetically-controlled species richness. Positive diversity–elevation trends in soil-banks of the Mojave Desert are the likely product of increasing moisture availability and reproductive frequency at higher elevations in dry mountain ranges.

Introduction

In deserts of North America, bryophyte diversity reflects the ability of individuals to reproduce, disperse and establish in the face of challenging abiotic conditions. Successful colonization results from at least one of three processes: 1) dispersal over distance; 2) soil-bank dormancy; and 3) vegetative expansion of existing plants (During 1979). Soil-banks are of particular importance, not only because they function as reservoirs of taxonomic and genetic diversity for bryophytes (Hock et al. 2008), but also because they allow plants to avoid risks associated with temporal fluctuations in stress and resource availability (During 1997). Organs and tissues from which a new plant can arise (hereafter referred to as “propagules”) can remain dormant and viable for nearly 50 years in dry soils (Whitehouse 1984), suggesting that soil-banks are likely to exist in deserts even in locations where surface plants may be absent. Assuming the persistence of propagules in soils of arid localities, soil-banks could be a key mechanism of “dispersal in time” which permits desert bryophytes to avoid harsh abiotic conditions and conditionally establish during favorable periods.

Despite the significant role of soil crust bryophytes for nutrient dynamics, hydrological cycling and soil stabilization in arid ecosystems (Eldridge and Greene 1994), we know little of how soil-banks might contribute to bryophyte diversity either locally or across arid landscapes. Elsewhere, bryophyte soil-bank diversity has been described from a variety of mesic habitats (reviewed by During 1997). Only a single study has investigated soil-banks from a semi-arid region (a dry savanna in Zimbabwe), where soil communities exhibited surprisingly high diversity compared to surface communities (During 2007) and featured one moss genus that was new to science (Zander and During 1999). These findings suggest that bryophyte soil-banks in desert shrublands might similarly harbor cryptic taxonomic richness.

The association of species richness with elevation is a fundamental concern of both plant ecology (Whittaker 1960) and biogeography (Lomolino 2008). In bryophyte communities surveyed along elevational gradients, species richness can vary in a positive (Austrheim 2002), negative (Geissler and Velluti 1996) or unimodal fashion (Wolf 1993), trends which depend on the length of the elevational gradient surveyed (Nogués-Bravo et al. 2008). Elevation–richness patterns of bryophytes are typically associated with moisture gradients that covary with elevation (Lee and La Roi 1979), reflecting the fact that bryophytes are highly dependent on external water for growth and reproduction. In deserts of the southwestern United States, persistent desiccation and water limitation restrict reproductive frequency, particularly at low elevations (Stark and Castetter 1987; Benassi et al. 2011). In the absence of successful propagule production and dispersal, meager deposition rates are also expected to be reflected by minimal species richness in low elevation soil-banks. While many low elevations (<1000 m) are typified by low species richness of surface bryophyte communities (Nash et al. 1977), the mechanisms maintaining diversity in sub-surface soil-banks may operate differently than in surface communities, and it remains to be seen if elevation–richness patterns are consistent between each profile.

The purposes of this study were to characterize the diversity of bryophyte soil-bank communities in the Mojave Desert and to quantify changes in sub-surface diversity along an elevational gradient of 1400 m. Because bryophyte reproduction in the region increases with elevation and increasing moisture availability, I hypothesized that three separate measures of soil-bank diversity would be positively related to elevation. Although similar approaches have been applied to other plant communities, to my knowledge this study represents the first to investigate a soil-bank community of bryophytes in a truly arid temperate region, and is the first to explicitly test the elevation–richness relationship for any bryophyte soil-bank.

Materials and Methods

Study area and field collections

The Spring Mountains are a dry mountain range in the Mojave Desert, approximately 40 km northwest of the city of Las Vegas in southern Nevada, U.S.A. (36.006°, –115.452°). On the eastern slopes of the Spring Mountains (Fig. 2.1), limestone outcrops and wooded foothills descend to sloping alluvial fans composed of shallow, well-drained, loamy-skeletal soils (Lato 2006). Much of the terrain is dissected by dry washes created during episodic rainfall events. Annual precipitation in the area is sparse and highly variable (mean = 283 mm; SD ± 127 mm; Fig. 2.2), mostly provided by winter rain-showers and occasional late-summer showers (National Climatic Data Center records for Spring Mountain State Park, 1152 m a.s.l., period 1977–2011).

At low elevations near 1000 m, local vegetation was dominated by the perennial evergreen shrub *Larrea tridentata* (DC.) Coville. Middle elevations (1200–1800 m) were characterized by the shrub *Coleogyne ramosissima* Torr., which intergraded at its upper limits with the small trees *Pinus monophylla* Torr. & Frém. and *Juniperus osteosperma* (Torr.) Little. Upper elevations (> 2000 m) were dominated by tall coniferous trees, mainly *Pinus ponderosa* Lawson & C. Lawson.

In late September and early October of 2011, I surveyed twelve sites (Table 2.1) arrayed along two parallel elevational gradients ascending the eastern slopes of the Spring Mountains (Fig. 2.3). The first transect (Kyle Canyon) included five sites spanning 1664–2235 m, while the second transect (Lee Canyon) included seven sites between 1019–2442 m. Sites were crudely spaced at intervals of ~200 m. The presence of mature vegetation and intact substrates at all sites indicated the absence of any recent fires or mechanical disturbances. I collected 4 soil cores (10 cm diameter × 3 cm depth) at each site from patches that were free of any large rocks, litter or surface plants (including existing patches of bryophyte shoots). The 48 soil cores were sealed and immediately transported to the lab at room temperature in dry darkness before germination. Some cores were breached during transport and were discarded, yielding a total of 40 cores.

For germination, I air-dried and sieved each soil sample (355 µm fine wire mesh) to remove small rocks, coarse organic matter and any remnant plant parts, then placed a 4 cm^3 subsample into sterile polystyrene culture dishes (35 mm diameter, Falcon item 351008, Becton-Dickinson, Franklin Lakes, NJ, USA). Cultures were moistened, loosely covered and maintained in a humid environment within a growth chamber (Percival model E30B, Boone, IA, USA) under a cycle of 12 hr light (20°C) and 12 hr dark (8°C). I also randomized two sterile soil samples among the culture dishes to detect unwanted aerial spore contamination. Soil cultures were monitored twice weekly for moisture and germination; any vascular plant germinants were immediately removed. Preliminary observations suggested that growth of microorganisms (e.g., fungi, cyanobacteria, algae) in non-sterile soil had only a nominal effect on moss germination rates compared to sterile soil. Soil cultures were grown for 5 months to allow all propagules to germinate to identifiable stages, and at monthly intervals I recorded the presence and identity of bryophyte species in each sample. Bryophyte nomenclature follows Norris and Shevock (2004), with the exception of the family Bryaceae, which follows the recent revisions of Spence (2011).

Statistical analyses

All analyses were performed in the R computing environment (version 2.15.0; R Core Development Team 2012) using supplemental packages as noted. To determine how climatic variables were associated with elevation, I obtained interpolated values for mean annual precipitation, temperature, relative humidity and soil moisture for each of the twelve field sites from the FetchClimate web service (http://fetchclimate.cloudapp.net/), and then calculated pairwise Spearman correlation coefficients (significant if $P \leq 0.05$) using the packages *Hmisc* and *corrplot*. The FetchClimate web service generates values based solely on climate data observations (National Oceanic and Atmospheric Administration records, 1948–2012, http://www.esrl.noaa.gov/psd/) without regard to elevation information.

For the species data, I assessed species compositions by calculating ordination site scores with non-metric multidimensional scaling (NMS; Kruskal 1964) based on Bray-Curtis distances and implemented in the *vegan* package. A two-dimensional solution was sought *a priori* from a maximum of 999 random starting configurations. Composition–elevation trends were assessed visually by plotting site scores in the ordination space according to elevation.

To assess the relationship between diversity and elevation, I first calculated three distinct measures of diversity for each of the 12 sites. The first diversity measure, species richness (SR), was the number of species in the pooled collection of soil cores at each site. The second measure was Shannon entropy (H′), calculated for each site according to Oksanen et al. (2011). This measure integrates the number of species at each site with the evenness in the abundances among species, where abundances were considered as the frequency of each species among each of the soil cores per site. The third measure, phylogenetic species richness (PSR) was essentially an estimate of the effective species richness of a site after accounting for taxonomic relatedness.

PSR was calculated in the *picante* package as the number of species at a given site multiplied by the phylogenetic distance ("branch length" in a phylogenetic tree) between those species (Helmus et al. 2007). Therefore, related species give lower values for a site, and distantly related species give higher values, ranging from a minimum of zero to a maximum equal to the number of species present at a given site. The tree upon which calculations were performed was manually constructed using taxonomic distinctions defined by the Bryophyte Names Authority List (http://www.mobot.org/MOBOT/tropicos/most/bryolist.shtml) of the Missouri Botanical Garden.

To detect diversity–elevation trends, I conducted separate Bayesian linear regressions for each of the three diversity response variables using the package *MHadaptive* (Chivers 2012). A Bayesian approach allows one to make a probability statement about the parameter of interest (in this case, the slope of the diversity–elevation trendline) given only the data at hand, rather than a statement about how frequently those data would be expected under a given null hypothesis (Gelman et al. 2004). Therefore, small sample sizes (in this study, N=12) are not a constraint, provided that observations are considered independent and exchangeable. Bayesian methods are based on the joint probability of observing the data given a hypothesis (calculated using a likelihood function) and the prior probability distribution of the hypothesis (the "prior"); this joint probability is proportional to the conditional probability distribution (the "posterior") for the parameter of interest, which is effectually the desired outcome. In this study, I used flat, uninformative priors, assumed normally-distributed errors, and sampled the posterior probability distribution with a Metropolis-Hastings algorithm (Chivers 2012) employing 10,000 iterations, of which the first 2,000 iterations (burn-in) were discarded.

Results

Among twelve sites on the eastern slope of the Spring Mountains, elevation was significantly and positively correlated with mean annual precipitation (Spearman correlation coefficient = 0.60), mean annual soil moisture (0.85) and mean annual relative air humidity

(0.85); elevation was negatively correlated with mean annual air temperature (–0.74). A total of 17 bryophyte species (and one fern) were present in the entire collection of soil samples (Table 2.2). Of all bryophyte species, 58% represented the taxonomic family Pottiaceae, Bryaceae 17%, Funariaceae 11%, Ditrichaceae 5% and Encalyptaceae 5%. There were few widespread species, and most species were present in only a few sites (Table 2.3). External contamination in the growth chamber was not detected by the sterile controls. The NMS ordination yielded two convergent solutions after ten random starts, with a final stress of 10.9%. The topology of NMS site scores plotted in species space indicated an association between species composition and elevation (Fig. 2.4). For example, communities at lower elevation sites were associated with xeric species including *Syntrichia caninervis* Mitt. and *Crossidium aberrans* Holz. & E.B. Bartram, while mesic species such as *Ceratodon purpureus* (Hedw.) Brid. were present at higher elevations (Table 2.3). The Bayesian regressions revealed that all three diversity measures (SR, H′, PSR) were positively associated with elevation (Table 2.1). Ninety-five percent Bayesian credible intervals for the regression slope parameter (β) did not include zero, consistent with a positive diversity–elevation hypothesis (Fig 2.5). Posterior means for each slope parameter were: SR = 2.47 species; H′ = 0.597; and PSR = 1.82 species per change in 1000 m.

Discussion

This study is the first to characterize species composition and diversity of bryophyte soil-banks in the driest desert of the southwestern United States, and the first to connect trends in soil-bank diversity to elevation. The most noteworthy finding was that soil-bank diversity in the Mojave Desert was positively associated with elevation. Elevation was itself significantly correlated with climatic variables including available moisture and temperature, indicating that elevation can be a useful indicator of the stresses which bryophytes experience. Moisture and elevation are tightly linked in desert mountain ranges of the southwestern United States, providing strong gradients which influence plant growth and reproduction (Smith et al. 1997).

Studies in the region have shown fidelity between elevation and bryophyte species compositions of surface communities, which change along gradients corresponding to vegetation and climate. For example, Clark (2012) documented compositional changes across 1000 m of vertical relief spanning three vegetation zones at Grand Canyon National Park in northern Arizona, revealing that acrocarpic, xeric mosses of the Pottiaceae and Grimmiaceae families predominated at lower elevations and were superseded by mesic mosses (plus several liverworts) at higher elevations. I observed very similar patterns in soil-banks of the Spring Mountains, where the Pottiaceae family was well represented, although the saxicolous family Grimmiaceae was conspicuously absent from soil profiles, perhaps because its members require lithic substrates for germination (Keever 1957). Outside of the southwestern United States, Stehn et al. (2010) and Slack (1977) have observed similarly changing species compositions in montane surface communities of the eastern United States, supporting the generality of the concept of compositional turnover along montane elevational gradients.

Like species compositions, area-wide species richness in bryophyte soil-banks of the Spring Mountains (17 taxa) corresponded well with the generally low species numbers found in the surface vegetation of other Mojave Desert sites. For example, Thompson et al. (2005) encountered 11 taxa (4 shared in common with the current study) in surface communities at other Spring Mountain locations between 1030 – 1440 m, Bowker et al. (2000) reported 6 taxa (5 shared) at 1494 m, and Nash et al. (1977) reported just 3 species (3 shared) from 1000 m, perhaps indicative of moisture limitations at lower elevations. The moisture limitation concept was supported by my finding strong positive correlations between elevation and indicators of moisture availability which included annual precipitation, soil moisture, and relative humidity. Curiously, there was no strong association between elevation and the seed-bank of vascular plants at similar locations in the Spring Mountains (Abella and Springer 2012), perhaps indicating that water availability has quite different effects depending on the extent to which different plant groups rely on external water.

The generally positive elevation–diversity trend observed among bryophyte soil-banks in this study appears to parallel the positive trends observed at moderate elevations both in the Mojave Desert and elsewhere in the world. For example, Bisang et al. (2003) suggested that soil-bank richness in a tropical rainforest may increase with elevation. However, above approximately 2000 m, bryophyte species richness in surface communities apparently declines, probably as a result of increasing stresses (e.g., moisture and temperature stresses) in some alpine zones (Geissler and Velluti 1996). Studies of very broad elevational gradients in excess of 3000 m (e.g., Wolf 1993; Grau et al. 2007) often reveal a hump-shaped, unimodal relationship for bryophyte species richness in surface vegetation, with low-elevation increases eventually peaking and tapering in high montane and alpine areas. Had the current study been extended through the conifer forest and above upper treeline into the alpine zone, a similar unimodal peak and decline might have been expected for soil-bank species. Despite covering three major vegetation–climate zones, the areas surveyed herein covered only the lower portion of a mountain range that extends upward to 3633 m. Observing only a portion of a larger elevation gradient could influence the apparent shape of the elevation–richness pattern (McCain and Grytnes 2010), which may explain the monotonic positive relationship which I observed in soil-banks of the Spring Mountains.

Bryophyte diversity at landscape scales is perhaps best viewed in a context where local communities are sustained by dispersal from the regional species pool (During and Lloret 2001; Leibold et al. 2004). In this regard, local richness and compositions are the product of immigration events which are then filtered by the capacity of bryophytes to tolerate local conditions. Like the “seed rain” of many vascular plants, the deposition of bryophyte spores (Miles and Longton 1992) and asexual propagules (Pohjamo et al. 2006) is expected to be greatest immediately around source plants, and declines rapidly with distance. This is true from scales of several dozens of meters (Lönnell et al. 2012) to several hundreds of kilometers (Sundberg 2012), suggesting that proximity to reproductive plants may be a strong determinant of the density and composition of spores that comprise soil-banks (but see Hylander 2009). I hypothesize that the accrual of propagules in soil-banks is the result of proximity to propagule-producing plants at higher elevations. Reproductive success increases with moisture and elevation in southwestern USA deserts (Stark and Castetter 1987), which suggests that soil-banks should be richest at higher elevations where productive propagule-producing plants occur more frequently. Conversely, low-elevation sites far from productive plants are expected to yield fewer soil-bank species, not necessarily because propagules cannot survive there, but because their arrival would require infrequent long-distance dispersal events originating from distant montane sources. Although this study did not directly measure distance-dependency, one way to verify these hypotheses would be to survey soil-bank richness (in tandem with spore deposition rates) at varying distances from known reproductive populations.

To summarize, this study documented 17 species of bryophytes in sub-surface soil-banks along an elevational gradient covering 1400 m in a temperate arid mountain range. The positive relationships of species richness, Shannon entropy, and phylogenetically-controlled species richness with increasing elevation indicate that future work should attempt to connect soil-bank diversity with distance from reproductive surface communities along the elevation gradient. The positive diversity–elevation trend present in the Mojave Desert suggests that similar patterns may exist in bryophyte soil-banks of other temperate arid regions where moisture and temperature influences are closely associated with changes in elevation.

Table 2.1. Site descriptions, three community measures and results of Bayesian linear regressions from soil-banks of the Spring Mountains. Soils were collected at twelve sites. Posterior means and credible intervals are in units of diversity per 1000 m change in elevation, all other values are in original units. See text for abbreviations.

