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Population Dynamics And Environmental Factors Influencing Herbs In Intact And Degraded Florida Rosemary Scrub

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POPULATION DYNAMICS AND ENVIRONMENTAL FACTORS INFLUENCING HERBS IN INTACT AND DEGRADED FLORIDA ROSEMARY SCRUB

by

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ABSTRACT

Species have complex and contextual relationships with their environment; both the relative contributions of life-history stages to population growth and the effect of environmental factors on each stage can be different among co-existing species. Timing and extent of reproduction, survival, and mortality determine population growth, species distributions, and assemblage patterns. I evaluate the role of habitat (intact, degraded) and microsite (shrub, leaf litter, bare sand) on population dynamics of Florida scrub herbs. Isolated overgrown shrubs and extensive bare sand areas in degraded scrub were expected to decrease seed predation, reduce competition of herbs with shrubs, and provide larger habitat for recruitment. I provide evidence that habitat and microsite variation influenced demography of five endemic and two common native species through effects on seed removal, emergence, and establishment. Habitat and species affected seed removal: endemic species with large seeds were removed in higher frequency in degraded habitat, likely by vertebrates, while species with small seeds were removed in higher frequency in intact habitat, by invertebrates. There was no evidence of differences in individual seed production between habitats for the two common species, *C. fasciculata* and *B. angustifolia*. Invertebrates were primarily responsible for seed removal of both species, although peak season of removal and microsite varied with species. Removal of seeds, emergence, and establishment increased with seed density. Matrix modeling indicated that population growth of *C. fasciculata* was greater in degraded habitat and greatest in litter microsites, and population growth of *B. angustifolia* was similar between habitats and greatest in bare sand. Contrasting responses among species to environmental factors in intact and degraded scrub indicated that natural disturbances are not ecologically equivalent to anthropogenic disturbances. Idiosyncratic species dynamics in common environments suggest that understanding relationships between life-history traits and environmental conditions will be required to facilitate restoration.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER ONE: INTRODUCTION

Life-history varies within populations and among species (Allen and Pizer 2008). Categorizing and analyzing factors affecting life-history trait variation is a central pursuit in ecology because the timing and extent of reproduction, survival, and mortality determine population growth, species distributions, and assemblage patterns. As species have complex and contextual relationships with their environment, both the role of each stage in the life cycle (de Kroon et al. 1986), and the effect of environmental factors on each stage (Schupp and Fuentes 1995), provide valuable ecological insight. Recruitment (e.g. Shelford 1907; Shaw 1926; Louda 1982; Roughgarden et al. 1985; Anderson 1989; Eissenstat and Newman 1990), establishment (e. g. Cowles 1899; Gleason 1917; Eriksson and Ehrlen 1992; Ostfeld et al. 1997; Wijdeven and Kuzee 2000), and population growth (e. g. Bell et al. 2003; Quintana-Ascencio et al. 2003; Bakker et al. 2009; Forbes et al. 2010) have been considered at length. However, many previous analyses focus on a single life-history stage, or examine species in isolation from their surroundings. The relative contribution of life-history stages to population growth must be considered in conjunction with environmental factors driving population dynamics (Silvertown et al. 1993; Crone et al. 2011) to elucidate mechanisms underlying life-history stage patterns. Relationships between life-history traits and environmental conditions can reveal species' life-history strategies, and facilitate predictions about which species may co-occur in novel or altered environments.

A complete analysis of a species' life cycle is necessary in order to understand the importance of different life-history stages to population growth (de Kroon et al. 1986). Positive effects of one stage on population growth (e.g. great recruitment) may be obscured by negative effects of another stage (e.g. great juvenile mortality) (Schupp and Fuentes 1995; Smit et al.

2006). Population growth is also affected by energy invested into particular life-history stages and trade-offs between life-history traits (e.g. growth vs. reproduction, size-number trade-offs in reproduction, current vs. future reproduction, reviewed in Allen and Pizer 2008). Changes in demographic rates are unlikely to be independent of one another (Benton et al. 2006); focusing on one or few life-history stages results in superficial or incomplete understanding of demographic patterns. Furthermore, predictions of species distributions are only possible with sufficient life-history data (Herrera et al. 1994) because individual stages may be affected differently by particular environmental factors (Schupp and Fuentes 1995; Benton et al. 2006).

Environmental conditions regulate recruitment, subsequent establishment, and population growth in two main ways: through resource (Sinclair 1975; Shulman 1984; Menge 2000, Chesson et al. 2004) and propagule availability (Andrewartha and Birch 1954; Andrewartha and Birch 1984; Poulsen et al. 2007). Plant species occur in heterogeneous conditions that determine accessible space, nutrients, water (Oswald and Neuenschwander 1993; Bisigato and Bertiller 1999; Jones and del Moral 2005; Parent et al. 2006; Smit et al. 2006), and competition from other plants (Eissenstat and Newman 1990; Kellman and Kading 1992; Liu et al. 2007; Coop and Givnish 2008; Ronnenberg et al. 2008; Badgery et al. 2008; Pihlgen and Lennartsson 2008). These factors influence seed production, survival of arriving seeds (Alcantara et al. 2000), and seedling establishment. Relatively low seed production, short dispersal distances, high seed predation, or a combination of these factors, may significantly decrease the number of seeds reaching appropriate habitat for recruitment (Ehrlén et al. 2006; Orrock et al. 2006). Without both availability of appropriate habitat / microsite conditions for recruitment and a substantial seed supply, plant populations fail to persist (Klinkhamer and de Jong 1989). As a result, habitat degradation, microsite availability, and seed density all have great potential, either individually or acting in synergy, to drive population dynamics of a given species.

Co-occurring species may respond similarly to environmental conditions (including degree or time-since-disturbance; Clements 1916; Braithwaite and Mallik 2011) during common life-history stages, or may be differentially affected by environmental conditions with distributions governed by complex relationships to biotic and abiotic factors (Gleason 1917). Organisms living in arid, unstable environments often display higher reproductive output, earlier reproduction, faster development or population growth than those living in moist, stable environments (Braby 2002). Biomass-destroying disturbance and abiotic stress affect plants synergistically: competitive plants often live in conditions of low stress and low disturbance, stress-tolerant plants are found in high stress and low disturbance, and ruderals in high disturbance and low stress (Grime 1977). However, as each species is unique, co-occurring species may have different resource requirements at different life-history stages. Habitat degradation may alter species relationships if changes in biotic or abiotic conditions alter reproduction, growth, or survival of individual species in distinct ways. For example, habitat degradation may provide a competitive advantage for species relying more heavily on open space for recruitment, but may be a disadvantage for species relying more on development of belowground storage organs for survival. A deeper understanding of the relationship between life-history traits and environmental conditions will help conservation biologists and land managers anticipate changes in species distributions resulting from anthropogenic habitat degradation. Species may co-exist in degraded habitats that do not co-occur in intact habitats, and vice versa.