Transect (canyon)	Elevation (m)	Latitude	Longitude	SR	H′	PSR
Lee	2442	36.358	-115.664	7	1.94	4.69
Lee	2346	36.353	-115.643	5	1.6	3.16
Kyle	2235	36.259	-115.638	7	1.94	4.69
Lee	2135	36.37	-115.627	5	1.6	2.99
Kyle	2002	36.272	-115.582	4	1.38	3.24
Lee	1802	36.394	-115.585	2	0.69	0.77
Kyle	1785	36.271	-115.544	6	1.79	3.45
Kyle	1702	36.267	-115.511	4	1.38	2.71
Kyle	1664	36.257	-115.521	5	1.6	2.82
Lee	1524	36.418	-115.546	5	1.6	2.47
Lee	1220	36.45	-115.503	4	1.38	2.24
Lee	1019	36.476	-115.47	2	0.69	1.47
Observed mean ± SD				4.64 ± 1.69	1.46 ± 0.43	2.89 ± 1.19
Observed range				2 – 7	0.69 – 1.95	0.77 – 4.69
Posterior mean of slope (β) parameter				2.47	0.60	1.82
95% Bayesian credible interval				0.48 – 4.56	0.01 – 1.11	0.35 – 3.15

Table 2.2. Species relative frequencies in soil samples collected at 12 sites in the Spring Mountains.

Abbreviation	Species	Family	Relative frequency (%)
Bryarg	*Bryum argenteum*	Bryaceae	33.3
Bryrec	*Bryoerythrophyllum recurvirostre*	Pottiaceae	8.3
Cerpur	*Ceratodon purpureus*	Ditrichaceae	16.7
Croabe	*Crossidium aberrans*	Pottiaceae	25.0
Didvin	*Didymodon vinealis*	Pottiaceae	16.7
Encint	*Encalypta intermedia*	Encalyptaceae	8.3
Entmuh	*Entosthodon muhlenbergii*	Funariaceae	8.3
Fern	Fern prothallus, not determined	not determined	8.3
Funhyg	*Funaria hygrometrica*	Funariaceae	58.3
Gemcae	*Gemmabryum caespiticium*	Bryaceae	41.7
Gymspp	*Gymnostomum sp.*	Pottiaceae	25.0
Phacus	*Phascum cuspidatum*	Pottiaceae	8.3
Pteova	*Pterygoneurum ovatum*	Pottiaceae	75.0
Ptytur	*Ptychostomum turbinatum*	Bryaceae	8.3
Syncan	*Syntrichia caninervis*	Pottiaceae	41.7
Synrur	*Syntrichia ruralis*	Pottiaceae	25.0
Torbre	*Tortula brevipes*	Pottiaceae	8.3
Torine	*Tortula inermis*	Pottiaceae	8.3

Table 2.3. Species presences and absences in soil samples collected at twelve sites in the Spring Mountains. Site elevations follow Table 2.1, species abbreviations follow Table 2.2.

Elevation (m)	Species																	
	Bryarg	Bryrec	Cerpur	Croabe	Didvin	Encint	Entmuh	Fern	Funhyg	Gemcae	Gymspp	Phacus	Pteova	Ptytur	Syncan	Synrur	Torbre	Torine
2442	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0
2346	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0
2235	1	0	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0
2135	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0
2002	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0
1802	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
1785	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	1	1
1702	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
1664	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0
1524	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0
1220	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0
1019	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0

Figure 2.1. Example of a mid-elevation soil collection site (1700 m a.s.l.) at Kyle Canyon on the eastern slopes of the Spring Mountain range in southern Nevada. Widely spaced *Coleogyne ramossissima* (blackbrush) shrubs are the dominant vegetation. Soils for germination were collected from vegetation-free areas in the open interspaces.

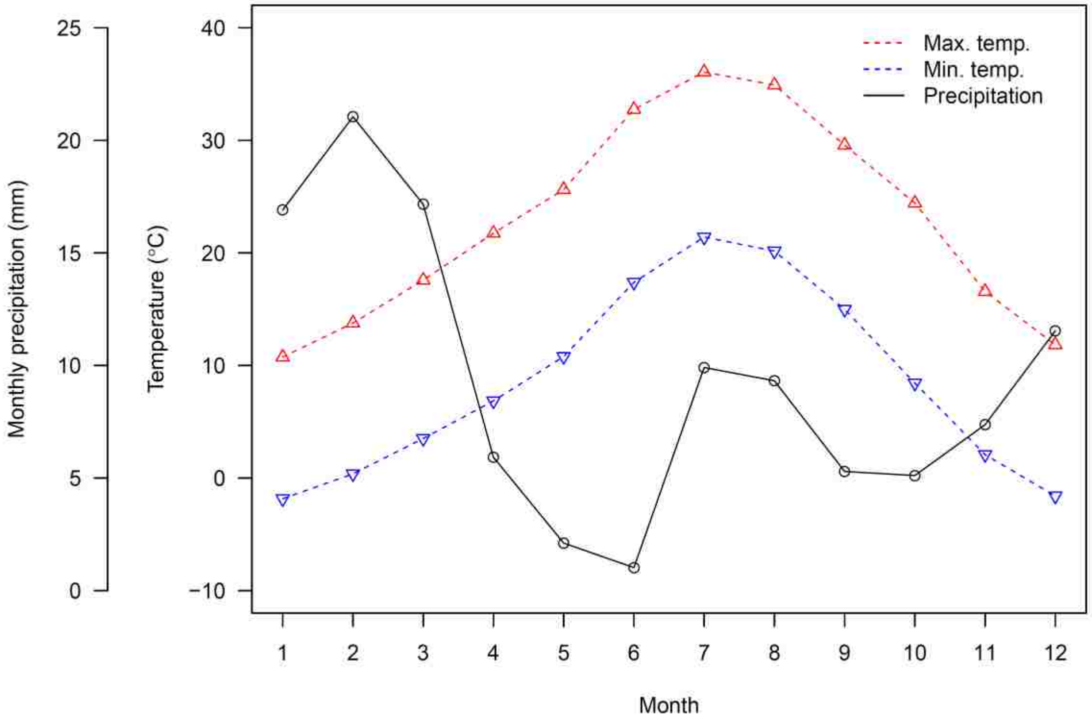


Figure 2.2. Mean monthly precipitation and air temperatures near the study area (National Climatic Data Center records for Spring Mountain State Park, 1152 m a.s.l., period 1977–2011).

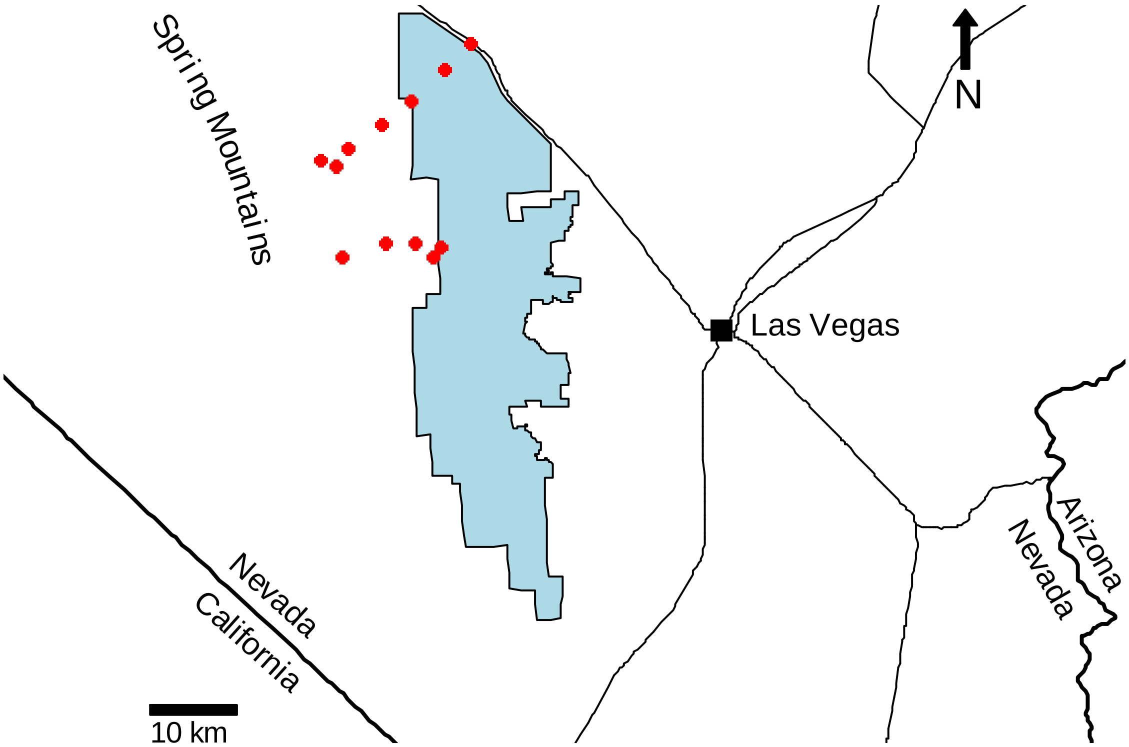


Figure 2.3. Map of study sites (red filled circles) in Red Rock Canyon National Conservation Area (shaded polygon) and adjacent public lands in the Spring Mountains of southern Nevada.

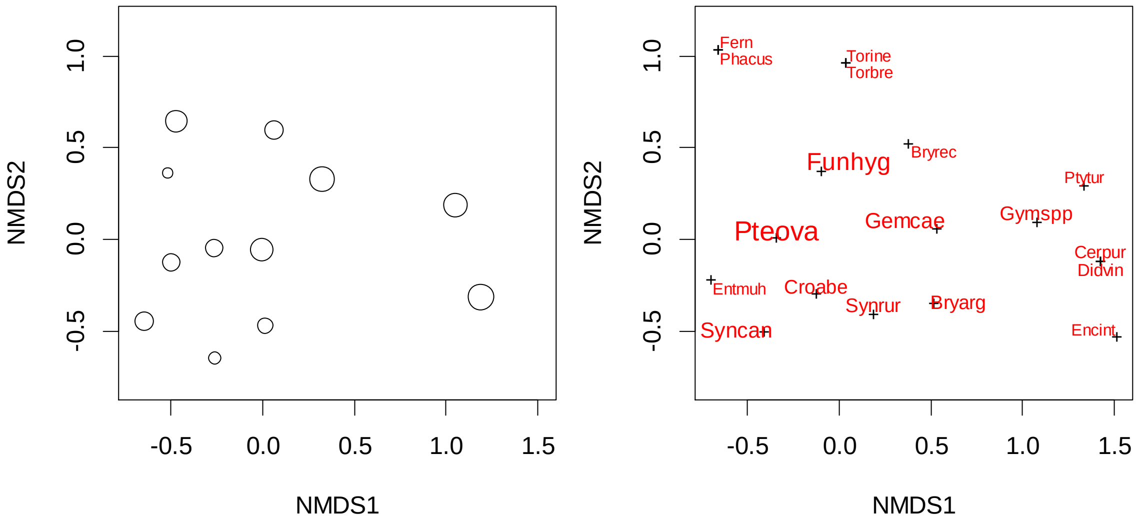


Figure 2.4. Results of NMS (non-metric multi-dimensional scaling) ordination of bryophyte soil-bank communities (two-dimensional solution, stress = 10.9%). Site scores in species space are sized by elevation (left diagram), and species scores in species space are sized by relative frequency (right diagram). Lower elevation sites (lower left-hand corners) correspond with xeric species including *Syntrichia caninervis*, *Crossidium aberrans*, and *Pterygoneurum ovatum*. Abbreviations follow Table 2.2.

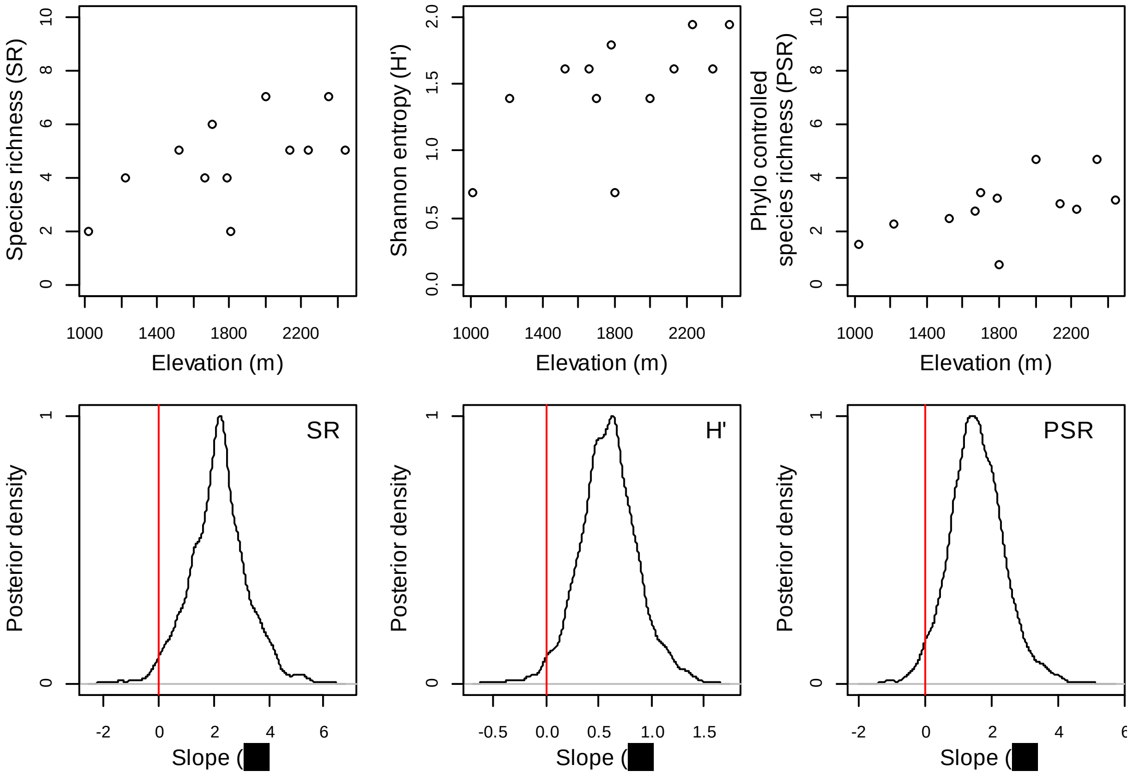


Figure 2.5. Three measures of diversity observed along the elevational gradient (top row), and posterior densities for the slope parameter (β) from Bayesian regressions of each diversity measure independently regressed on elevation (bottom row). Values of β indicate the estimated change of the response variable for every 1000 meters of change in elevation, where values above zero (red vertical lines) correspond to a positive relationship between each response and elevation. Note the difference in scales.

CHAPTER 3

POST-FIRE RECOVERY OF DESERT MOSSES: EFFECTS OF FIRES AND DISPERSAL IN TIME AND SPACE

Abstract

As changing fire regimes modify North American deserts, fires of greater severity and frequency could negatively impact the recovery of non-vascular plants which are not adapted to such disturbances. Post-fire recovery of bryophytes can initiate by *in situ* survival of existing surface plants, survival of dormant propagules in sub-surface soil-banks (dispersal in time) or aerial immigration into burned sites (dispersal in space). I characterized bryophyte communities at six burned sites along a post-fire chronosequence spanning three decades and three profiles (surface, soil and aerial). I asked whether communities differed among profiles and among sites where fires had different severities, ages and potential fuels; I also tested the hypothesis that wildfires negatively affect soil-bank propagules. Burn severity was associated with differences in beta-diversity, species composition and richness, while burn age was associated only with different composition and richness; there was no effect of fuel availability. Significant differences among profiles explained more variation in composition than other fire attributes, and species richness (but not beta-diversity) was greater in soil profiles than in aerial spore rain or existing surface communities. Soils from the oldest and least severe burns had more species than recent and severe burns, indicating that the recovery of bryophyte communities from soil-banks may begin (but not necessarily conclude) within 30 years after wildfires. In the near future, communities could be perturbed from historical patterns as fire regimes undergo extensive changes.

Introduction

The assembly of communities following wildfire disturbances is the result of species' adaptations to historical fire regimes (Bond and Keeley 2005) and their capacity to colonize disturbed areas. Successful post-fire recovery is therefore a process which integrates species' traits and life histories with the frequency, extent and severity of wildfires. Although North American deserts have not been historically prone to fire, disturbance regimes in the southwestern United States are currently undergoing drastic changes due to introductions of non-native, fire-stimulating plants (D'Antonio and Vitousek 1992; Brooks et al. 2004; Abella 2009). The proliferation of invasive plants reduces ecosystem resilience through positive feedback cycles of increasing fire frequency (Brooks and Chambers 2011) and by the creation of continuous fuel-loads that promote fire spread across desert landscapes (Fig. 3.1). These changes radically alter soil and community properties and create deleterious changes in nutrient availability, productivity, erosion and biodiversity, which persist in the presence of invasive non-natives (Allen et al. 2011). Following fires, plants that do not survive fires must rely on colonization from at least one of three sources: 1) regeneration from surface communities that escape fires; 2) germination from soil-banks; or 3) aerial dispersal/immigration. The relative contributions of surface, soil and aerial community profiles remain uncertain for desert plants that are not adapted to fire.

Non-vascular plants inhabiting deserts are exceptionally sensitive to damage and mortality from fires because they do not possess perennating organs or seeds capable of enduring the direct effects of fire. Non-vascular plants, including mosses and liverworts ("bryophytes" hereafter), are essential members of biotic soil crust communities in arid shrublands and grasslands worldwide. Bryophytes are important components of arid ecosystems, playing vital roles in nutrient fixation, nutrient retention and hydrological cycling, as well as housing a variety of fungal, invertebrate and bacterial symbionts (Belnap et al. 2001). Bryophytes are also responsible for initial soil stabilization and nutrient dynamics following fires in dry regions (de las Heras et al. 1994; Hardman and McCune 2010). The loss of this collection of functions could potentially alter the nature of desert ecosystems as bryophytes are increasingly impacted by global changes both directly (e.g., carbon dioxide enrichment) and indirectly (e.g., altered fire regimes; Slack 2011).

Determining whether plant populations are sustained by spatial dispersal or by temporal storage is an ongoing challenge (Alexander et al. 2012). It is currently unknown whether desert bryophytes colonize disturbed ground primarily from aerial immigration or generation from soil-banks, or even whether latent propagules frequently survive fires within soil. In the absence of disturbance, propagules can remain viable for up to 50 years in dry soil (Whitehouse 1984). Soil-banks are sources of bryophyte colonization following disturbances of natural (Furness and Hall 1982; Miles and Longton 1992) and human (Jonsson 1993; Hassel and Söderström 1998) origin. While diversity in bryophyte soil-banks has been extensively characterized in temperate grasslands, temperate forests and polar regions (e.g., During 1997; During 2001; Lewis-Smith and Ochyra 2006), less is known about soil diversity in arid and semi-arid regions, especially localities that may experience fire disturbances. In one study of a semi-arid African savanna, post-fire soil samples exhibited surprisingly high diversity compared to surface communities (During and Moyo 1999; During 2007). As soil-banks function as reservoirs of taxonomic and genetic diversity (Zander and During 1999; Hock et al. 2008), ecologists and practitioners require a better understanding of their role in post-fire colonization and knowledge of whether projected increases in fire frequency and severity (Brooks and Matchett 2006) can deplete these biological resources. An appreciation of soil-bank dynamics will be crucial for resource managers who have the capacity to manipulate mechanical and pyrogenic disturbances to desert soils.

The purposes of this study were to characterize the relative influences of spatial and temporal dispersal and to assess how fires might shape bryophyte diversity in deserts. Using site surveys and emergence germination methods, I measured species richness and diversity of bryophytes at six burn sites along a chronosequence spanning three decades and three community profiles in the Mojave Desert of the southwestern United States. First, I hypothesized that species richness, composition and beta-diversity would differ among the surface, soil and aerial profiles as a result of different life history traits among species. Second, I hypothesized that communities that experienced more recent and/or severe fires would exhibit lower diversity and lower richness as a result of fire mortality. Accordingly, I also expected differences among microhabitats because of apparently different fuel loads under perennial shrubs vs. open sites between shrubs. Finally, I hypothesized that more recent and/or severe burns would exhibit species-poor, low-diversity soil-banks because of severity-dependent mortality and because time is required for the gradual re-accumulation of species following fires (i.e., a soil-bank "depletion" hypothesis). Support for these hypotheses could indicate that changing patterns of fire severity and burn frequency in the Mojave Desert may negatively impact future native plant communities as bryophyte diversity and related functions are lost.

Materials and Methods

Study sites

Red Rock Canyon National Conservation Area (36.135° N, –115.427°; 1149 m a.s.l.) is approximately 25 km west of the city of Las Vegas in southern Nevada, U.S.A., on the southern flanks of the Spring Mountain range. The immediate area has experienced at least fourteen fires >10 ha between the years 1980 and 2011 (BLM 2012; Engel and Abella 2011). I surveyed six of these burned areas along with paired, unburned reference sites (Figs. 3.1 and 3.2). The years 1980, 1993 and 2005 were represented by two burns each, with burned areas ranging from 12 to 1,619 ha (Table 3.1). Reliable records for fires older than 1980 were not available and were excluded from further consideration. All sites were typified by the dominant shrub *Coleogyne ramosissima* (blackbrush), although the shrub *Larrea tridentata* or the small tree *Pinus monophylla* were co-dominant at the lower or upper elevation extremes, respectively. Regional substrates were shallow, rapid-draining, skeletal soils derived from calcareous sandstone, dolomite and limestone parent materials (Lato 2006). Annual rainfall in the area is sparse (mean

= 283 mm; SD ± 127 mm), falling mainly as winter showers and occasional late-summer monsoons (NCDC records for Spring Mountain State Park, 1152 m a.s.l., period 1977–2011).

Macroplot and microplot placement

At each of six previously burned sites (Fig. 3.2), I randomly located four macroplots within burned areas and four macroplots in adjacent unburned locations (equal in size to the burned area), yielding a total of 48 macroplots across the entire study area. Macroplots were circles with a radius of 34.7 m (area = 0.38 ha), consistent with Forest Health Monitoring standards used for non-vascular vegetation surveys on U. S. National Forests and other public lands (Tallent-Halsell 1994). At the center of each macroplot, I obtained site descriptors including geographic coordinates, elevation, aspect, slope and topographic position, as detailed by Engel and Abella (2011). I also estimated *post hoc* fire severity with an ordinal severity score ranging from 1 (severely burned) to 5 (unburned), based on remnant vegetation and litter in burned plots as compared to unburned reference plots (Lutes et al. 2006). An independent severity estimation method (mean minimum branch diameter method; Moreno and Oechel 1989) gave qualitatively similar results, so the simpler categories of Lutes et al. (2006) were retained.

Nested within each macroplot, I randomly placed 5 microplots (square frames 15 × 15 cm) under *Coleogyne* shrub canopies on their north side and 5 microplots in open spaces between shrubs (minimum 1 m from nearest shrub canopy). I set a minimum distance of 5 m between neighboring microplots and excluded locations consisting only of shrub stems, downed wood or solid rock. In both macroplots and microplots, I sampled bryophyte communities belonging to three community profiles: surface, soil and aerial.

Community sampling in surface, soil and aerial profiles

I visually estimated areal cover class values (Peet et al. 1998) for bryophyte species in the 480 microplots, and likewise categorized the areal cover of lichens, shrubs, forbs, grasses, coarse litter (>5 mm), fine litter (≤ 5 mm), soil and rock. Despite obvious phylogenetic dissimilarity, spore-bearing ferns were included as a single “pseudo-species” of bryophyte because of similar dispersal, life-cycle and autecology. Species unidentifiable in the field were returned to the lab for verification. Nomenclature followed the Bryophyte Names Authority List of the Missouri Botanical Garden (http://www.mobot.org/MOBOT/tropicos/most/bryolist.shtml).

Concurrent with surface profile sampling, I sampled the soil profile for latent moss species. First, I gently removed any large rocks, litter or surface plants (including existing patches of bryophyte shoots) from just outside the same 480 microplots mentioned above. I extracted 480 soil cores (10 cm diameter × 3 cm deep; volume ≈ 235 cm^3) which were immediately transported to the lab at room temperature in dry darkness before the germination step. For this, I homogenized and sieved soil samples (355 µm fine wire mesh) to remove rocks, coarse organic matter and any plant parts. A 2-cm^3 subsample of the sieved soil was spread thinly in each well of a 12-well polystyrene culture plate (item 665102, Greiner Bio-one, Monroe, NC, USA). To detect unwanted spore contamination, I also randomized two sterile soil samples among every ten samples in the 12-well culture plates. Cultures were loosely covered and maintained in a moist environment within a growth chamber (Percival model E30B, Boone, IA, USA), under a cycle of 12 hr light (20°C) and 12 hr dark (8°C). Cultures were monitored twice weekly for moisture and germination and any vascular plants were immediately removed. Pilot studies suggested that growth of microorganisms (e.g., fungi, cyanobacteria, algae) in non-sterile soil had only a nominal effect on moss germination rates and species composition. Soil cultures were grown for 8 months to allow propagules to reach identifiable stages, and at monthly intervals I recorded the presence and identity of bryophyte species in each sample.

In the field, I established aerial propagule traps (hereafter “spore traps”) at the centers of the 48 macroplots. Polyethylene capture funnels (30 cm diameter × 40 cm deep) were filled at the bottom with 50 cm^3 of sterilized, sifted native soil which had been autoclaved at 121.0°C for 45 minutes (Amsco LG 250 Laboratory Steam Sterilizer, Steris Corporation, Mentor, OH, USA). Spore traps were elevated 1 m above ground level on sturdy wire frames and were exposed for 30–34 days before being sealed and transported in dry darkness to the laboratory for the germination step. Germination of spore-trap samples followed the procedure given above for soil cultures, including temperature and light regimes. At monthly intervals, I recorded the presence and identity of bryophyte species in each sample.

Analyses: beta-diversity, composition, richness

I compared beta-diversity with a permutational test for homogeneity of multivariate dispersion (PERMDISP; Anderson et al. 2006), performed in the R computing environment (version 2.15.0; R Core Development Team 2012) using the functions ‘betadisper’ and ‘permutest’ from the *vegan* package. Because beta-diversity can be defined as the variability of species compositions, the PERMDISP method effectively describes differences in beta-diversity among pre-defined groups (e.g., among different profiles, microsites, burn severities and burn years). For this analysis, I pooled species occurrences among every 5 microplot replicates having identical attributes (i.e., same fire, same macroplot and same position relative to shrub microsite), then calculated Sørenson distances (binary Bray-Curtis distances) because the standardizations inherent to Bray-Curtis distances can complicate interpretation (Anderson et al. 2006).

Differences in species compositions were examined with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) implemented with the ‘adonis’ function in the *vegan* package; calculations were based on pooled species occurrences, Bray-Curtis distances, and 999 permutations. Fixed effects were profile, microsite, burn severity and burn year (indicating time since fire), and permutations were stratified among macroplots to account for spatial autocorrelation. PERMANOVA requires no assumptions of multivariate normality and is insensitive to heterogeneity of multivariate dispersion (Anderson and Walsh 2012). I supplemented this analysis by graphically depicting species compositions in a non-metric multidimensional scaling ordination (NMS; Kruskal 1964) that employed Bray-Curtis distances based on Hellinger-transformed species data from which zero-sum rows had been removed (Legendre and Gallagher 2001). Solutions were computed independently for 2 and 3 dimensions using a maximum of 999 random starts, and the solution with the lowest stress was retained.

Differences in species richness were examined with a mixed-effects linear model using the 'PROC MIXED' procedure implemented in SAS software (version 9.3; SAS Institute Inc., Cary, NC, USA). This is a restricted maximum-likelihood estimation procedure that is analogous to a fixed-effects analysis of variance, but that can also account for random effects and partially hierarchical, unbalanced study designs (SAS Institute 2011). Species richness (the number of species detected in each 0.225 m^2 microplot) was considered in response to profile, microsite, burn severity and burn year (fixed effects, nested as appropriate), and macroplot (a random effect accounting for spatial autocorrelation, nested within each of the above effects). From the saturated full model, interactive effects were removed if contributory main effects were not significant, and the final reduced model was selected based on minimized values of Akaike's Information Criterion and the Bayesian Information Criterion.

Testing soil-bank depletion

To test the hypothesis of depleted soil banks from more recent or severe fires, I repeated the above tests of beta-diversity (PERMDISP), species composition (PERMANOVA) and species richness (PROC MIXED) using only the data from laboratory-grown soil germinants. Where permissible, fixed effects were microsite, fire severity and fire year (time since fire), and macroplot was a random effect. Soils with significantly lower beta-diversity, differing species compositions and lower richness were considered evidence in support of soil-bank depletion.

Results

Community characterizations

Twenty-seven taxa were present across all studied sites (Table 3.2), including 25 acrocarpic moss species (chiefly representing the xerophilic family Pottiaceae), one liverwort and one fern. Taxa were distributed unevenly among different profiles and sites with different fire attributes (Table 3.3; Figs. 3.3–3.6). For example, of the 480 randomly placed sample points, bryophytes occurred in 142 (29.6 %) of the surface samples and in 382 (79.6 %) of the soil samples, while only 1 of the 48 aerial spore-traps (2.1 %) contained viable bryophytes. Of the 27 total taxa, 25 were present in the soil profile (13 were unique to this profile), 13 in the surface profile (2 unique), and 1 in the aerial profile (0 unique; Table 3.4). Based on searches of herbarium records (CNABH 2012) and state checklists (Brinda et al. 2007), one species which emerged from the soil bank (*Riccia cavernosa*) was not previously known within at least 250 km of the study area. Propagule contaminants were not detected in sterile controls during the germination assays.

Beta diversity, composition and richness

There were significant differences in beta-diversity (multivariate group dispersion) among burns of different severity (Table 3.5); however, beta-diversity did not differ significantly among sites from the same profile, burn year or microsite (i.e., beneath shrub canopies vs. interspaces) with similar fuel availability (Fig. 3.7). These differences were also demonstrated by the NMS ordination, which revealed differing multivariate dispersions among sites grouped by burn severity, but not among sites from the same profile, burn year or microsite (Fig. 3.8).

Species composition (multivariate group position) differed significantly among the surface, soil and aerial community profiles (Fig. 3.8; Table 3.6). Composition also differed significantly among different fire severities and burn years, but not among different microsites (Table 3.6). Differences among profiles explained the greatest proportion of variation in species composition (R^2 = 0.17), although fire severity also had good explanatory value (R^2 = 0.13).

Species richness differed significantly among profiles, burn years and burn severities, but not among different microsites (Table 3.7; Fig. 3.9); there was a significant interaction between profile and burn severity, with soil profiles having more dramatic reductions at greater levels of severity (Fig. 3.9).

Testing soil-bank depletion

Beta-diversity, species composition and species richness of the soil profile differed significantly among fires of different ages and severities, but not among different microsites

(Tables 3.8, 3.9 and 3.10). A greater proportion of variation in species composition was explained by fire severity (R^2 = 0.09) than by burn year (R^2 = 0.04). Although soil-bank species richness did not increase monotonically with time since fire, it was greatest in the oldest burns (soil-bank richness 1980 > 2005 > 1993; Fig. 3.9). Similarly, richness did not monotonically decrease with burn severity, although the two most severe burn classes had the lowest richness (Fig. 3.9).

Discussion

I characterized bryophyte community structure and propagule source dynamics across three spatial profiles and three disturbance intervals, and addressed whether the age and severity of each fire disturbance was associated with changes in community diversity, composition and richness. While fire age and severity were associated with measurable negative effects on community characteristics, dispersal in space and time appear to be leading factors affecting the recovery of bryophyte communities following wildfires in the Mojave Desert.

Dispersal in time: bryophyte soil-banks

Dispersal in time via soil-bank storage is essential for post-fire colonization and population maintenance of bryophytes in the Mojave Desert. In temporally variable environments, the primary advantage of dispersal in time is risk reduction. Many vascular desert plants (Venable et al. 2008) and some non-vascular plants (Hock et al. 2004) escape unfavorable periods through soil-bank dormancy, which appears to be the case in the Mojave Desert, where heat and desiccation stresses impose seasonal obstacles to reproduction and establishment of bryophytes (Barker et al. 2005). I documented high levels of diversity and richness in soil-banks, implying that dispersal in time could help maintain populations when propagule availability is otherwise constrained.

Soil-banks exhibited much greater richness than either surface or aerial profiles, featuring many species (14 of 27 total) which were otherwise apparently absent. The ability of bryophyte soil-banks to sustain regional species pools is demonstrated by the single occurrence in soil of the liverwort *Riccia cavernosa*, whose nearest previous report was ~250 km distant at the western fringes of the Mojave Desert in California and which had been reported in Nevada only once previously (Brinda et al. 2007; CNABH 2012). The presence of cryptic species suggests that soil-banks act as diversity reservoirs with hidden contributions to regional species pools.

Dispersal in space: aerial propagule rain

Aerial dispersal contributes to the accrual of spores in soil-banks and to initial colonization after disturbances. Elsewhere, early post-fire communities are typically dominated by short-lived, pioneer "fire mosses" which are associated with ubiquitous aerial dispersal (Ryömä and Laaka-Lindberg 2005). However, I detected only one of these species (*Funaria hygrometrica*) in the air and soil, but not in surface profiles. *Funaria* is frequent in other temperate-zone soil-banks despite being absent in surface profiles (During 1997; During 2007; Caners et al. 2009). The absence of *Funaria* in surface profiles at Red Rock Canyon suggests that environmental constraints control establishment more than propagule limitation. Specifically, *Funaria* germination fails in the absence of soil modifications generated immediately after fires (Southorn 1976; Southorn 1977), even when viable propagules are provided (During 1987). Other common post-fire colonists (e.g., *Ceratodon purpureus*, *Polytrichum* spp., *Marchantia polymorpha*) have similar requirements (Clément and Touffet 1990; Thomas et al. 1994), yet I detected these species only at low frequencies (if at all), probably reflecting their biogeographical scarcity in the Mojave Desert more than indicating establishment limitations.

Successful detection of bryophytes in aerial profiles can depend on regional availability, sampling methodology and proximity to source colonies. I detected only a single species in 48 aerial samples exposed for a month at Red Rock Canyon; sampling across multiple seasons likely would have yielded greater species capture. Most studies reporting comparably low species richness (e.g., Marshall and Convey 1997) collected aerial samples from ≥ 1 meter above ground-level as in the current study, which likely detects only low-density, long-range dispersal. Elsewhere, estimates of up to 22 species in the aerial profile (Ross-Davis and Frego 2004) were the likely result of sampling at the air–soil interface, where high-density, local dispersal is expected, especially near source plants. The typically leptokurtic density distributions associated with aerial dispersal (Nathan and Muller-Landau 2000) suggest that future studies must define whether local- or landscape-scale dispersal is the primary interest.