I aimed to understand the relationship between life-history traits and environmental drivers of population dynamics by studying herbs in Florida scrub, a threatened habitat (Florida Natural Areas Inventory, 2000). Florida scrub herbs are tolerant of harsh xeric conditions (abiotic stress) and rely on fire (disturbance) to maintain appropriate habitat and microsite structure for recruitment (open canopy with bare sand gaps between shrubs). These species recruit from the seedbank and are often challenged by low recruitment and survival. An examination of these species in mechanically disturbed scrub (a more extreme disturbance) provided an opportunity to examine the effect of changing biotic and abiotic factors on demographic patterns. I first investigated post-dispersal seed predation, germination, and seedling survival of five rare Florida Scrub species in intact and degraded habitats (Dissertation Chapter 2). Studied species (scrub blazing-star (*Liatris ohlingerae*), scrub eryngium (*Eryngium cuneifolium*), tufted wireweed (*Polygonella basiramia*), Highlands scrub hypericum (*Hypericum cumulicola*), paper nailwort (*Paronychia chartacea* subsp. *chartacea*)) represented a gradient of seed sizes, which enabled an examination of seed size effects on seed dynamics in the two habitats. I also studied two more common native species partridge pea (*Chamaecrista fasciculata*), coastalplain honeycombhead (*Balduina angustifolia*)) to evaluate the role of habitat (intact, degraded), microsite (bare sand, leaf litter, shrubs), and seed density on seed bank and seedling dynamics (Chapter 3). I used deterministic matrix models based on these empirical data to examine the influence of habitat and microsite on population demography of *C. fasciculata* and *B. angustifolia* (Chapter 4). I used stochastic models to evaluate scenarios of changing seed density and frequency of habitats and microsites through succession on population growth rate of these short-lived species.

Results of my studies will disentangle factors influencing herb species distributions. I evaluated habitat and microsite requirements for co-occurring species, and the consequences of ecological disturbance. Anticipating demographic challenges to target species in areas slated for restoration will enable conservation biologists and land managers to implement proper preventative (e.g. animal exclosures) and compensatory measures (e.g. drastically increasing seed availability) to reach restoration goals. The synthesis of empirical data and matrix models in my research provides a useful framework for approaching restoration of any habitat.

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CHAPTER TWO: POST-DISPERSAL SEED PREDATION, GERMINATION AND SEEDLING SURVIVAL OF FIVE RARE FLORIDA SCRUB SPECIES IN INTACT AND DEGRADED HABITATS

Stephens, Elizabeth L., Castro-Morales, Luz, and Quintana-Ascencio, Pedro F. 2012. Post-Dispersal Seed Predation, Germination, and Seedling Survival of Five Rare Florida Scrub Species in Intact and Degraded Habitats. *The American Midland Naturalist*, 167: 223-239.

Abstract

Knowledge of seed ecology is important for restoring ecosystems degraded by anthropogenic activities. Current efforts to preserve and reintroduce populations of plant species endemic to Florida are hindered by lack of information on demographic responses to human alteration. Comparisons of seed removal, germination and establishment in both intact and degraded habitats will aid management decisions for species needing protection. Our objectives were to assess the effect of post-dispersal seed predation on plant populations in degraded and intact habitats, and to investigate effects of habitat and microsite on seed germination and establishment. For five rare Florida scrub species with different seed sizes (*Liatris ohlingerae*, *Eryngium cuneifolium*, *Polygonella basiramia*, *Hypericum cumulicola*, *Paronychia chartacea* subsp. *chartacea*), we conducted a seed removal experiment with seeds exposed to both insects and vertebrates, to insects only, with a no-access control. We also planted seeds in replicated degraded and intact scrub sites (Spring Field Trial: bare sand; Winter Field Trial: in bare sand, litter only, and under shrubs with litter), and determined background germination rates in a growth chamber. The contrasting pattern of seed removal among treatments suggested that habitat and species affect the likelihood of removal in Florida scrub. Species with large seeds such as *L. ohlingerae* were removed in higher frequency in degraded scrub, likely by vertebrates. Species with small seeds such as *H. cumulicola* and *P. chartacea* were removed by invertebrates and in higher frequency in intact scrub. *E. cuneifolium* had significantly more seedlings in degraded scrub and *P. chartacea* had significantly greater germination in intact scrub in the Spring Field Trial. *E. cuneifolium*, *H. cumulicola* and *P. chartacea* had higher germination in bare sand than in litter only or under shrubs. Our data indicate that scrub herbs are differentially vulnerable to seed predation and abiotic factors at particular life-history stages, and that this vulnerability can be context dependent. Restoration success will require careful assessment of potential seed predators and abiotic conditions favoring germination and survival of endemic Florida plant species in degraded habitat; increased heterogeneity in areas slated for restoration likely will promote establishment of multiple targeted species.

Introduction

Current efforts to preserve and reintroduce populations of protected plant species are limited by lack of specific information on demographic responses to human alteration. Habitat disturbance can affect multiple life-history stages of species in areas acquired for protection and restoration, including seed survival and seedling establishment. Seed predation often varies with habitat quality or type (Bossard 1991; Holl and Lulow 1997; Tallmon et al. 2003); these patterns can be further affected by predator preferences for seed characteristics such as seed size (Booman et al. 2009). Anthropogenic disturbance can either diminish (Coates et al. 2006; Schleuning, 2009) or enhance seedling establishment (Schupp and Fuentes 1995; Pugnaire and

Lozano 1997; Cole et al. 2004). The direction of this influence often depends on whether disturbance historically maintained the habitat (Hellström et al. 2009), or on the growth form or functional group of the species (Zimmer et al. 2010).

Habitat restoration is essential to conservation of protected species in threatened habitats such as Florida scrub (Florida Natural Areas Inventory 2000). Florida scrub is restricted to the southeastern United States, and is valuable to local and global biodiversity because it hosts a large number of rare and endemic species, several of which are endangered or threatened (Turner, Wilcove and Swain 2006). The Lake Wales Ridge of south-central peninsular Florida contains some of the best remaining examples of intact Florida scrub; this habitat is rapidly diminishing due to commercial, agricultural, and residential development (Weekley et al. 2008).

There is a need to elucidate factors affecting recruitment of native species because goals for re-establishing scrub species are rarely achieved due to mortality of seeds, seedlings and adults. Previous studies on the demography of Florida endemic species in their natural habitats provided insight about critical features affecting the scrub ecosystem, such as gap dynamics and fire (Satterthwaite, Menges and Quintana-Ascencio 2002; Quintana-Ascencio, Menges and Weekley 2003; Menges and Quintana-Ascencio 2004). These factors are important to many scrub endemics, which occur as multiple patchy populations that depend on habitat configuration and regional population dynamics for persistence (Quintana-Ascencio and Menges 1996). Here, we focus on post-dispersal seed predation - the consumption of seeds after they initially disperse from parent plants - germination, and seedling establishment. Comparing demographic responses of endemic herbs in intact and degraded Florida scrub will advance understanding of requirements for seed and seedling survival, and suggest introduction procedures to increase plant numbers and population viability.

Our objectives were two-fold: (1) assess the effects of post-dispersal seed predation on seed germination in degraded and intact scrub habitats using a seed removal experiment, and (2) investigate effects of habitat and microsite on seed germination and establishment using field and growth chamber experiments. We selected five scrub endemics representing a gradient of seed size for our study species; seed size often determines which species' seeds appeal to seed predators, or which seeds can be easily handled. We expected seed size to influence seed predator preferences and subsequent removal from the different habitats. For our seed removal experiments, we assumed that removal should generally represent post-dispersal seed predation in this system because seeds of study species do not have eliasomes (lipid attachments) or fleshy fruit, giving animals little incentive to move them without consumption. We also assumed that wind movement was not responsible for seed removal because we anchored species having pappi (modified calyx composed of bristles or featherlike hairs aiding wind dispersal) in sand. Because we did not follow seed fate after removal, and animals may sometimes drop seeds they intend to consume, our design provides a conservative estimate of predator-mediated seed mortality. Even though seed removal is not equivalent to predation, this method can reveal limitations on seed availability (Mϋnzbergová and Herben 2005). For one of our germination experiments, we examined the effect of single species and mixed species treatments (seeds of all study species planted). For a given study species, comparing these two treatments revealed whether seeds of other species and conspecifics affected germination differently.