Effects of fire severity, age, and fuels

Wildfires have direct impacts on bryophyte communities, in addition to less-obvious effects on propagule reserves and colonization. There are at least two possible scenarios that explain bryophyte recolonization after wildfires. The first is that fires immediately kill plants and propagules, followed by subsequent immigration from outside of burns; this scenario was supported by the finding of initially depressed levels of diversity and richness following wildfires at Red Rock Canyon. The second scenario is that propagules or plant fragments regenerate after surviving fires *in situ*, which was supported by the finding of a generally diverse soil-bank. A mixture of these two scenarios appears to be the case for Mojave Desert bryophytes, suggesting both that fires directly affect surface and soil communities, and that at least some plants or propagules can survive fires below ground. Although plant communities of the Mojave Desert have not historically experienced frequent fires, soil-bank richness at this location corresponds well with an African savanna subjected to repeated burning, where a species-rich soil-bank apparently survived multiple surface fires as a result of soils buffering extreme temperatures (During 2007). Propagule survival via soil buffering has been reported for ferns (Dyer and Lindsay 1992) and vascular plants (Beckstead et al. 2011). In Mojave Desert shrublands, fire temperatures decrease by 48°C just 2 cm below the soil surface (Brooks 2002), suggesting that soil buffering could similarly protect bryophyte soil-banks below this depth.

Plants of surface communities can survive fires by quite different mechanisms than soil communities. Despite lacking special adaptations to fire, bryophytes leave biological legacies in small-scale fire refugia (Hylander and Johnson 2010) which are determined by available fire fuels (Esposito et al. 1999). Refugia in desert systems could consist of rocky outcrops, open spaces between shrubs and other areas where fuels are sparse. Fuel loads concentrated immediately beneath shrubs have been associated with peak fire temperatures of 135°C, more than double the temperatures in adjacent open spaces during a Mojave Desert experimental burn (Brooks 2002). Therefore, I expected (but did not observe) differences in community measures between shrub and open microsites. While this lack of a relationship could result from variability in burn severity, it does not negate the role of fire refugia: where fuel-free sites were not obviously available, I documented clearly negative effects of increasing severity on bryophytes, underscoring the need for conserving small-scale refugia and landscape heterogeneity in localities where wildfire severities may be increasing.

Patterns at Red Rock Canyon were consistent with observations that fires in dry regions are associated with initial reductions in non-vascular vegetation cover, diversity and richness (Johansen et al. 1984; Hilty et al. 2004) and altered species compositions afterwards (Hardman and McCune 2010). Elsewhere, the very earliest stages of succession are typified by rapid expansion of pioneering species which form distinctive colonist stages (de las Heras et al. 1992), yet the low abundance of colonists I observed at recently burned sites suggests that mechanisms of early succession in hot deserts may operate differently than more temperate systems. In any case, the chronosequence approach may not have detected rapid species turnover had it occurred in the very earliest months and years after fires (Walker et al. 2010). By establishing plots immediately after fires, a permanent plot approach could complement the chronosequence approach and might clarify early-stage bryophyte succession.

Soil-bank depletion and potential ramifications

In support of the soil bank depletion hypothesis, I observed significantly different species compositions and richness among soil profiles collected from different fires. For example, richness was lowest among younger and more-severe fires. Similar depletion occurred in the seed-bank of a woody shrub community only 2 years after a wildfire (Odion and Davis 2000). Recovery at Red Rock Canyon became more apparent over periods of time approaching 30 years post-fire. Successional dynamics in desert plant communities are notoriously slow and difficult to document, and may further be conditioned on historical events, pre-disturbance vegetation and variations in local environments (Engel and Abella 2011). More rigorous tests of the soil-bank depletion hypothesis could be gathered by experimentally exposing propagules to simulated wildfires.

It is currently unclear whether changes in bryophyte communities induced by shifting fire regimes will have consequences for the structure and function of desert ecosystems. While the intriguing topics of ecosystem resilience and functionality are beyond the scope of this study, I expect that local extirpation of bryophytes and depletion of their soil-bank reserves will have consequential effects on arid terrestrial ecosystems. Losses of soil-crust species are associated with corresponding declines in ecosystem functions (Bowker et al. 2010) including erosion and soil degradation (Chaudhary et al. 2009). Bryophytes exhibit low functional redundancy, as each species contributes individualistically to multiple simultaneous functions (Bowker et al. 2011). While further evidence is needed to validate the soil-bank depletion hypothesis, I infer that the effects of losing bryophyte species will be non-trivial and could lead to novel ecosystem states that share little in common with historical patterns in arid terrestrial ecosystems.

Implications for management in a world of increasing fire

Several strategies are available to resource managers hoping to retain bryophytes and associated ecosystem functions. First, rapid assays of cryptic soil-bank diversity could be performed in locations where fire management is planned, simply by collecting and germinating soil in covered greenhouse pots. Although taxonomic expertise will continue to limit the ability of managers to perform such assays, rapid inventories can quickly identify places where prescribed burning may be imprudent and can help prioritize locations for future fire suppression. Second, in the event of severe disturbances, it may be useful to supplement natural immigration by adding propagules when accelerated recovery is desired. A restoration approach could augment communities through direct transplants (Cole et al. 2010) and propagule inoculations (Belnap 1993; Bowker 2007). Managers can facilitate post-fire recovery of bryophyte communities by working cooperatively with dispersal in space and time, and by accounting for the direct influences of fires on communities. In view of changing fire regimes in the Mojave Desert and in other arid lands where exotic plant invasions promote fires, an understanding of post-fire colonization will be fundamental to guiding ecologists and practitioners towards scenarios that preserve biodiversity and the functional integrity of arid ecosystems.

Table 3.1. Site descriptions for fire survey sites at Red Rock Canyon NCA, southern Nevada.

Map ID	Fire name	Latitude	Longitude	Elevation (m a.s.l.)	Fire year	Fire size (ha)	Lutes fire severity[a]
1	Hillside	36.002°	–115.482°	1596	1980	12	4
2	Cottonwood	35.985°	–115.450°	1350	1980	1619	3
3	Red Rock 1993	35.994°	–115.449°	1287	1993	97	1
4	Blue Diamond	36.089°	–115.447°	1184	1993	16	2
5	Overlook	36.120°	–115.437°	1135	2005	25	4
6	Red Rock 2005	36.140°	–115.389°	1056	2005	17	2

[a] Lutes fire severity was a *post hoc* fire severity score ranging from 1 (severely burned) to 5 (unburned), based on remnant vegetation and litter in burned plots as compared to unburned reference plots (Lutes et al. 2006).

Table 3.2. Species checklist and key to abbreviations.

Abbreviation	Species	Family
Anohan	*Anoectangium handelii*	Pottiaceae
Bryarg	*Bryum argenteum*	Bryaceae
Brycae	*Bryum caespiticium*	Bryaceae
Cerpur	*Ceratodon purpureus*	Ditrichaceae
Croabe	*Crossidium aberrans*	Pottiaceae
Croser	*Crossidium seriatum*	Pottiaceae
Crosqu	*Crossidium squamiferum*	Pottiaceae
Didaus	*Didymodon australasiae*	Pottiaceae
Didvin	*Didymodon vinealis*	Pottiaceae
Encint	*Encalypta intermedia*	Encalyptaceae
Entmuh	*Entosthodon muhlenbergii*	Funariaceae
Fern	(not determined)	(not determined)
Funhyg	*Funaria hygrometrica*	Funariaceae
Griano	*Grimmia anodon*	Grimmiaceae
Gymaer	*Gymnostomum aeruginosum*	Pottiaceae
Micsta	*Microbryum starckeanum*	Pottiaceae
Phacus	*Phascum cuspidatum*	Pottiaceae
Ptelam	*Pterygoneurum lamellatum*	Pottiaceae
Pteova	*Pterygoneurum ovatum*	Pottiaceae
Ptesub	*Pterygoneurum subsessile*	Pottiaceae
Riccav	*Riccia cavernosa*	Ricciaceae
Syncan	*Syntrichia caninervis*	Pottiaceae
Synrur	*Syntrichia ruralis*	Pottiaceae
Toratr	*Tortula atrovirens*	Pottiaceae
Torbre	*Tortula brevipes*	Pottiaceae
Torine	*Tortula inermis*	Pottiaceae
Weiand	*Weissia andrewsii*	Pottiaceae

Table 3.3. Species relative frequencies according to fire and profile attributes (expressed as a percentage of the number of samples per category). Species abbreviations follow Table 3.2.

Species	Microsite		Profile			Burn severity					Burn year		
	Shrub	Open	Surface	Soil	Air	1	2	3	4	5	1980	1993	2005
Anohan	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.6	0.0	0.0	0.3	0.0	0.0
Bryarg	16.9	20.5	6.0	33.3	0.0	7.1	2.4	41.1	31.0	16.7	28.9	9.5	17.9
Brycae	21.3	21.8	6.0	39.2	0.0	17.9	4.2	42.9	27.4	19.8	35.1	12.8	16.7
Cerpur	0.6	0.6	1.3	0.0	0.0	0.0	0.0	0.6	0.0	1.0	1.8	0.0	0.0
Croabe	6.9	5.9	0.0	13.3	0.0	3.6	0.6	10.7	13.1	6.2	10.1	2.4	6.5
Croser	1.3	0.8	0.0	2.1	0.0	0.0	1.2	0.0	0.0	1.6	2.4	0.6	0.0
Crosqu	0.8	0.6	0.6	0.8	0.0	0.0	0.0	0.6	1.2	1.0	1.8	0.0	0.3
Didaus	9.6	9.8	2.5	17.9	0.0	0.0	1.2	23.8	27.4	6.5	12.2	1.5	15.5
Didvin	2.1	1.3	0.2	3.3	0.0	0.0	1.2	5.4	0.0	1.2	3.6	0.9	0.6
Encint	2.1	1.5	0.0	3.8	0.0	2.4	1.8	2.4	0.0	1.8	2.1	2.1	1.2
Entmuh	0.6	0.6	0.0	1.3	0.0	1.2	0.0	0.0	3.6	0.4	0.3	0.3	1.2
Fern	1.5	1.5	0.0	3.1	0.0	0.0	0.6	2.4	0.0	2.0	2.7	1.2	0.6
Funhyg	7.7	6.4	0.0	14.6	2.1	3.6	8.9	6.0	1.2	8.3	6.8	8.0	6.3
Griano	0.0	0.8	0.8	0.0	0.0	0.0	0.0	1.2	0.0	0.4	0.6	0.0	0.6
Gymaer	0.4	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.6	0.0	0.0
Micsta	4.0	3.0	0.0	7.3	0.0	0.0	0.0	7.1	20.2	1.2	3.6	0.0	6.8
Phacus	1.0	0.2	0.0	1.3	0.0	0.0	0.0	0.6	0.0	1.0	1.8	0.0	0.0
Ptelam	0.2	0.0	0.0	0.2	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Pteova	10.4	10.2	5.4	16.3	0.0	13.1	1.2	14.3	3.6	12.7	12.5	14.9	3.6
Ptesub	0.8	2.1	2.3	0.8	0.0	0.0	1.2	0.0	0.0	2.6	3.3	0.9	0.3
Riccav	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.3	0.0
Syncan	12.1	17.4	19.8	11.5	0.0	2.4	0.6	12.5	26.2	20.6	11.0	18.5	15.2
Synrur	6.7	6.4	7.1	6.7	0.0	0.0	0.0	7.7	0.0	10.5	18.5	0.6	0.6
Toratr	0.4	0.2	0.0	0.6	0.0	0.0	0.0	1.2	0.0	0.2	0.6	0.3	0.0
Torbre	1.3	0.6	0.0	1.9	0.0	0.0	0.6	0.0	1.2	1.4	0.0	1.2	1.5
Torine	6.0	2.3	0.6	7.9	0.0	3.6	0.6	3.0	0.0	6.3	5.7	5.7	0.9
Weiand	1.7	1.7	0.2	3.3	0.0	0.0	0.0	3.6	0.0	2.2	5.1	0.0	0.0
Sample size	480	528	480	480	48	84	168	168	84	504	336	336	336

Table 3.4. Species richness and beta-diversity summaries according to fire and profile attributes. Beta diversity was measured as the mean distance to group centroid in a principal coordinates analysis (Anderson et al. 2006); sample sizes differ from other analyses because uninformative zero-sum plots were removed (e.g., "Air" profile).

	Microsite		Profile			Burn severity					Burn year		
	Shrub	Open	Surface	Soil	Air	1	2	3	4	5	1980	1993	2005
Mean plot richness	1.16	1.16	0.53	1.91	0.02	0.56	0.26	1.88	1.56	1.26	1.71	0.82	0.96
SE plot richness	0.06	0.06	0.05	0.07	0.02	0.10	0.05	0.14	0.17	0.06	0.09	0.06	0.07
Cumulative total taxa	24	25	13	25	1	10	14	20	11	25	24	19	18
Cumulative unique taxa	2	3	2	13	0	1	0	1	0	2	5	2	0
Mean beta-diversity	0.513	0.491	0.463	0.446	--	0.406	0.481	0.333	0.387	0.508	0.461	0.472	0.506
SE beta-diversity	0.016	0.015	0.025	0.013	--	0.048	0.039	0.020	0.037	0.014	0.019	0.021	0.016
Beta-diversity sample size	71	71	49	93	--	11	14	24	12	81	53	45	44

Table 3.5. Tests for differences in beta-diversity: PERMDISP results for the full community data, based on Sørenson distances and 999 permutations of each factor.

Factor		Df	Sum sq.	Mean sq.	*F*-value	*P*(>*F*)	
Microsite	Groups	1	0.0173	0.0173	0.8087	0.366	
	Residuals	140	2.9915	0.0214			
Profile	Groups	1	0.0458	0.0458	2.0739	0.154	
	Residuals	140	3.0891	0.0221			
Burn severity	Groups	4	0.6934	0.1734	8.7540	0.001	***
	Residuals	137	2.7130	0.0198			
Burn year	Groups	2	0.0429	0.0215	1.0019	0.400	
	Residuals	139	2.9771	0.0214			

Table 3.6. Tests for differences in species composition: PERMANOVA results for the full community data, based on Bray-Curtis distances and 999 permutations of each factor.

Factor	Df	Sum sq.	Mean sq.	*F*-value	R^2	*P*(>*F*)	
Microsite	1	0.1500	0.1503	0.8370	0.0039	0.476	
Profile	1	6.3910	6.3908	35.5770	0.1668	0.001	***
Burn severity	4	4.9720	1.2431	6.9200	0.1298	0.001	***
Burn year	2	2.9120	1.4562	8.1070	0.0760	0.001	***
Residuals	133	23.8910	0.1796	0.6235			
Total	141	38.3170	1.0000				

Table 3.7. Test for differences in species richness: PROC MIXED (mixed-effects linear model) results for the full community data, based on restricted maximum likelihood estimation and Type III tests.

Factor	Df_{num}	Df_{den}	*F*-value	*P*(>*F*)	
Microsite	1	179	1.23	0.268	
Profile	1	179	128.17	< 0.0001	***
Burn severity	4	179	13.68	< 0.0001	***
Burn year	2	179	4.61	0.011	*
Profile × Burn severity	4	179	7.11	< 0.0001	***

Table 3.8. Test for differences in beta-diversity: PERMDISP results for the soil profile data, based on Bray-Curtis distances and 999 permutations of each factor.

Factor		Df	Sum sq.	Mean sq.	*F*-value	*P*(>*F*)	
Microsite	Groups	1	0.077875	0.077875	4.56825	0.047	
	Residuals	378	6.443806	0.017047	NA	NA	
Burn severity	Groups	4	2.274902	0.568726	31.79348	0.001	***
	Residuals	375	6.708044	0.017888	NA	NA	
Burnyear	Groups	2	0.626813	0.313406	16.6323	0.001	***
	Residuals	377	7.103897	0.018843	NA	NA	

Table 3.9. Test for differences in species composition: PERMANOVA results for the soil profile data, based on Bray-Curtis distances and 999 permutations of each factor.

Factor	Df	Sum sq.	Mean sq.	*F*-value	R^2	*P*(>*F*)	
Microsite	1	0.43	0.42981	1.4806	0.00346	0.186	
Burn severity	4	10.943	2.73575	9.4242	0.08807	0.001	***
Burnyear	2	4.899	2.44947	8.438	0.03942	0.001	***
Residuals	372	107.988	0.29029	0.86905			
Total	379	124.26	1				

Table 3.10. Test for differences in species richness: PROC MIXED (mixed-effects linear model) results for the soil profile data, based on restricted maximum likelihood estimation and Type III tests.