Methods

Study Species

We studied five state and federally endangered herbs: *Liatris ohlingerae, Eryngium cuneifolium, Polygonella basiramia, Hypericum cumulicola,* and *Paronychia chartacea* subsp. *chartacea.* These species are either restricted to the Lake Wales Ridge or central Florida (Wunderlin and Hansen 2008). *Liatris ohlingerae* occurs both inside and outside of gaps, or patches of bare sand, in the scrub. The other four species are gap specialists that are concentrated inside gaps (Petrů and Menges 2003; Schafer et al. 2010). All five species are reproductive in Florida scrub from fall to early winter, and their seeds represent a gradient of seed size from *L. ohlingerae* as the largest to *P. chartacea* as the smallest (Table 1). Seed size is relevant to seed predation because it determines which seeds appeal to seed predators, or which seeds can be easily handled (Ivan and Swihart 2000). Invertebrates (Koprdová et al. 2010; Honek et al. 2011) tend to take smaller seeds than vertebrates (Reader 1993; Howe and Brown 2000; Perez et al. 2006). We separated individual seeds from seed heads (*L. ohlingerae*, *E. cuneifolium*) or from fruits (*H. cumulicola*) to minimize any potential effect of seed presentation on predator preferences.

Study Sites

Study sites were located in Highlands County, Florida, at Archbold Biological Station (ABS; 2,104 hectares), the adjacent Archbold Reserve (Reserve; 1,476 ha), and the McJunkin Tract of the Lake Wales Ridge Wildlife and Environmental Area to the northwest of ABS (McJunkin; 303 ha). Archbold Biological Station is a globally significant natural preserve that features rosemary scrub, among other habitat types. Rosemary scrub occurs in areas of locally high elevation with well drained, low nutrient soils. Several herbaceous species, many of them rare and endemic, grow in gaps of bare sand between shrubs (Abrahamson et al. 1984; Menges et al. 2008). Most of these herbs recover from fire and other disturbances by seedling recruitment, whereas surrounding shrubs primarily resprout (Menges and Kohfeldt 1995).

Archbold's Reserve includes pastureland and degraded scrub, which were roller chopped and lightly grazed by cattle, with cattle on site until 2002. The McJunkin Tract is managed by the Florida Fish and Wildlife Conservation Commission and includes degraded scrub that was once ranchland. The ABS sites served as reference scrub sites for the degraded scrub sites within the Reserve and McJunkin Tract; all sites were selected on Archbold and Satellite soils, and shared topography characteristics associated with rosemary scrub / scrubby flatwoods in the reference scrub. Species composition in the degraded scrub was similar to intact rosemary scrub sites, except for the presence of nonnative grasses. However, in degraded scrub, shrubs were overgrown, bare sand areas surrounding shrubs were more extensive, and species distributions and relative abundance differed from intact rosemary scrub (E. Menges, pers. comm.; Navarra et al. 2011). The degraded scrub sites are currently under treatments to reestablish native habitat structure and scrub species.

Seed Collection

We collected seeds at Archbold Biological Station immediately before each experiment. We separated intact, fully pigmented seeds under a dissecting microscope, sorted them into groups with forceps and sealed them in foil, and stored them in a refrigerator (4° C) before their deployment in the field (Table 1).

Seed Removal

We evaluated the role of predators on seed fate using animal exclosures in intact and degraded Florida scrub (June 2007 – April 2008). We exposed seeds of each species in replicated exclosure treatments using a complete factorial design, with 5 replicates x 3 exclosure types x 4 sites x 2 habitats; 120 total sampling units. The three exclosure types were: (1) a no access treatment that used a wire mesh cylinder with plastic covering to exclude vertebrates and invertebrates; (2) an invertebrates-only treatment that used a wire mesh cage to exclude vertebrates; and (3) an open-access control.

For the no access treatment, we constructed each exclosure from a rectangular piece of wire mesh (30.5 cm x 76.2 cm, 1.3 cm mesh, 19 gauge galvanized hardware cloth) that we shaped into an upright cylinder. We attached a square piece of wire mesh to the top of each cylinder to prevent birds from accessing the seeds through the top. We secured cylinder seams with wire and covered the outside of the cylinder with heavy-duty clear plastic sheeting to within a few centimeters from the cylinder's top. We applied a layer of Tangle-Trap Sticky Coating (Tanglefoot) to the upper rim of the plastic sheeting to prevent access by invertebrates. For the invertebrates-only treatment, we used square cages made from wire mesh (22.9 cm x 22.9 cm x 11.4 cm, 0.6 cm mesh) with no plastic sheeting or sticky coating. The open-access control treatments had no equipment, only wire-stake flags marking treatment locations.

We arranged experimental units in triplets with one of each treatment type positioned within 3 m of each other). We placed a sand-filled Petri dish (100 mm diameter, 10 mm height) on the ground inside each unit, and sprinkled seeds (avoiding skin contact) onto the sand-filled dish. Petri dishes were used to easily relocate seeds and reduce displacement by wind or water. We used more seeds per unit for the smaller-seeded species than for the largest-seeded species (5 for *L. ohlingerae,* 10 for *E. cuneifolium*, *P. basiramia,* and *P. chartacea,* and 20 seeds for *H. cumulicola*). After 48 h, we collected the sand-filled dishes and counted remaining seeds under a microscope. Preliminary trials and other studies suggested that 48 h is well suited to assess differential removal rates (Fedriani et al. 2004). We used the no-access treatments to confirm that all deposited seeds could be recovered under conditions of no animal access.

Germination and Establishment

We used three growth chamber studies (one with a greenhouse counterpart) and two field experiments to evaluate the effects of habitat and microsite on germination and establishment of the study species in intact and degraded Florida scrub.

Germination (background laboratory trials)

We observed background germination rates of the five study species in a growth chamber (CONVIRON CMP 4030) to determine the maximum potential field germination of seeds in the field. We allocated 30 seeds per species from those sorted for each of two field germination trials. We deposited these seeds into Petri dishes with a moist filter paper and exposed them to conditions mimicking those in the field. For our Spring Chamber Trial (May 2008, initiated simultaneously with our Spring Field Trial), we set the chamber to late spring conditions at Archbold Biological Station (daily minimum 22° and maximum 27.2 °C; Archbold Biological Station Weather data, Appendix A). For our Winter Chamber Trial (February 2009, initiated simultaneously with our Winter Field Trial), we used winter temperatures (daily minimum 20° and maximum 22° C; Appendix A). We moistened seeds and checked for germination daily, and we terminated trials after seeds ceased germinating. *Liatris ohlingerae* seeds were not available for the Winter Chamber Trial.

Germination (GA_3 laboratory and greenhouse trials)

We also stimulated seeds (*L. ohlingerae*, *E. cuneifolium*, and *P. chartacea*) with gibberellic acid (GA_3, 90% product purity), a plant hormone commonly used to promote germination in growth chamber and greenhouse studies. We allocated 264 seeds per species to this study from those sorted for the Winter Field Trial. We tested seeds in two different environments: the growth chamber (daily minimum 21° C and maximum 29° C) and a hoophouse with uncontrolled temperatures (daily minimum 18° C and maximum 50° C) from May to July 2008. In both environments, we used three different concentrations of GA_3: 100 ppm, 50 ppm, 5 ppm, and a control with no hormone applied. The solution of GA_3 was made with powder dissolved in a small amount of 91% isopropyl alcohol and then mixed with distilled water.

We used three replicates per treatment in each environment; each GA_3 treatment was applied once at experiment initiation. In the growth chamber, we distributed 10 seeds to each replicate (total 120 seeds per species), and were arranged Petri dishes randomly in the growth chamber. In the greenhouse, we planted 36 seeds per treatment per species at twelve seeds per flat. We buried seeds ≤ 5 mm using forceps into sand collected from Archbold Biological Station and sterilized at 90° C for 8 h in a Fisher Scientific oven. We arranged flats randomly in the greenhouse, watered with ambient water, and checked daily for germination.