Factor	Df_{num}	Df_{den}	*F*-value	*P*(>*F*)	
Microsite	1	88	1.48	0.227	
Burn severity	4	88	16.52	< 0.0001	***
Burn year	2	88	3.73	0.028	*

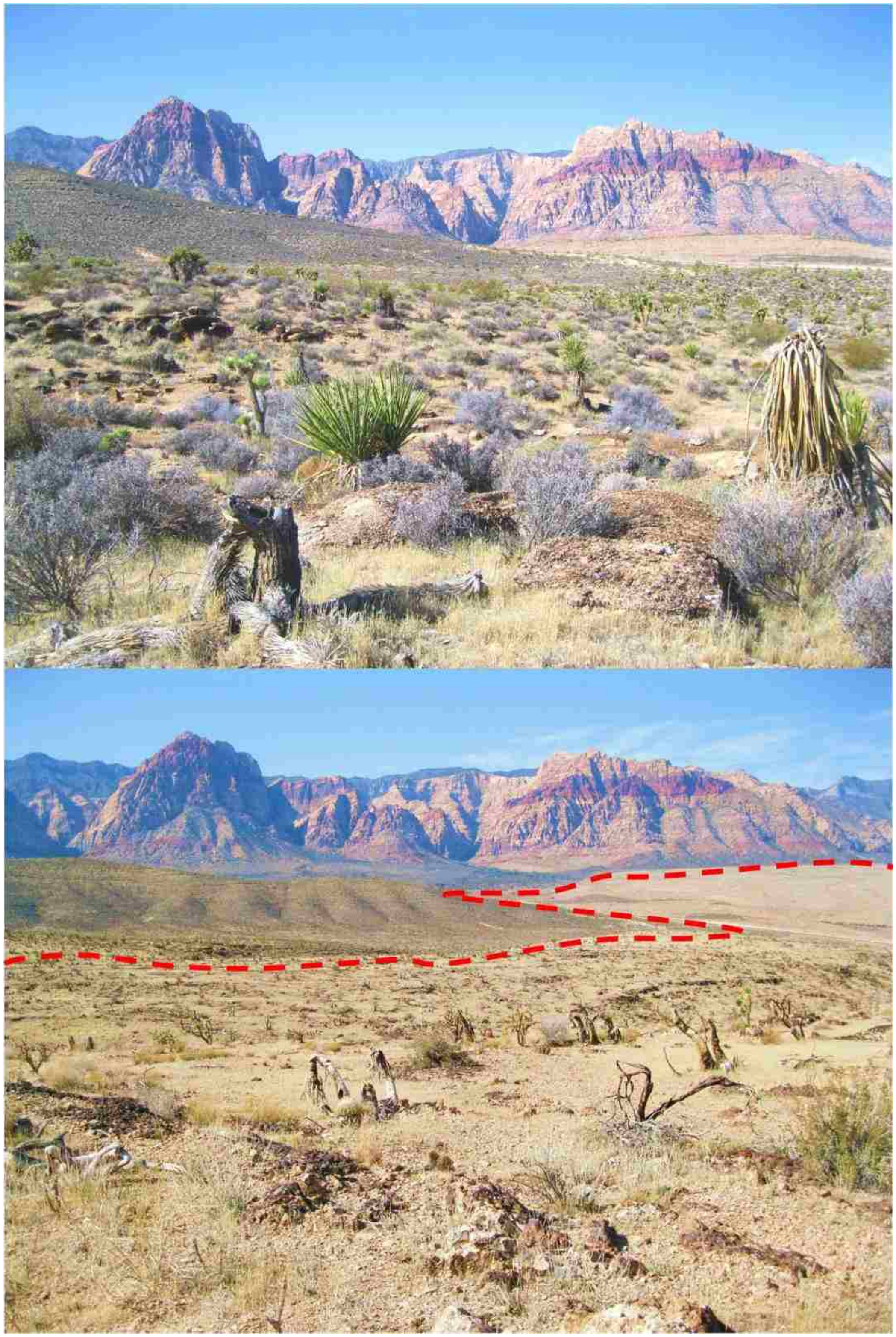


Figure 3.1. Intact (top) and burned (bottom) landscapes at Red Rock Canyon National Conservation Area. The "Overlook" fire of 2005 removed most native shrubs and promoted the proliferation of invasive, fire-stimulating annual grasses (light tan vegetation) in burned areas (below red dotted line in lower photo).

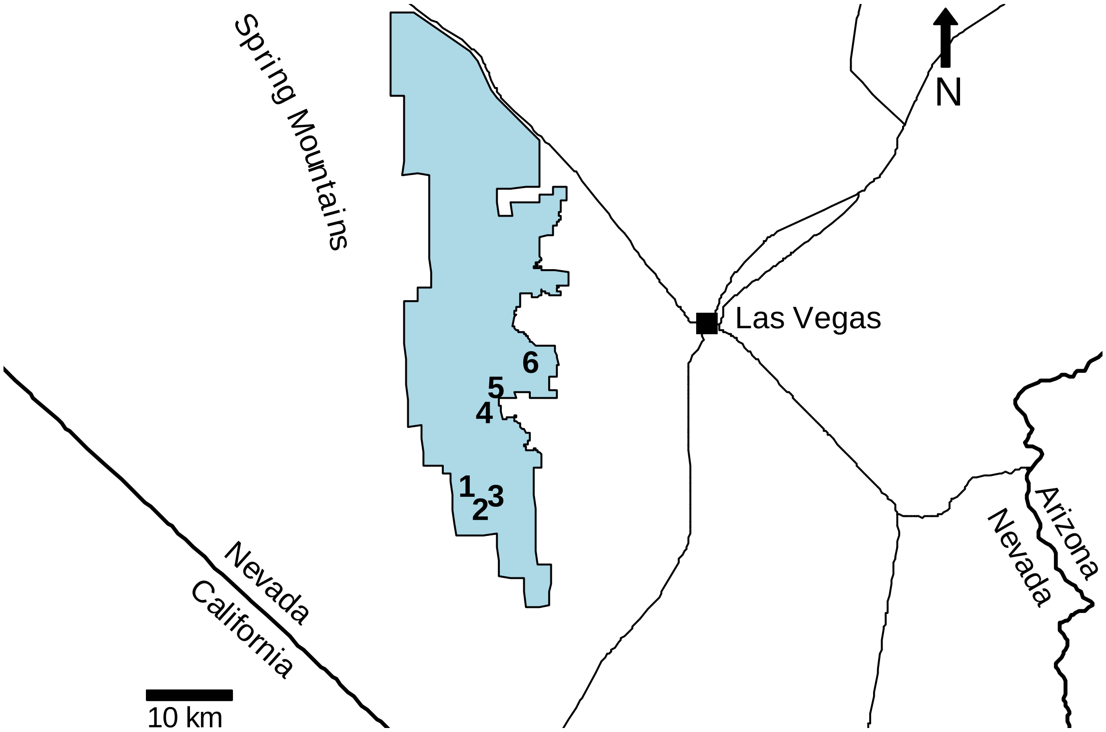


Figure 3.2. Map of study sites (numbered according to Table 3.1) at Red Rock Canyon National Conservation Area (shaded polygon) near the Spring Mountains of southern Nevada.

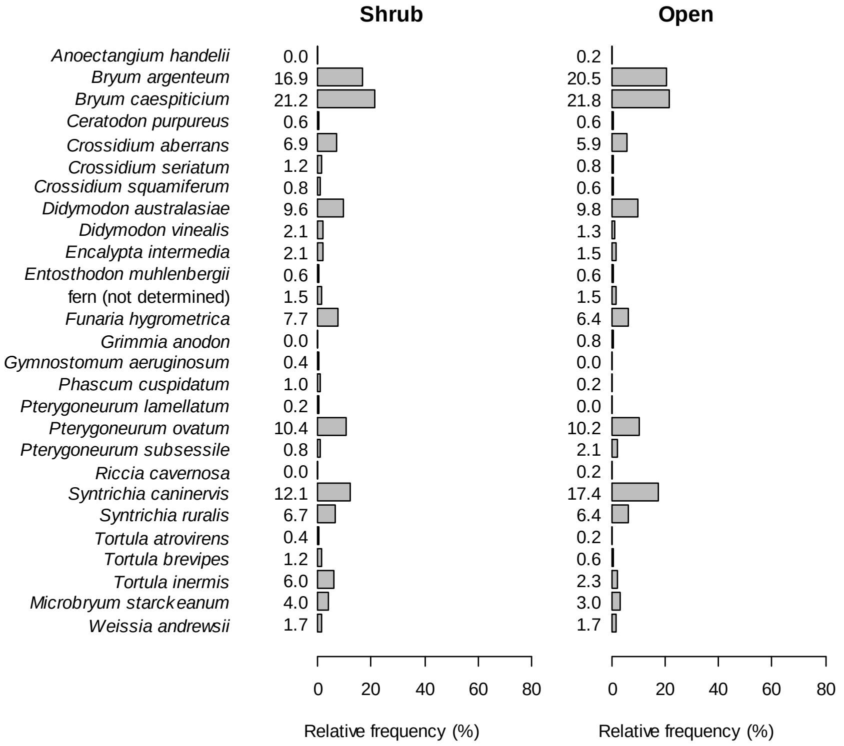


Figure 3.3. Species relative frequencies in each of two microsites.

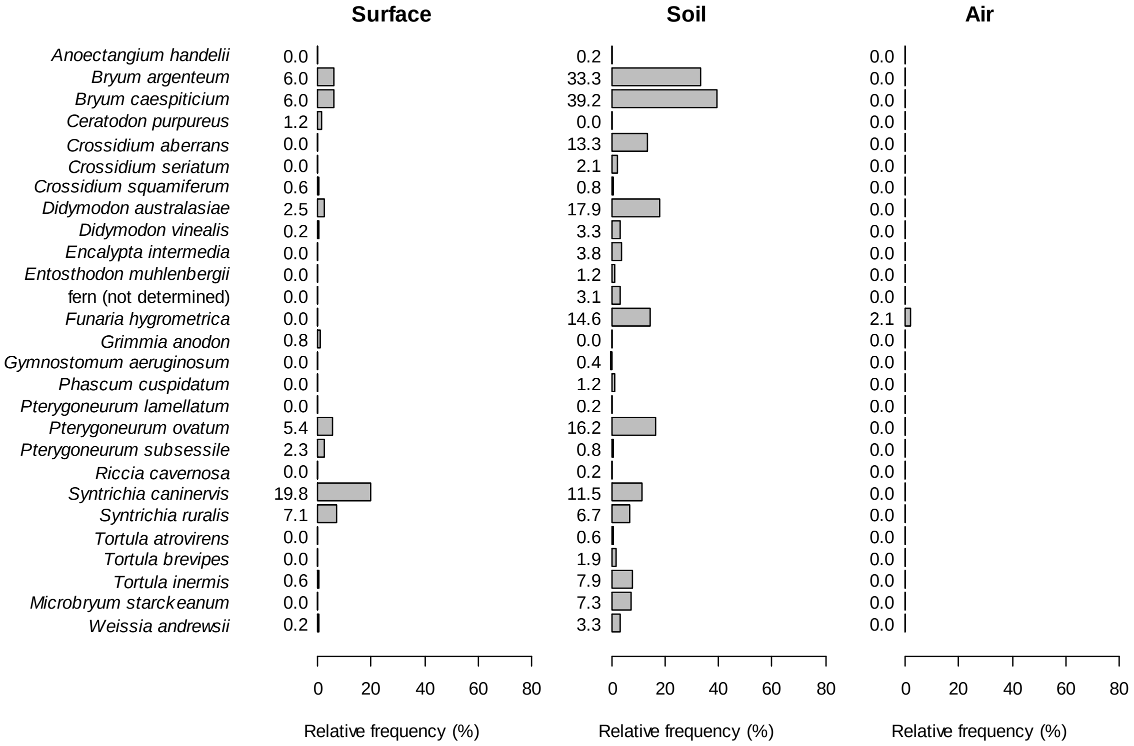


Figure 3.4. Species relative frequencies in each of three profiles.

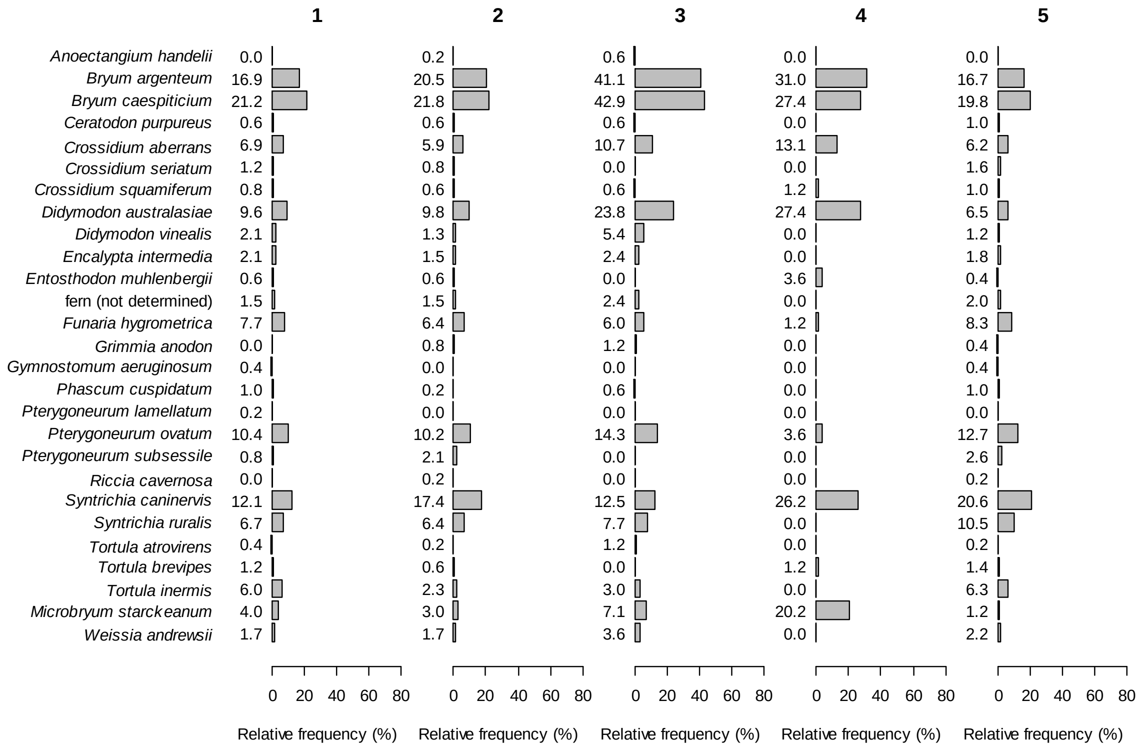


Figure 3.5. Species relative frequencies in each of five burn severity classes, based on a *post hoc* severity score ranging from 1 (severely burned) to 5 (unburned).

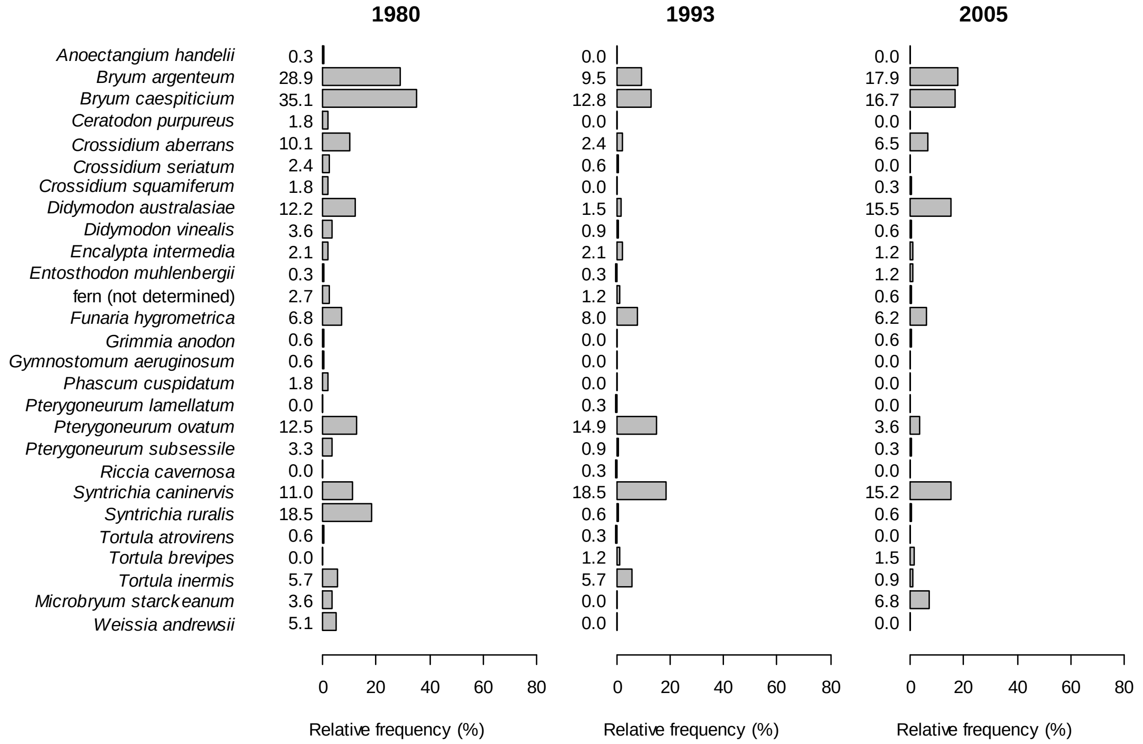


Figure 3.6. Species relative frequencies in each of three burn years.