Germination / establishment (Spring Field Trial)

We initiated our Spring Field Trial in May 2008 by planting seeds in open areas in each habitat. We initiated our Winter Field Trial in February 2009 by planting seeds in replicated microsites within each habitat. We planted all seeds within PVC rings 10.2 cm diameter x 7.6 cm deep, which we partially buried in the sand (approximately 3.5 cm) to keep seeds in place. We then covered seeds with sand, protected them with a wire mesh vertebrate exclosure to reduce removal, and marked them with wire-stake flags.

The Spring Field Trial included four degraded scrub sites (two Reserve, two McJunkin) and two reference scrub sites, with four plots per site (6 sites x 4 plots; 24 total plots). We employed six treatments in each plot, with a separate PVC ring for each treatment: 6 seeds of *L. ohlingerae* only, 20 seeds of *E. cuneifolium* only, 20 seeds of *P. basiramia* only, 20 seeds of *H. cumulicola* only, 20 seeds of *P. chartacea* only, a mixture of all of the above species (2 *L. ohlingerae* seeds, 4 *E. cuneifolium,* 4 *P. basiramia,* 8 *H. cumulicola*, 8 *P. chartacea*), and a control with no seeds planted. We used the control treatment to detect any seeds arriving from extant adult plants (Turnbull et al., 2000; Clark et al., 2007). We randomly assigned planting locations for each treatment in each plot. We evaluated seedling recruitment once a week from May to August and then once a month from September to February 2009 to evaluate seedling recruitment, and considered seedlings that survived to the end of the experiment to be established.

Germination / establishment (Winter Field Trial)

In the Winter Field Trial, we set up two transects in each of four sites: two degraded scrub (one Reserve, one McJunkin) and two reference scrub sites. We randomly assigned distances along the transect, species planted, and microsite type (bare sand, litter with no shrub, or underneath shrub with litter) to each experimental location. After we located a random point along the transect, we moved perpendicular until we encountered the assigned microsite type. We used three treatments: single species (seeds of one species), mixed species (seeds of the five study species), and a control (no planted seeds), all of which had PVC collars and exclosures. We planted 20 seeds in single species treatments, and 2 *L. ohlingerae,* 4 *E. cuneifolium,* 4 *P. basiramia,* 8 *H. cumulicola,* and 8 *P. chartacea* seeds in mixed species treatments. Due to limited seed availability, we reduced the number of *H. cumulicola* units and only included *L. ohlingerae* in mixed species units. In total, we established 144 planting locations (26 *E. cuneifolium,* 26 *P. basiramia*, 22 *H. cumulicola,* 26 *P. chartacea,* 24 mixed species, 20 controls) and planted 2,624 seeds. We monitored sites for seedlings once a month after planting until February 2010, and considered seedlings that survived to the end of the experiment to be established.

Analytical Methods

We estimated seed removal by invertebrates as the difference between the number of seeds removed from no-access treatments and the number of seeds removed from the invertebrates-only. We then estimated seed removal by vertebrates as the difference between the number of seeds removed from the invertebrates-only and the open-access control. We used nominal logistic regression to test the null hypothesis that the independent variables species, habitat type, and exclosure treatment influenced the dependent variable seed recovery, and to test whether habitat type and microsite influenced the dependent variables germination and seedling establishment. We coded PVC rings in the seed removal study as either loss of seeds (≥ 1 seed removed) or all seeds recovered. In germination trials, we coded each PVC ring as having germination / establishment (≥ 1 germinant seedling) or no germination / establishment. In some cases, too many zeroes precluded use of logistic regression; in these cases we conducted Kruskal-Wallis analyses using total counts of germinants or seeds removed.

Results

Seed Removal

The largest seeds, *L. ohlingerae*, were removed the least frequently, and the small seeds, *H. cumulicola,* were removed the most frequently (Figure 1). In total, from largest to smallest seed size, 79 of 600 (13.2%) *L. onlingerae* seeds were removed, 354 of 1800 (19.7%) *E. cuneifolium*, 391 of 1200 (32.6%) *P. basiramia*, 1421 of 2380 (59.7%) *H. cumulicola*, and 376 of 1200 (31.3%) *P. chartacea* seeds were removed.

We found different removal rates for different species (P < 0.001; *P. chartacea* B = 1.437, SE =0.156; *P. basiramia* B =1.489*,* SE = 0.157; *E. cuneifolium* B =2.136, SE = 0.178*; L. ohlingerae* B = 1.216, SE = 0.223; DF = 1, relative to *H. cumulicola*), greater removal in intact scrub than in degraded scrub (P = 0.020, B = -0.309, SE = 0.133, DF = 1), and greater removal from the open-access control than the no-access treatment (P < 0.001, B = 2.205, SE = , DF = 1).

There were significantly more seeds removed from the invertebrates-only than from the no access treatment in intact scrub (P < 0.001, B = -0.640, DF = 1). Relative to *H. cumulicola*, *L. ohlingerae* had significantly more seeds removed in degraded scrub (P < 0.001, B = -1,330, DF = 1) and from open-access than from the invertebrates-only treatment (P = 0.002, B = 0.590, DF = 1), *P. basirami*a had significantly more seeds removed in intact scrub (P = 0.064, B = -0.270, DF = 1) and from open-access than from the invertebrates-only treatment (P < 0.001, B = 3.266, DF

= 1), and *E. cuneifolium* had more seeds removed from open-access than from the invertebrates-only treatment (P < 0.001, B = 1.256, DF = 1) (Table 2, Figure 1).

Species with large seeds tended to be removed more frequently in degraded scrub by vertebrates, whereas species with smaller seeds tended to be removed more frequently in intact scrub by invertebrates (Figure 1). For the smallest seeds (*H. cumulicola*, *P. chartacea*), we did not have complete seed recovery from the no access treatments. We also observed that the smallest seeds adhered more to organic matter than the other species and were the most difficult to locate.

Germination and Establishment

Germination (laboratory and greenhouse)

Our Spring Chamber Trial demonstrated substantial viability for the seeds of each species. *H. cumulicola* and *P. basiramia* (each 86.7%) had the highest germination, *E. cuneifolium* and *L. ohlingerae* had the next highest (each 83.3%), and *P. chartacea* had the lowest germination (56.7%). In the Winter Chamber Trial (without *L. ohlingerae*), *P. chartacea* had the highest germination (86.0%), *P. basiramia* had the next highest (57.5%), *H. cumulicola* had low germination (33.3%) and *E. cuneifolium* had no germination. There was notable difference in germination between seasonal conditions, as germination was much lower for all species in the Winter Chamber Trial except for an increase in *P. chartacea*. In the GA_3 growth chamber study, we observed little to no stimulatory effect of the hormone treatments, as there was no significant difference in number of germinants among treatments (Figure 2). There was no germination in the greenhouse for any of the treatments.

Germination (Spring Field Trial)

We found significant differences in germination between habitats for one of our study species. For the Spring Field Trial (Figure 3a, Table 3), in which all seeds were planted in bare sand, *L. ohlingerae* had no significant difference in germination between habitat types (P=0.528, B=-0.395, SE=0.626, Wald=0.398, DF=1). Logistic regression analyses revealed significantly greater germination in degraded than in intact habitat for *E. cuneifolium* (P = 0.026, B = 1.449, SE = 0.649, Wald = 4.985, DF = 1). *P. basiramia* had only one germinant in the intact scrub, and few in the degraded scrub (Figure 3a, Table 3) and *H. cumulicola* had only one germinant in the intact scrub, and no germinants in the degraded scrub (Figure 3a, Table 3). Low sample size precluded tests for these last two species.

We did not find a significant difference in germination of *P. chartacea* seeds planted in intact and degraded scrub (P = 0.372, B = 0.588, SE = 0.658, Wald = 0.797, DF = 1). However, we observed many *P. chartacea* seedlings in plots of other study species and controls, more so in the intact scrub than in the degraded scrub (P < 0.001, chi square = 32.250, DF = 1). We analyzed this observational data in order to develop further hypotheses about the seed availability of *P. chartacea* in intact and degraded scrub.

Establishment (Spring Field Trial)

Only *L. ohlingerae*, *E. cuneifolium*, and *P. basiramia* had established seedlings that survived to the end of the study (Figure 3b). At this time, *P. chartacea* seedlings had germinated too recently to be considered established. Logistic regression analyses of establishment for the Spring Field Trial indicated no significant differences between the two habitats, either for individual species (*L. ohlingerae*, P = 0.831, B = 0.136, SE = 0.637, Wald = 0.046, DF = 1; *E.*

cuneifolium, P = 0.998, B = -19.516, SE = 10048.243, Wald = 3.772E-06, DF = 1; *P. basiramia* P = 0.998, B = -19.257, SE = 10048.243, Wald = 3.673E-06, DF = 1) or across species (P = 0.225, B = -0.611, SE = 0.504, Wald = 1.471, DF = 1).

Germination (Winter Field Trial)

The total number of germinants per species per site, whether from a single or a mixed species treatment, were used for analysis due to low overall numbers of germinants (Table 3, Figure 3c). There were no differences in germination between habitat types for *L. ohlingerae* (P = 0.190, B = 1.273, SE = 0.971, Wald = 1.719, DF = 1) or *E. cuneifolium* (P = 0.874, B = -0.105, SE = 0.662, Wald = 0.025, DF = 1), but there was weak evidence of *E. cuneifolium* germinating most in bare sand regardless of habitat. Our data were insufficient to conclude on the difference between habitat types for *P. basiramia* (P = 0.064, B = -1.598, SE = 0.862, Wald = 3.434, DF=1). There were no differences between habitat types for *H. cumulicola* (P = 0.998, B = 18.067, SE = 8569.170, Wald = 4.445E-06, DF = 1).

For those points where we planted *P. chartacea* seeds, our data was insufficient to determine if germination was different between habitats (P = 0.064, B = 2.507, SE = 0.786, Wald = 10.176, DF = 1). There was significantly greater germination in bare sand than in litter only (P = 0.004, B = -2.708, SE = 0.931, Wald = 8.462, DF = 1). However, we again found many *P. chartacea* seedlings in plots of other study species and controls, more so in the intact scrub than in the degraded scrub (P = 0.001, B = 2.507, SE = 0.786, Wald = 10.176, DF = 1). Germination was significantly higher in bare sand (P = 0.014, B = -2.035, SE = 0.831, Wald = 5.995, DF = 1) and in litter only (*p* = 0.046, B=1.688, SE=0.847, Wald=3.970, DF=1) than under shrubs with litter.

When all species from the Winter Field Trial were analyzed together, we did not find a significant difference in germination between the two habitats, but we did find significant differences in germination among microsite types (Table 4). Significantly more planting points in bare sand had germination than those in litter only or in litter under shrubs. Germination in litter only and under shrubs with litter was not significantly different.

Establishment (Winter Field Trial)

P. chartacea had significantly more establishment in degraded vs. intact scrub ($P < 0.001$, $B = 2.379$, $SE = 0.642$, $Wald = 13.749$, $DF = 1$). An analysis of all species together indicated significantly more established seedlings in intact scrub than in degraded scrub ($P = 0.003$, $B = 1.145$, $SE = 0.388$, $Wald = 8.736$, $DF = 1$), with most of those seedlings in the bare sand and second most in the litter only (bare sand vs. shrub $P = 0.033$, $B = -0.930$, $SE = 0.437$, $Wald = 4.525$, $DF = 1$; bare sand vs. litter only $P = 0.001$, $B = -1.587$, $SE = 0.478$, $Wald = 11.020$, $DF = 1$; shrub vs. litter $P = 0.001$, $B = -1.587$, $SE = 0.478$, $Wald = 11.020$, $DF = 1$) (Figure 3d).

Discussion

Our results have implications for effective habitat restoration and preservation of biodiversity in Florida scrub. Our data indicate that scrub herbs are differentially vulnerable at particular life-history stages, and that this vulnerability can be context dependent. Both habitat and microsite type were found to be influential for the recruitment of our study species, although conditions favoring establishment were species specific.

Three of our study species (*E. cuneifolium*, *P. basiramia, H. cumulicola*) appear less limited in degraded scrub than in intact scrub, either through decreased seed removal (*P. basiramia, H. cumulicola)* or greater germination success (*E. cuneifolium)*. Other studies have found lower seed removal in disturbed than intact habitat; *Prunus avium* seeds were removed less frequently in treefall gaps than in closed woods of Minnesota, likely due to the reduced protective cover in gaps (Webb and Willson 1985). Research in grasslands (Eriksson and Eriksson 1997; Leps 1999; Hellstrom et al. 2009; Schleuning et al., 2009) and forests (Flory and Clay 2009; Munier et al. 2010) has similarly demonstrated that habitat disturbance can promote germination. For instance, seedling recruitment was positively influenced by mowing in a Czech Republic study of meadow species (Leps 1999). Mechanical disturbance also stimulated germination and seedling establishment for the perennial grassland plant *Trifolium montanum* in central Germany (Schleuning et al. 2009), for grassland herbs in northern Finland (Hellström et al. 2009), and for small-seeded pasture species in semi-natural pastures (Eriksson and Eriksson, 1997). Forest studies of the conifer *Picea mariana* in the Mealy Mountains of Canada (Munier et al. 2010) and of native and invasive species in southern Indiana (Flory and Clay 2009) also observed enhanced seedling emergence with physical soil disturbance or with proximity to forest roads.

Two of our study species appear more limited in degraded scrub than in intact scrub, either through increased seed removal (*L. ohlingerae)* or decreased germination (*P. chartacea)*. Other studies have found that seed predators may preferentially forage in degraded areas. For example, bird species hunted and consumed more seeds in degraded areas than in intact habitats of the Sierra Nevada foothills (Bossard 1991). Harvesting of seeds by vertebrates (including rodents) was greater in treefall gaps than in undisturbed understory in Costa Rica and Panama

(Schupp 1988; Schupp and Frost 1989). Seed removal in southeastern New York was also found to be greater at 5 and 10 meters into old fields than in intact forest, although not for all years of the study (Ostfield et al. 1997). Degree of disturbance has been shown to influence seed removal, as *Uvularia* seeds were removed more in mowed fields than in woods, but were not different between woods and tree-fall gaps (Webb and Willson 1985).

Disturbance can also reduce recruitment (Leps 1999; Aschero and Vasquez 2009; Mazia et al. 2010). Our observational data indicated that more *P. chartacea* seedlings grew in the intact than in the disturbed scrub; more seeds may be available from the intact scrub seed bank due to higher mean seed density (Navarra 2010). A more random spatial distribution for *P. chartacea* in the degraded scrub seed bank and aggregated distribution in intact scrub could explain the difference between our experimental and observational data for this species (Navarra 2010). Other examples of soil disturbance inhibiting establishment include an Argentinian study in which armadillo-like diggings exerted antagonistic effects on tree recruitment, and simulated burrowing prevented seedling emergence in relict grassland (Mazia et al. 2010). In this study, reduced emergence was attributed to reduced soil moisture, increased seed burial, and predation in excavated patches. In the Czech Republic, seedling recruitment of a small portion of the studied species was negatively influenced by mechanical disturbance (Leps 1999), indicating that this pattern may be species specific. Moreover, suppression of anthropogenic degradation was found to result in higher adult tree recruitment in protected plots in the Monte Desert (Aschero and Vasquez 2009). In addition to soil disturbance, the fire suppressed state of the degraded scrub may reduce seedling establishment, as fire has been shown to promote seedling recruitment (Carrington 1999; Hartnett and Richardson 1989; Menges and Gordon 1996; Menges and Kimmich 1996; Weekley and Menges 2003).