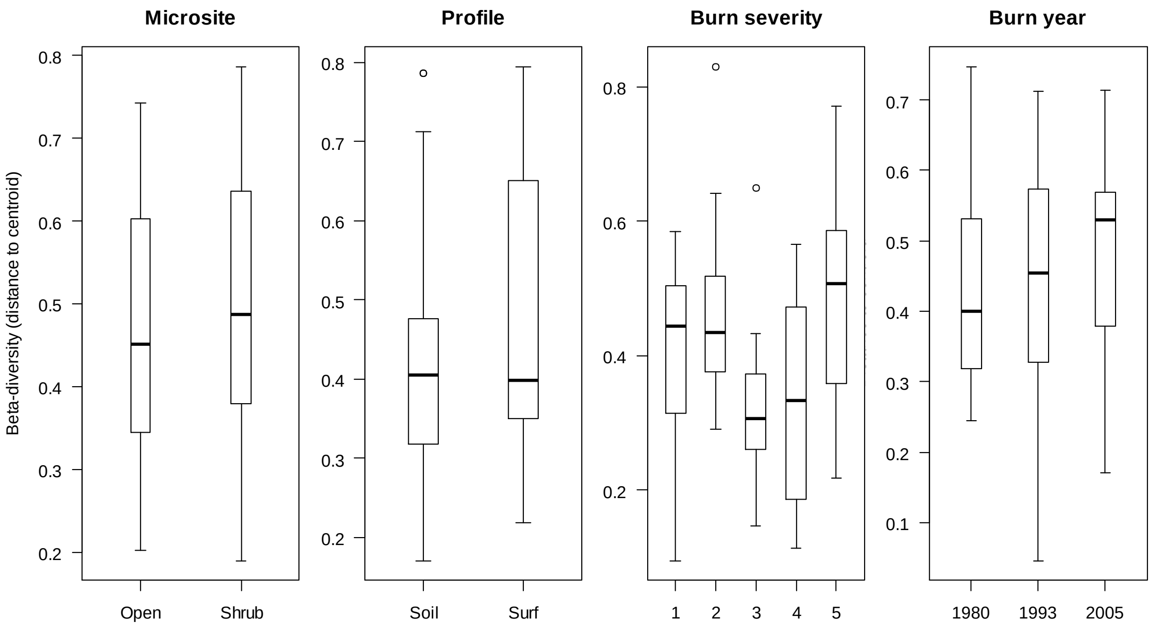
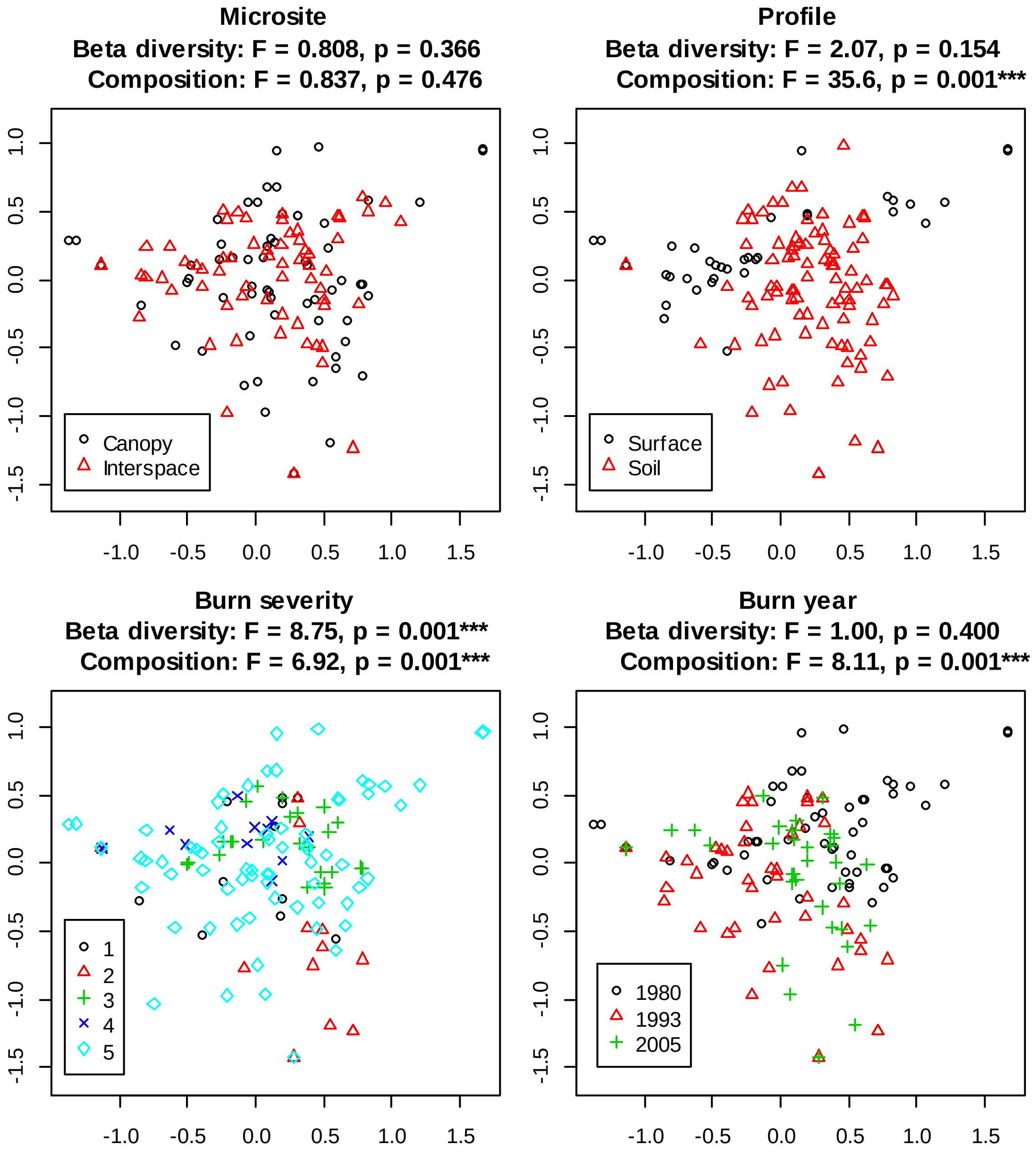


Figure 3.7. Beta-diversity of plots according to fire and profile attributes. Bold central bars are median values of beta-diversity (measured as distance to multivariate centroid), box ends are 1st and 3rd quartile values, whisker ends are ±1.5 times the interquartile range, and circles are outliers beyond the 1.5 interquartile range.


Microsite
Beta diversity: F = 0.808, p = 0.366
Composition: F = 0.837, p = 0.476

Profile
Beta diversity: F = 2.07, p = 0.154
Composition: F = 35.6, p = 0.001***

Burn severity
Beta diversity: F = 8.75, p = 0.001***
Composition: F = 6.92, p = 0.001***

Burn year
Beta diversity: F = 1.00, p = 0.400
Composition: F = 8.11, p = 0.001***

Figure 3.8. Results of NMS (non-metric multi-dimensional scaling) ordination of bryophyte communities at Red Rock Canyon. Plots (points) were ordinated in species space in the first two of three NMS dimensions (stress = 0.149). Plot scores were based on Bray-Curtis distances using the frequency of each bryophyte species in 5 replicated microplots. See text for tests of beta-diversity (multivariate dispersion) and composition (multivariate position).

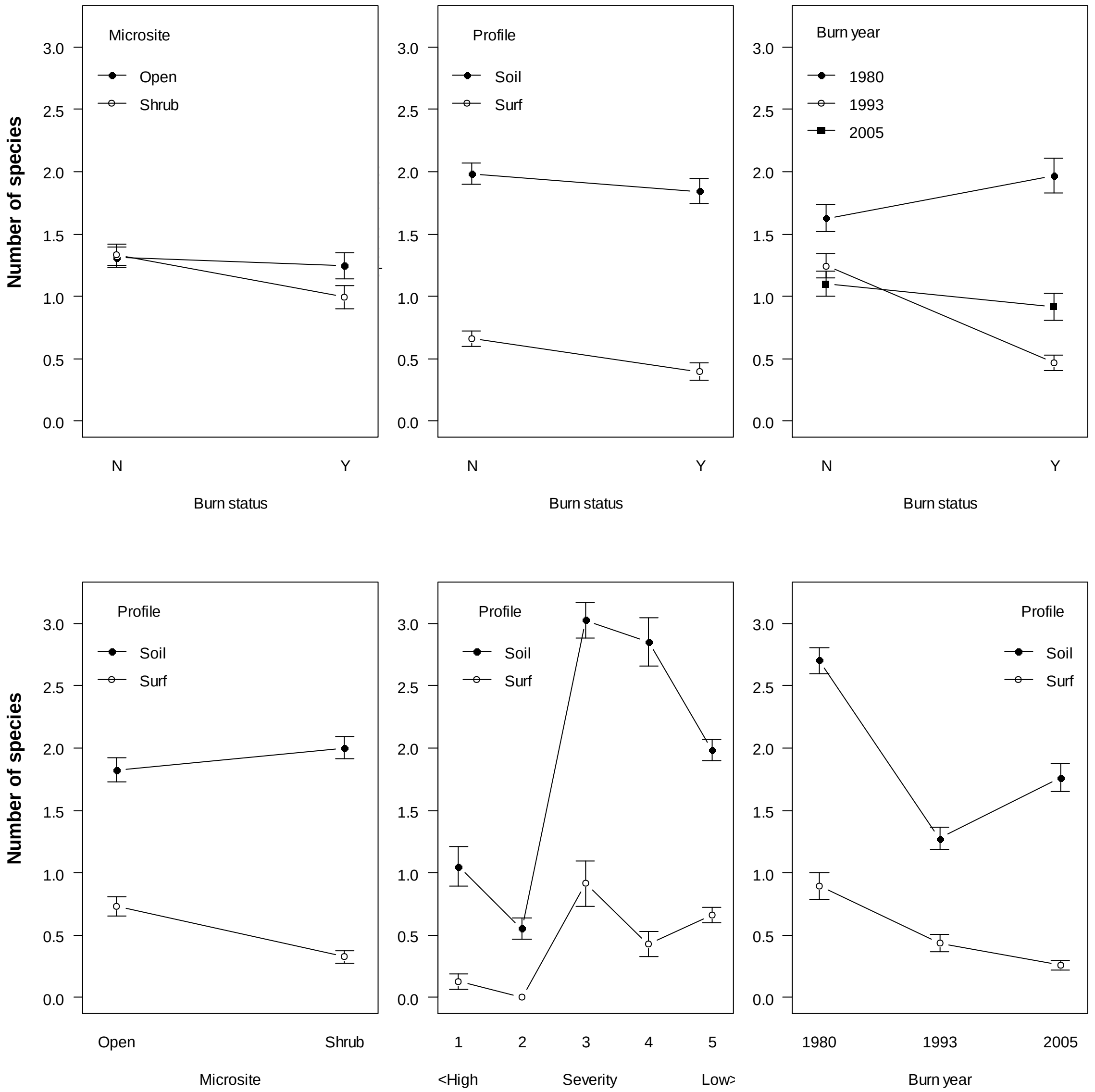


Figure 3.9. Species richness of plots according to fire and profile attributes. Symbols are mean values and whiskers are ±1 standard error. Severity was a *post hoc* fire severity score ranging from 1 (severely burned) to 5 (unburned).

CHAPTER 4

LOCAL HABITAT OR DISPERSAL: CONSTRAINTS ON NON-VASCULAR PLANT DIVERSITY IN THE MOJAVE DESERT

Abstract

In desert plant communities of the southwestern United States, patterns of diversity can be shaped by processes that are either environmental (e.g., habitat limitation) or spatial (e.g., dispersal limitation), and whose strength and relative influence can vary across scales. This information is essential for practitioners tasked with preserving biodiversity and identifying potential habitat types. I surveyed diversity in a stable xeric bryophyte community within a regular sampling grid of 1000 adjacent cells. Eigenvector mapping and variation partitioning revealed that purely environmental processes accounted for little of the variation in community composition (2.0%); most variation was attributed either to environments that were spatially structured (25.6%) or to purely spatial dispersal influences (28.0%). At three nested scales, influential environmental factors were related to topography (broad-scale >5 m^2), shrub "islands" (meso-scale 1−5 m^2), and physical substrate characteristics (fine-scale < 1 m^2). Patterns of dispersal limitation were less obviously scale-dependent at the community level, yet were important when considering individual species, which showed a wide range of spatial autocorrelation across scales (Moran's *I* range = –0.003 to 0.601). I also delineated seven habitat types using a predictive classification method based on four predictors: south exposure, slope, shrub cover, and lichen cover. These findings suggest that bryophyte diversity is the joint result of spatial dispersal limitations and the distinctive spatially patterned environment of desert shrublands. Conservation efforts must not only account for dispersal limitations of individual species of concern, but should also seek to retain native shrubs and consequent landscape physiognomy. The approach used in this study demonstrates the utility of pairing multi-scale landscape surveys with predictive regression trees to identify suitable habitats for non-vascular desert plants.

Introduction

The preservation of biodiversity requires knowledge of how species are distributed, in addition to understanding the causal processes that underlie distributions. While niche concepts have traditionally emphasized the role of environmental and biotic interactions in local plant communities, recent advances in metacommunity ecology have profitably integrated spatial dispersal into conventional frameworks (Cottenie 2005; Leibold and McPeek 2006). Metacommunity perspectives depict local communities as subsets drawn from the regional species pool, and the composition of local communities as the product of species being able to both arrive at sites and tolerate local conditions. Therefore, local community composition is "an integrative response" (Dray et al. 2012) which reflects the collective environmental, spatial, and historical influences experienced by a given plant community. Assessing community composition across landscapes will help resource managers not only document and manage diversity, but also make inferences about formative processes.

One way to clarify how species arrive and persist in local communities is by "partialling out" the unique contributions of environmental and spatial processes (Legendre et al. 2012). *Unique* contributions can be supplemented by *joint* environment–space influences which are defined by spatial autocorrelation (when nearby points share greater environmental similarity than more distant points; Legendre 1993). Such spatially structured environments include, for example, many limiting resources in North American deserts (e.g., nutrients, water, shade) which decline with increasing distance from perennial shrubs (Schlesinger et al. 1996). Distinguishing influences that are [a] purely environmental, [b] purely spatial, or [a∩b] the joint result of spatially structured environments will help ecologists and practitioners identify some of the latent processes that organize communities.

Principles concerning environment–space processes can be demonstrated most clearly in undisturbed systems where competitive interactions are not strong; this is an apt description for bryophyte communities comprising biotic soil crusts in arid regions. The minor consequence of competitive interactions among bryophytes (Bates 1988; During and Lloret 2001) suggests that patterns of their diversity are largely the result of abiotic environments and spatial processes possibly related to dispersal. Despite their limited stature, bryophytes are well adapted to the Mojave Desert of the southwestern United States, where they stabilize soils, capture and distribute nutrients, regulate seed germination, and colonize disturbed areas (Belnap and Lange 2001). Although desert bryophytes are commonly assumed to disperse quite freely (Zander 1979), successful spore production in the Mojave Desert is often complicated by mate limitation (Stark et al. 2005) and excessive abiotic stress (Stark 2001), leaving open the question of dispersal limitation. Although it is challenging to directly measure dispersal, spatially explicit surveys can resolve cases of propagule- or dispersal-limitation by their tell-tale spatial signatures.

Resource managers and conservation practitioners require predictive methods to fulfill mandates not only for documenting biodiversity, but also for cataloging community types and classifying habitats to guide management actions like restoration or fire suppression. Multivariate regression trees (MRT; De'ath 2002) are one solution for creating classifications based on community responses to environments, and could easily be paired with existing landscape-scale site surveys. The MRT approach resembles a multivariate version of linear regression in which species responses can be predicted by values of environmental variables – the product is a decision tree in which splits are based on threshold values of significant environmental predictors, and terminus branches indicate unique community or habitat types. Predictive classifications have previously been applied to non-vascular plant communities in Australia (Read et al. 2008), and could help classify similar communities in the Mojave Desert.

In this study, I addressed three major questions regarding desert bryophytes in a case-study community. First, what are the relative contributions of processes associated with [a] environment, [b] space, and [a∩b] spatially structured environment? I expected that species composition would be filtered most strongly by stressful abiotic environments, whether spatially structured or not, and very little evidence of dispersal limitation. Second, what are the influential factors associated with each of these three processes as observed at different scales? I expected broad-scale environmental control to predominate over fine-scale influences. And finally, which environmental factors can successfully predict habitat types based on community composition? I identified factors related to water availability and shrub islands as possible effective predictors. In general, environmental influences (spatially structured, or not) were expected to predominate over purely spatial dispersal processes in determining species compositions.