Microsite type was found to be influential for the germination or establishment of several of the study species as well: bare sand was least limiting for *H. cumulicola* and *P. chartacea,* and slightly less limiting for *E. cuneifolium* than the other microsites; litter only was slightly less limiting for *L. ohlingerae*. Shrub microsites limited germination or establishment the most, although germinants of *L. ohlingerae* and *E. cuneifolium* were sometimes able to grow under shrubs. In previous Florida scrub studies, litter was found to prevent the recruitment and persistence of many rare plant species (Hawkes and Menges 1996; Menges and Kimmich 1996; Quintana-Ascencio et al. 2003; Rickey et al. 2007). Similarly, bare soil was found to promote establishment of *Trifolium montanum*, a declining perennial grassland plant in central Germany, whereas thick litter negatively affected establishment (Schleuning et al. 2009). A study of quaking aspen establishment in the Canadian Rocky Mountains found that the vast majority of seedlings became established on bare mineral soil in contrast to intact forest floor microsites (Landhäusser et al. 2010).

Our data indicate that successful translocation of Florida scrub endemics in native and degraded habitat can be affected by both where the species are introduced, and whether they are protected from animals. Even though some of the study species (*E. cuneifolium*, *P. basiramia, H. cumulicola*) appear less limited in degraded scrub than in intact scrub, either through decreased seed removal or greater germination success, their establishment is still dependent on a substantial supply of seeds. Vertebrate exclosures are best employed for species with relatively larger seeds such as *L. ohlingerae*, *E. cuneifolium*, and *P. basiramia*. This protection will improve the chances that seeds survive until they germinate. For those species most limited in their germination and seedling survival (*P. basiramia, H. cumulicola*), it may be more beneficial to transplant adult individuals reared in greenhouse conditions than to plant seeds. *H. cumulicola* transplants have been successful in intact scrub at Archbold Biological Station (Quintana-Ascencio and Menges 1996; C. Oakley, pers. comm.).

It is important to recognize that certain species will require more intervention than others. Species challenged by synergism of high seed removal and low germination may depend on a greater investment of time and resources. For example, it may take several attempts to successfully establish *H. cumulicola* in scrub undergoing restoration. A combination of both planted seeds and transplants should augment the establishment of such species in degraded habitat. On the other hand, species such as *L. ohlingerae,* which have relatively low seed removal and high germination, may require fewer total introduced seeds and trials.

Our results emphasize the need for creating a variety of microsite types in habitat undergoing restoration. Only heterogeneous habitats with different microsites are able to accommodate multiple species with individual requirements for germination and protection from seed predators. Patchy burns can contribute to creation of these heterogeneous habitats (Rocca 2009; Russell-Smith 2002), especially in landscapes that are naturally patchy. However, land management alone is insufficient for restoration success. As we have demonstrated, demographic monitoring can provide critical information about native species targeted in restoration. It is only through an understanding of the demographic contributions of different life-history stages that we can understand what is required in native species establishment. A partnership between carefully planned demographic studies and land management is key to restoring degraded habitat as closely as possible to intact scrub conditions.

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Tables and Figures

Table 1. Mean seed length and width, estimated seed size (length x width), and total seeds per species used for each study. Totals for spring germination / establishment include Spring Field Trial and Spring Chamber Trial; totals for winter germination / establishment include Winter Field Trial, Winter Chamber Trial, and the gibberellic acid study (growth chamber and greenhouse germination).

Species	**Seed length and width (µm)**	**Seed size (µm^2)**	**Total seeds for removal study**	**Total seeds for spring germ / estab study**	**Total seeds for winter germ / estab study**
L. ohlingerae	102 / 16	2749.5	600	222	342
E. cuneifolium	22 / 17	303.8	1800	606	934
P. basiramia	28 / 7	240.5	1200	606	910
H. cumulicola	7 / 4	23.8	2400	702	926
P. chartacea	6 / 4	22.3	1200	702	1006

Table 2. Logistic regression of seed recovery for *L. ohlingerae*, *E. cuneifolium*, *P. basiramia*, *H. cumulicola*, and *P. chartacea* by species, habitat (degraded vs. intact), and treatment (open-access control (O), invertebrate access only (I), and no access (N)). DF = degrees of freedom, B = slope from logistic regression. Significant P values (< 0.05) are marked with an asterisk.

	DF	**B**	**Sig.**
P. chartacea	1	1.437	<.001*
P. basiramia	1	1.489	<.001*
E. cuneifolium	1	2.136	<.001*
L. ohlingerae	1	1.216	<.001*
Habitat	1	-0.309	0.020*
O vs. I	1	0.168	0.213
O vs. N	1	2.205	<.001*
P. chartacea * Habitat	1	0.074	0.663
P. basiramia * Habitat	1	-0.640	<.001*
E. cuneifolium * Habitat	1	0.140	0.518
L. ohlingerae * Habitat	1	1.330	<.001*
P. chartacea * O vs. I	1	0.001	0.997
P. basiramia * O vs. I	1	0.590	0.002*
E. cuneifolium * O vs. I	1	1.256	<.001*
L. ohlingerae * O vs. I	1	3.266	<.001*
P. chartacea * O vs. N	1	-0.027	0.912
P. basiramia * O vs. N	1	0.060	0.799

	DF	B	Sig.
L. ohlingerae * O vs. N	1	13.700	0.935
Habitat O vs. I	1	-0.270	0.064
Habitat O vs. N	1	0.243	0.172
Intercept	1	-1.067	<.001*

Table 3. Percentage germination of total seeds planted for each species (single and mixed species treatments combined) in Spring and Winter Field Trials. Percentages were calculated by dividing the total number of germinants within intact scrub, degraded McJunkin scrub (degraded 1) or degraded Reserve scrub (degraded 2) by the total number of seeds planted there. In Winter Field Trial, data for degraded scrub represents the Reserve only.

	Spring Field Trial			Winter Field Trial	
Species	**Intact**	**Degraded 1**	**Degraded 2**	**Intact**	**Degraded 2**
L. ohlingerae	20.3%	51.6%	23.4%	29.2%	38%
E. cuneifolium	7.8%	18.8%	18.8%	3.9%	4.2%
P. chartacea	25.0%	8.9%	3.1%	0.9%	2.8%
H. cumulicola	0.5%	0%	0%	0%	0.3%
P. basiramia	0.5%	4.7%	5.7%	21.3%	1.8%

Table 4. Logistic regression of germination of *L. ohlingerae*, *E. cuneifolium*, *P. basiramia*, *H. cumulicola*, and *P. chartacea* by habitat (degraded vs. intact) and microsite (shrub / litter, litter only, bare sand) from Winter Field Trial. B = slope from logistic regression, SE = standard error, DF = degrees of freedom. Significant P values (< 0.05) are marked with an asterisk.