Materials and Methods

Study site

The study site at Red Rock Canyon National Conservation Area (NCA) is ~25 km southwest of the city of Las Vegas in southern Nevada (36.006° N, –115.452°; 1334 m a.s.l.; Fig. 4.1). The site consisted of an open alluvial fan at the base of calcareous sandstone cliffs, sloping gently (~6%) to the northeast. Substrates were shallow, well-drained, loamy-skeletal soils derived from calcareous sandstone, dolomite, and limestone (Lato 2006), which are typical of the region. Annual rainfall in the vicinity is very sparse (mean = 283 mm; SD ± 127 mm), falling mainly as winter showers and occasional late-summer monsoons (NCDC records for Spring Mountain State Park, period 1977–2011). Local vegetation was dominated by the perennial evergreen shrub *Coleogyne ramosissima* Torr. (blackbrush), although other frequent vascular plants included *Ephedra nevadensis* S. Watson, *Encelia farinosa* A. Gray ex Torr., *Thamnosma montana* Torr. & Frém., *Yucca schidigera* Roezl ex Ortgies, and *Yucca baccata* Torr. (Fig. 4.2). At least 104 taxa comprise the bryophyte species pool in the Red Rock Canyon vicinity (CNABH 2012). The site was selected for its relatively undisturbed condition and abundant bryophyte soil crusts to minimize ambiguous joint absences of species (Legendre and Legendre 2012), and to eliminate spatial patterns possibly produced by unobserved disturbances. While livestock grazing in the area is likely to have occurred in the last 100 years, and feral burros and horses have access to the site, there was no apparent evidence of disturbance to soil crusts or other vegetation.

Likewise, the intact state of mature evergreen shrubs and perennial forbs implied that no wildfires have recently disturbed the site, contrary to nearby sites in the region.

Field measurements

I established a 1 m × 40 m survey plot, bounded by reference string lines and oriented with the long axis running approximately SE–NW along a 124° azimuth (Fig. 4.2). Minor topographic features crossed the plot perpendicular to the long axis (two dry washes < 2 m vertical relief; Fig. 4.3*a*). A regular, uniform grid of contiguous square (20 × 20 cm) sample cells completely covered the survey area, (5 × 200 cells in dimension; N = 1000), and each was assigned unique geospatial coordinates corresponding with its northwest corner. Within each cell, I visually estimated the percent areal cover of bryophyte species using a 0 – 10 categorical abundance scale (Peet et al. 1998); the same scale was used to estimate aerially projected cover of other plants and substrates including shrubs, forbs, grass, litter, soil, and three classes of rock size (rock diameters 0.1–2 cm, 2–10 cm, and > 10 cm). I recorded presence/absence of shrub stems in each cell according to shrub species, as well as presence/absence of localized rodent activity shown by obvious soil disturbance (Table 4.1). I measured slope and aspect for later calculation of two synthetic variables: a heat load index calculated with Eq. 3 in McCune and Keon (2002), and a “south exposure” index indicating absolute angular divergence from 360° north. All field measurements occurred on clear, sunny days in late April and early May of 2012.

Statistical analyses

I used spatial eigenvector mapping in conjunction with variation partitioning and multivariate regression trees to examine scale-dependent variation in the community. Species data were relativized by column totals, and environmental data were scaled and centered to *z*-scores prior to analysis. Significance criteria were $P \leq 0.05$ unless otherwise specified. All analyses were performed in the R computing environment (version 2.15.0; R Core Development Team 2012) using the supplemental packages *ape, packfor, spacemakeR, ade4, spdep, vegan, PCNM, MVPARTwrap,* and their dependencies.

The spatial eigenvector technique, (principal coordinates of neighbor matrices, PCNM; Borcard and Legendre 2002), was essentially an ordination of the community as constrained to forward-selected environmental and spatial explanatory variables (cf. Dray et al. [2006] and Blanchet et al. [2008] for detailed procedures). In a parallel analysis, I parsed the global PCNM model into three complementary sub-models (Borcard et al. 2011) representing nested broad-, medium-, and fine-scale patterns across the 40 m^2 area; respectively, these scales approximated areas > 5 m^2, 1−5 m^2, and < 1 m^2.

Complementary to the multivariate PCNM analyses, I identified the degree of univariate spatial autocorrelation (a proxy for dispersal limitation) specific to each individual species by calculating Moran's *I* statistic with 999 Monte Carlo permutations (Cliff and Ord 1981). I also identified the influence of selected environmental variables by testing for differences in species richness (using *t*-tests) among sample cells defined by environmental thresholds (e.g., north vs. south slopes, shrub cover present or not, litter shallow or deep, lichen cover present or not). Despite that spatial autocorrelation could violate the *t*-test's assumption of independence among observations, I relaxed this assumption because the intent was to confirm the influence of specific factors suggested by the multivariate tests (which explicitly accounted for spatial autocorrelation).

To partition the amount of variation in community composition due to [a] environmental, [b] spatial, and [a∩b] spatially structured environmental contributions, I performed a redundancy analysis (RDA) of the community data based on the environmental and spatial explanatory variables used in the PCNM analysis, and examined the significance of partitions with permutational analysis of variance (Oksanen et al. 2011). This variation partitioning was performed both on the global PCNM model as well as the scale-specific sub-models, but I report only results for the global model to simplify interpretation.

I classified habitat types using multivariate regression trees (MRT; De'ath 2002), based on sixteen environmental variables (Table 4.1). The criterion for final model selection was minimization of cross-validated relative error (CVRE). Unlike other clustering methods, this technique is appealing in that it is predictive – each node of the final selected tree represented a threshold value for a selected predictor, so the tree may be used as a “decision tree” for site or habitat classifications.

Results

General community patterns

Bryophyte species were present in 635 of 1000 cells of the sampling grid; 9 species were recorded in the entire 40 m^2 study area. The dominant bryophyte was *Syntrichia caninervis* (Table 4.2), which formed short turfs across most of the area (597 of 1000 sample cells). Species richness in individual 20 × 20 cm sample cells ranged from 0 – 5 bryophyte species (mean = 0.63; SD ± 0.48), and was significantly greater in sample cells located on north aspects, those located outside shrub canopies, those with less than 10 mm of litter, and those with greater than a trace of lichen cover (Table 4.3). Species differed in their individual distributions over the 1000-cell sampling grid (Fig. 4.3), and also differed in their degree of spatial autocorrelation across scales (Fig. 4.4).

Spatial eigenvector mapping and variation partitioning

The forward selection yielded a subset of 177 positive eigenvectors modeling broad to fine spatial scales from the 715 extracted from the spatial matrix. Of the 16 original environmental variables, 11 were chosen by forward selection. Based on these, the global PCNM analysis explained 55.6% of the variation in the community data along 9 global canonical axes, while spatial decomposition yielded 8, 7, and 5 significant canonical axes for the broad, medium, and fine spatial scales, respectively. Variables correlated with broad-scale axes were characterized by macrotopography (south exposure, slope, heat load, and topographic position relative to dry washes). Medium scales were characterized by substrate variables and shrub patterning (positive associations with lichen and rock cover absent under shrubs, and negative associations with grass and soil cover found under shrubs). Fine-scale patterns were negatively related to substrate variables including litter cover, but these patterns were weak and fine-scale canonical axes explained little of the total variation (first axis $R^2 = 0.004$).

The entire set of environmental and spatial variables explained 55.6% of the variation in the global community data. Of this, 2.0% was attributed to environmental variables alone, 28.0% was attributed to spatial variables alone, and 25.6% was the joint influence of spatially structured environments ($P < 0.005$ for estimable partitions).

Habitat classification analysis

The selected MRT had a cross-validated relative error (*CVRE*) = 0.913 and featured seven habitat types as characterized by environmental variables and species (Fig. 4.5). Tree splits (nodes) were based on combinations of the following predictors: south exposure, slope, lichen cover, and shrub cover.

Discussion

This investigation of a bryophyte community in the southwestern United States revealed nearly equal influences of habitat and dispersal limitations, although patterns of each varied according to spatial scale and individual species. Topography, soil moisture, shade, and litter created heterogeneous substrate patches which interacted with dispersal limitations. I also classified seven habitat types based on species responses to environmental patterning, and assessed the utility of these methods for applications to resource management situations.

General community patterns

Species composition and richness (9 species) at Red Rock Canyon corresponded well with those found at nearby Mojave Desert sites. I recorded two more bryophyte species than were found ~20 km north at similar elevations within Red Rock Canyon NCA (Bowker et al. 2000), and two fewer species than were found at a site ~45 km north (Thompson et al. 2005). At a more distant low-elevation site (Rock Valley, Nevada, 1000 m a.s.l.), Nash et al. (1977) reported only 3 bryophyte species in an area > 50 times larger than the grid used in the current study, a discrepancy which likely reflects some combination of differing sampling methods, elevation and disturbance history between sites.

Contributions of environmental and spatial processes

Agreeing with expectations, much variation in community composition at Red Rock Canyon was attributed to environments that were spatially structured (25.6%), while an unexpectedly small amount was explained by purely environmental processes (2.0%), suggesting that spatially structured habitats are more important than those where environmental factors change independently of location. I also found substantial evidence of purely spatial influences (28.0% of community variation) which are attributable to dispersal limitation. Similar levels of environmental control have been documented in temperate-zone bryophyte (Heino et al. 2011) and fern communities (Gilbert and Lechowicz 2004; Karst et al. 2005), as well as tropical fern communities (Tuomisto et al. 2003; Jones et al. 2008).

The amount of variation explained by the global model (55.6%) is comparable with other studies employing similar analytical methods (e.g., Legendre et al. 2009). Unexplained variation is likely the result of unmeasured environmental variables (Borcard et al. 2004). While variation partitioning could overestimate the spatial component (Gilbert and Bennett 2010; Smith and Lundholm 2010), this study nevertheless accounted for spatial autocorrelation (non-independence between close sites) and found strong support for the role of dispersal limitation in this desert bryophyte community. To conclusively eliminate historical disturbance or demographic events that might yield similar spatial patterns (Borcard et al. 2011), future studies could use permanent plots to track temporal dynamics.

Scale-dependent habitat limitation

Influential environmental factors differed characteristically at three nested scales. Broad-scale community patterns (> 5 m^2) reflected the influence of physical topography, especially as related to the orientation of dry washes where northerly and easterly aspects exhibited lower heat loads and presumably longer periods of moisture retention. Aspect–moisture relations limit the abundance of desert soil crust organisms (Bowker et al. 2006), constraining most bryophytes to north slopes, as confirmed by the significantly higher species richness on these aspects in the current study. Marginal habitats subjected to intense solar radiation (e.g., flat or south-facing slopes) are more likely to be inhabited only by long-lived, stress-tolerant species (i.e., the dominant *Syntrichia caninervis*), while favorable low-stress sites (e.g., north-facing slopes) can sustain more species, as observed at Red Rock Canyon (Fig. 4.3*f*).

At intermediate scales (1 – 5 m^2), spatially structured habitats were important. Shrub patterning had apparent facilitative effects on non-vascular plants at Red Rock Canyon, as observed elsewhere in southwestern U.S. deserts for shrubs and perennials (Walker et al. 2001; Miriti 2007), annuals (Venable et al. 2008), and non-vascular plants (Bowker et al. 2005). However, bryophytes were rarely found directly beneath shrubs, instead being frequent immediately outside the dripline of shrub canopies, as noted at other Mojave Desert sites (Bowker et al 2000; Thompson et al. 2005). While shade, soil moisture, and nutrients are spatially structured relative to shrubs (Walker et al. 2001; Bolling and Walker 2002), leaf litter (which inhibits bryophytes) also accumulates directly beneath shrubs (Martinéz et al. 2006), which may have a suppressive effect on bryophyte establishment or growth. This suggests that areas directly adjacent to (but not within) the zone of litter deposition beneath shrubs represent optimal locations for desert mosses at intermediate scales. Because of the major role that shrub islands play in determining meso-scale patterns of bryophyte diversity, the preservation of shrubs and accompanying landscape structure will be critical to maintaining suitable habitat for non-vascular desert plants.

Fine-scale (< 1 m^2) environmental control of non-vascular plant diversity was less definitive than at broader scales. Bryophyte diversity patterns only weakly related to a few fine-scale environmental variables (e.g., soil texture, lichen cover), and were scarcely distinguishable from patterns resulting from undetected historical events (e.g., disturbances, demographic processes) which become more evident at small scales (Borcard et al. 2011). While this study design accounted for spatial relationships, it was not able to resolve temporal relationships resulting from unmeasured disturbance or demographic processes, reflecting limitations of this approach that a permanent plot study might better clarify.

Scale-independent dispersal limitation

I found evidence of spatial dispersal limitation in this Mojave Desert community, signifying that local dispersal ability is a key determinant of bryophyte community structure in environmentally heterogeneous desert habitats. These findings agree with observations of local dispersal limitation among epiphytic (Löbel et al. 2006), epiphyllous (Zartman and Nascimiento 2006), and saxicolous (Virtanen and Oksanen 2007) bryophyte communities in forested areas. Dispersal limitation depended on the scale of observation in the community, and species had individualistic dispersion patterns ranging from weakly regular to strongly aggregated. For example, the congeners *Pterygoneurum ovatum* and *P. subsessile* exhibited opposing patterns of dispersal limitation, which were also evident in their mapped distributions (Figs. 4.3*h* and 4.3*i*). Making such species-specific information available to resource managers could streamline restoration efforts, as only those species that demonstrate spatial limitations need be targeted for restoration or reintroduction efforts. Species that appeared locally dispersal-limited within the sampling grid (e.g., *Bryum argenteum, Pterygoneurum subsessile*; Fig. 4.3) are not necessarily limited at the landscape level, as all species reported are regularly encountered elsewhere at Red Rock Canyon.

Habitat classification

The MRT successfully identified seven habitat types based on important environmental predictors (south exposure, percent slope, lichen cover, and shrub cover). Measuring these predictors in future surveys should be relatively fast and efficient, and need not use the intensive grid-sampling method. Despite the utility of the MRT approach for broader applications, in this study the final tree explained little community variation, probably because species were responding to unmeasured environmental variables that limit explanatory power (De'ath 2002).

For example, while I measured physical soil characteristics, I assumed that soil chemistry was not important because bryophyte mineral nutrient acquisition occurs primarily via atmospheric deposition, not from soil uptake (Bates 2000; Ayres 2006; but see Bowker et al. 2005). Measuring soil nutrients and soil moisture will likely improve the explanatory value of MRT for future delineation of community and habitat types at Red Rock Canyon.

Conservation applications and conclusion

Collectively, my findings suggest that the species composition of a bryophyte community was the joint result of spatial dispersal limitations and spatially patterned habitats in desert shrublands. When dispersal- and propagule-limitation are concerns, the maintenance of local diversity may require propagule supplementation for individual species of concern. Mojave Desert bryophytes, already particularly susceptible to local disturbances, commonly fail to reproduce and disperse; annual reproductive frequency in some populations is estimated to be as low as 3% (Bowker et al. 2000). Dispersal limitation can be overcome through transplants of mature colonies (Cole et al. 2010) and propagule inoculations (Belnap 1993). Because I found that dispersal interacted strongly with the spatial structure of the environment, management efforts should also seek to retain the physical structure of perennial shrub islands that sustain habitat heterogeneity. In particular, fire suppression at Red Rock Canyon would benefit bryophytes directly (by preventing burn mortality), and indirectly (by preserving landscape physiognomy provided by shrubs).

Pairing multi-scale landscape surveys with predictive decision trees is valuable for identifying suitable habitats for non-vascular desert plants. Multivariate regression trees provide predictive classifications, giving managers a better idea about which habitats to protect, where to target restoration efforts, and which species are appropriate to select for reintroduction to a given habitat. The task of collecting community data to fit a classification model benefits from grid-based surveys used in this study, yet a grid-based approach is not required. Instead, extending my findings from the local to the landscape level will require only a nominal modification of techniques to make study plots smaller and more numerous across landscapes. Extending the scope of observation from local to regional levels is more realistic for land managers whose areas of responsibility often cover many thousands of hectares.

Table 4.1. Environmental variables used in analyses of bryophytes at Red Rock Canyon.

Variable	Units	Median	Mean	SE	Range
Verbatim aspect	Degrees	121	166.40	3.37	0 – 359
Folded aspect	Degrees	73	67.25	0.99	0 – 171
Percent slope	Degrees	5	5.92	0.15	0 – 55
Heat load	Unitless index	0.97	0.96	0.00	0.56 – 1.09
Topographic position	Categorical[a]	3	2.96	0.03	1 – 5
Grass cover	Cover class[b]	3	3.70	0.06	0 – 9
Litter cover	Cover class	4	4.68	0.09	0 – 10
Litter depth	mm	5	10.53	0.37	0 – 62
Rock cover (< 2 mm)	Cover class	5	4.74	0.08	0 – 9
Rock cover (2 – 10 mm)	Cover class	6	5.01	0.09	0 – 9
Rock cover (> 10 mm)	Cover class	0	0.84	0.07	0 – 10
Bare soil cover	Cover class	2	2.53	0.07	0 – 9
Forb cover	Cover class	0	0.32	0.02	0 – 9
Lichen cover	Cover class	1	1.45	0.05	0 – 7
Shrub cover	Cover class	3	3.77	0.11	0 – 10
Shrub stem	Presence/absence	0	0.10	0.01	0 – 2
Rodent disturbance	Presence/absence	0	0.07	0.01	0 – 1

[a] Topographic position values: 1= ridgetop, 2 = ridge shoulder, 3 = slope side, 4 = slope foot, 5 = drainage. See text for calculations of south exposure and heat load.

[b] Cover classes follow Peet et al. (1998).

Table 4.2. Relative frequencies, spatial autocorrelation, and autecological characteristics of bryophyte species at Red Rock Canyon. Species are sorted by decreasing relative frequency.