	B	**SE**	**DF**	**Sig.**
Habitat	0.671	0.425	1	0.114
Microsite			2	0.032*
Shrub vs. Bare sand	-1.151	0.571	1	0.044*
Litter vs. Bare sand	-1.276	0.569	1	0.025*
Habitat* Microsite			2	0.356
Intact habitat by Shrub	0.788	0.733	1	0.282
Intact habitat by Litter	-0.397	0.736	1	0.590
Intercept	-1.046	0.322	1	0.001

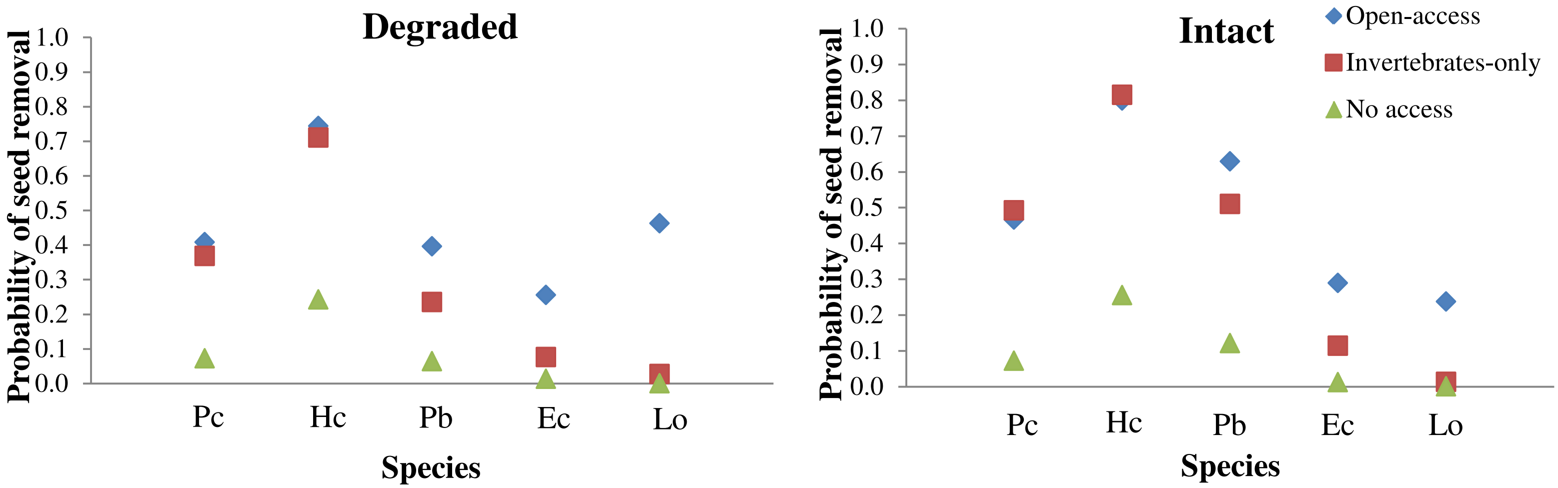


Figure 1. Predicted values for probability of seed removal in each habitat-treatment combination with species as an independent variable. Pc = *P. chartacea*, Hc = *H. cumulicola*, Pb = *P. basiramia*, Ec = *E. cuneifolium*, Lo = *L. ohlingerae*.

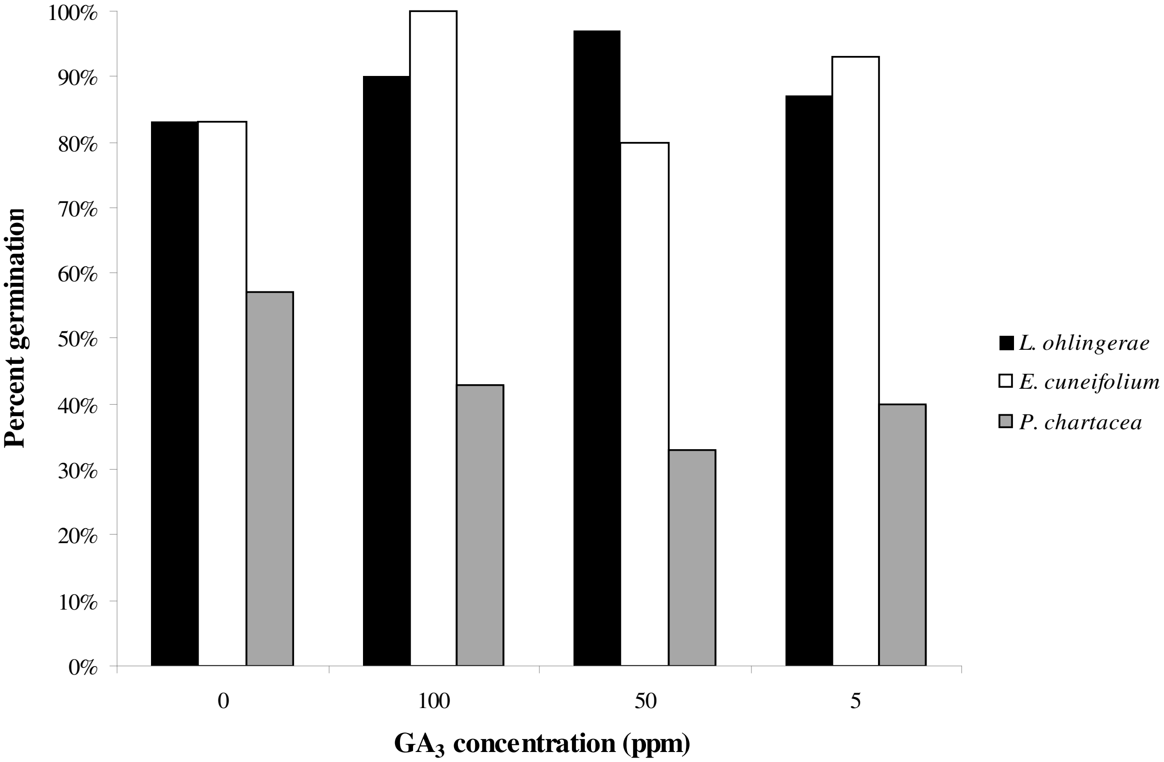


Figure 2. Percentage germination per species in GA_3 (gibberelic acid) growth chamber trial. *H. cumulicola* and *P. basiramia* were not available for this study.