Species code	Species	Relative frequency	Moran's *I* (*P*-value)[a]	Spore size (µm)	Specialized asexual propagules	Sexual condition[b]
Syncan	*Syntrichia caninervis*	59.7 %	0.588 ($P = 0.001$)	7–8	None	Dioicous
Pteova	*Pterygoneurum ovatum*	17.9 %	0.257 ($P = 0.001$)	25–38	None	Autoicous
Brycae	*Bryum caespiticium*	11.1 %	0. 235 ($P = 0.001$)	8–14	Infrequent tubers	Dioicous
Bryarg	*Bryum argenteum*	9.5 %	0.568 ($P = 0.001$)	8–15	Abundant bulbils	Dioicous
Ptesub	*Pterygoneurum subsessile*	7.9 %	0.601 ($P = 0.001$)	25–38	None	Autoicous
Torine	*Tortula inermis*	4.8 %	0.119 ($P = 0.001$)	11–15	None	Autoicous
Griano	*Grimmia anodon*	2.3 %	0.079 ($P = 0.001$)	8–10	None	Autoicous
Croser	*Crossidium seriatum*	0.6 %	0.186 ($P = 0.001$)	11–13	None	Autoicous
Synrur	*Syntrichia ruralis*	0.3 %	–0.003 ($P = 0.039$)	11–15	None	Dioicous

[a] Moran's *I* measures spatial aggregation: values close to 0 represent spatial randomness, values close to 1 represent spatial clustering, and negative values represent spatial regularity. Values in this table show Moran's *I* at a separation distance of 0.2 m.

[b] Reproductive characteristics derived from BFNA (2007). Sexual condition is strongly associated with high reproductive frequency for autoicous species, low frequency for dioicous species (Gemmell 1950).

Table 4.3. Results of tests for differences in mean species richness between influential habitats (one-sided univariate *t*-tests). North aspects were < 90° and > 270°; south aspects were the reverse.

Habitat variable	Habitat value	Mean number of species	Sample size	*t*-value	*P*-value
Aspect	North	1.32	584	6.170	< 0.0001
	South	0.89	416		
Shrub canopy cover	0–1%	1.59	502	14.486	< 0.0001
	≥1%	0.68	498		
Litter depth	< 10 mm	1.51	642	16.799	< 0.0001
	> 10 mm	0.48	358		
Lichen cover	≥1%	1.85	481	25.065	< 0.0001
	0–1%	0.48	519		

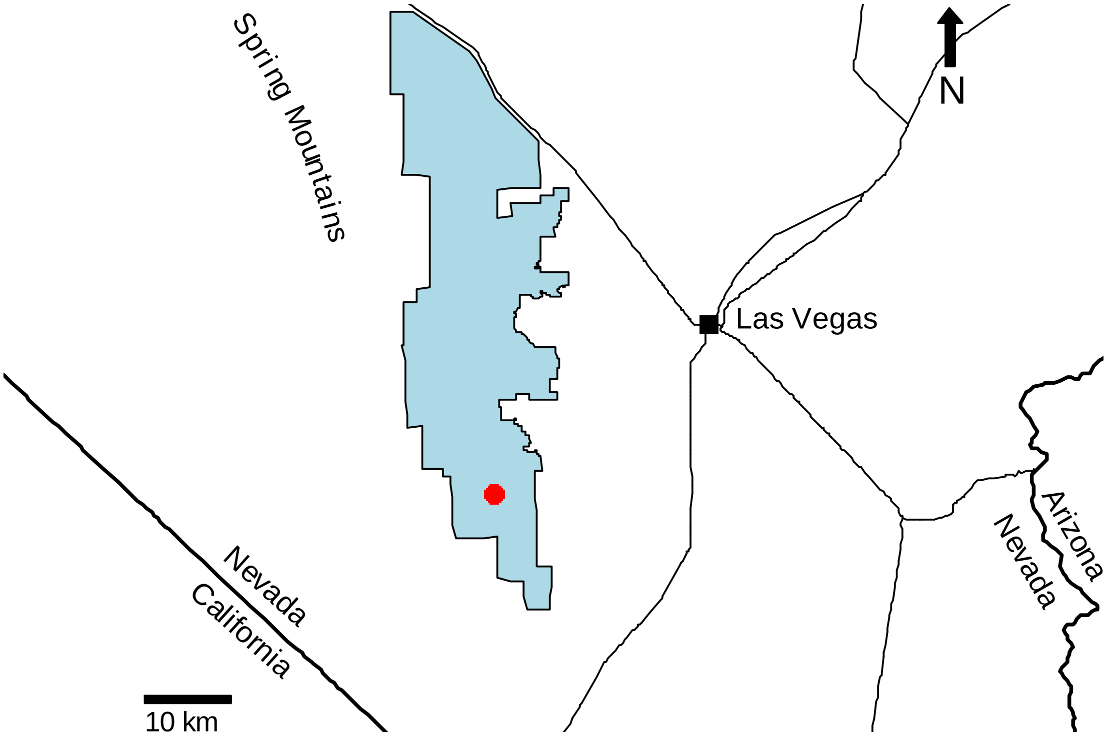


Fig. 4.1. Map of the study site (red filled circle) at Red Rock Canyon National Conservation Area (shaded polygon).

Figure 4.2. The 40 m^2 sampling area at Red Rock Canyon. Thin white lines define the boundaries of the surveyed area, within which were nested 1000 sample units (each 20 × 20 cm^2).

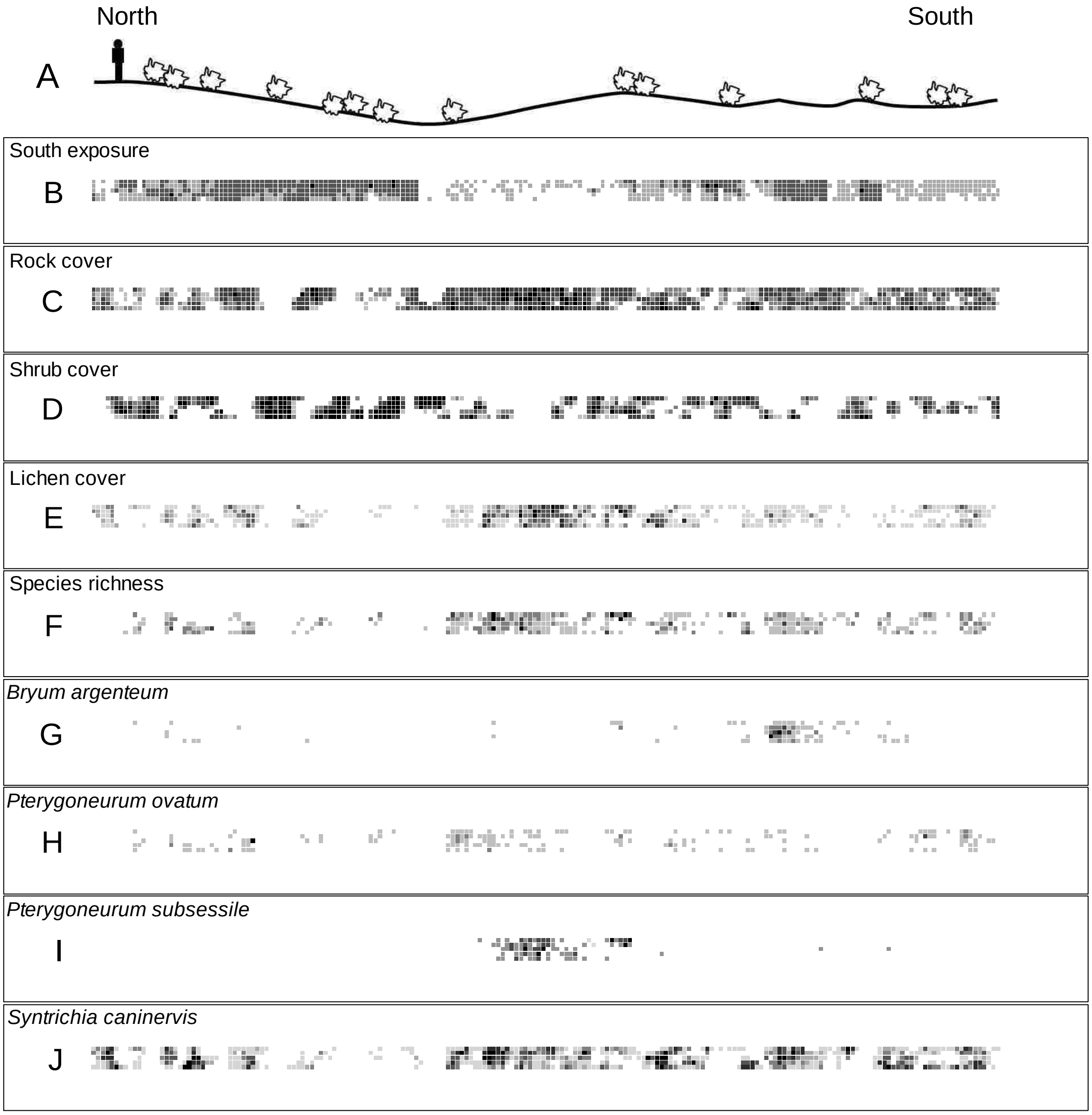


Figure 4.3. Graphical representations of the 40 m^2 sampling area at Red Rock Canyon. A side-view approximation of the site with scale shown by a hypothetical person and shrubs (panel A). Variables for selected environment (B–E) and species (F–J) data mapped onto the 40 m^2 sampling area, with darker shades indicating greater relative values. See text for units of measurement.

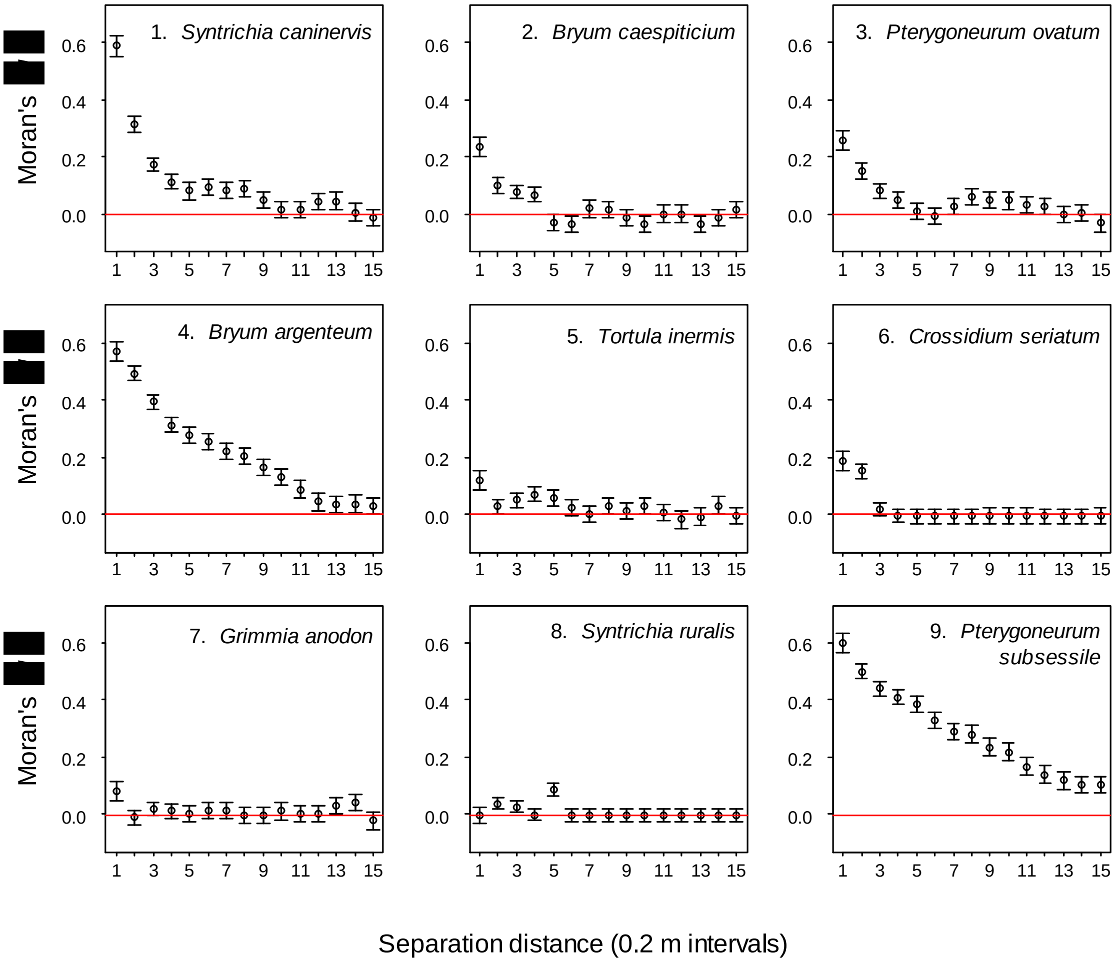


Figure 4.4. Spatial autocorrelograms for each of nine species. Moran's *I* values are plotted against increasing separation distances (at 0.2 m intervals). The Moran's *I* statistic measures the degree of spatial aggregation: values close to 0 represent spatial randomness, values close to 1 represent clustering, and negative values represent regularity. Species are ordered (1–9) according to decreasing relative frequency.

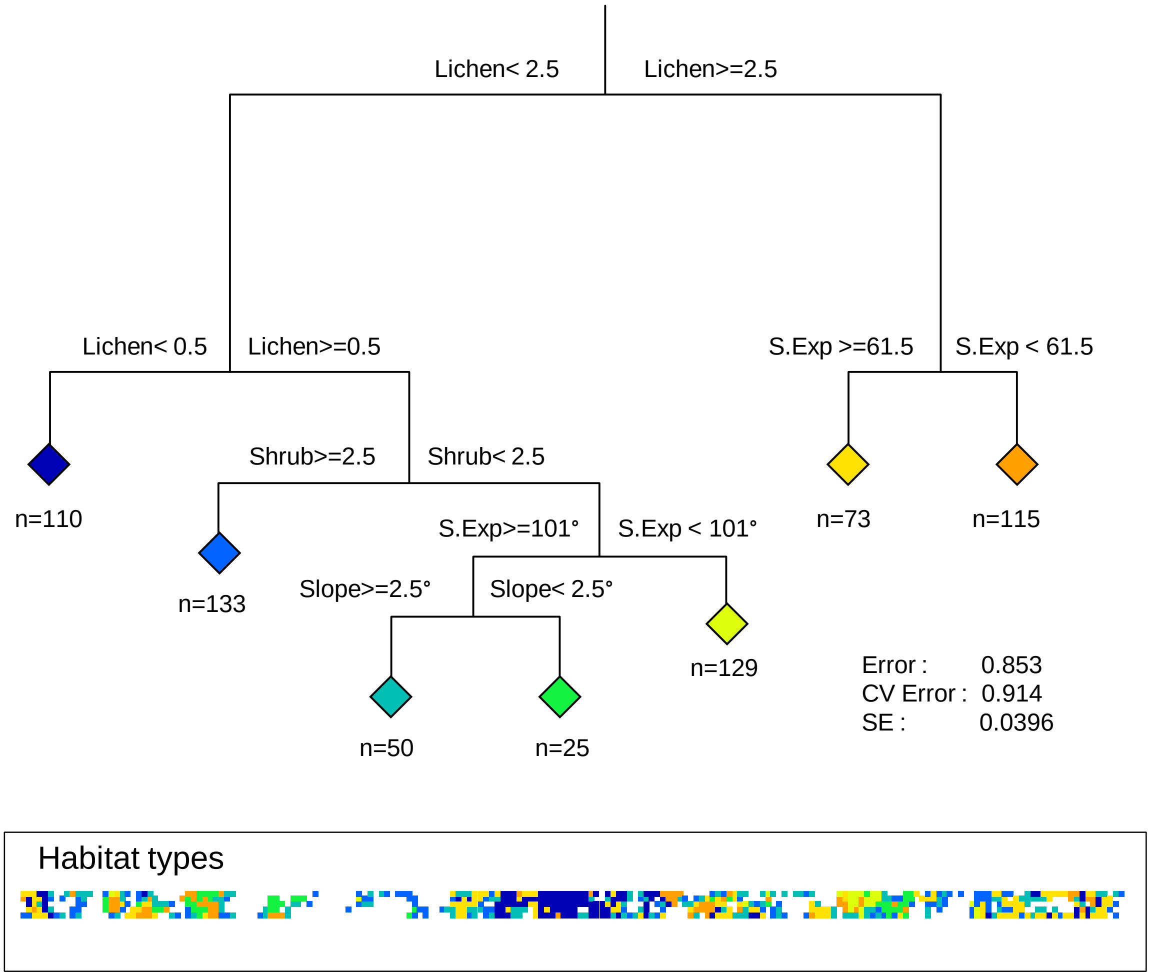


Figure 4.5. Membership in each of seven habitat types from a multivariate regression tree (color-coded branch tips; top) is plotted in geographic space onto the 40 m^2 sample grid (bottom). Threshold values of measured environmental variables are indicated at nodes preceding partitions, where cover classes are according to Peet et al. (1998). Labels: *Lichen* = lichen cover; *Shrub* = shrub cover; *Slope* = degree of slope; *S.Exp* = south exposure (aspect in degrees from 180°); *n* = number of plots per habitat type.

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Presentations:

Smith, R. J. 2012. Mining for mosses: Metacommunity dynamics at Red Rock Canyon, Nevada. Ecological Society of America, Portland, OR.

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