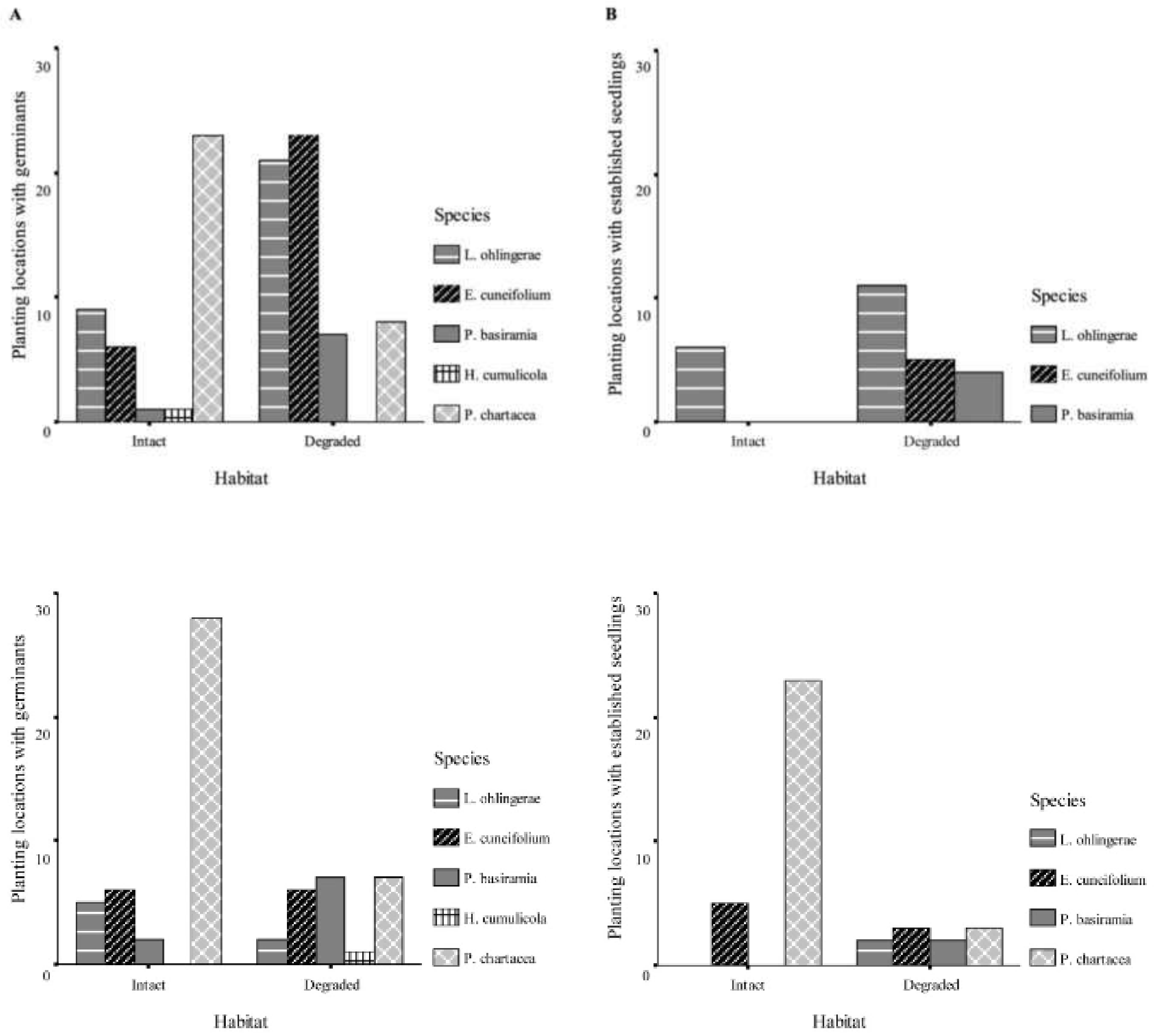


Figure 3. Number of planting locations with germination (A) and established seedlings (B) by February 28th, 2009, in intact and degraded scrub habitats from Spring Field Trial. *P. chartacea* individuals were still germinants at this sampling date. Number of planting locations with germination (C) and established seedlings (D) in intact and degraded scrub habitats by February 24th, 2010, from Winter Field Trial. Bars for *P. chartacea* represent both background germination and germinants from planted seeds.

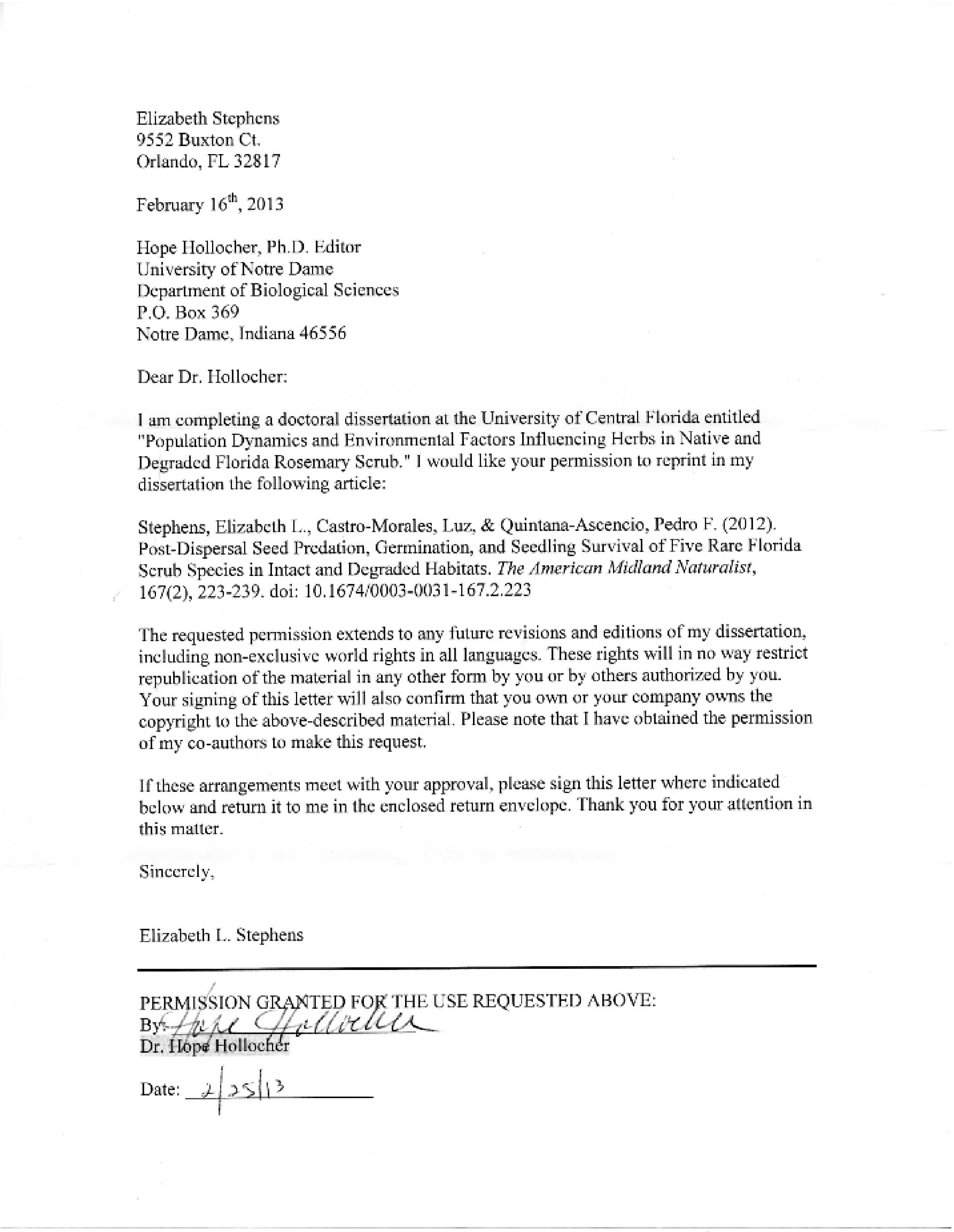
Appendix A: Temperature and Light schedule for Spring and Winter Chamber Trials.

Fluorescent and Incandescent Indicate Number of Bulbs of Each Type Illuminated Each Hour

Time	**Spring C**	**Winter C**	**Fluorescent**	**Incandescent**
0:00	22.0	20.0	0	0
1:00	22.0	20.0	0	0
2:00	22.5	20.0	0	0
3:00	23.0	20.0	0	0
4:00	23.5	20.0	0	0
5:00	24.0	20.0	0	0
6:00	24.5	20.5	0	1
7:00	25.0	20.5	1	1
8:00	25.5	21.0	1	1
9:00	26.0	21.0	1	2
10:00	26.5	21.5	1	2
11:00	27.0	22.0	2	2
12:00	27.2	22.0	2	2
13:00	27.0	22.0	2	2
14:00	26.5	21.5	1	2
15:00	26.0	21.0	1	2
16:00	25.5	21.0	1	1
17:00	25.0	20.5	1	1
18:00	24.5	20.5	0	1

Time	**Spring C**	**Winter C**	**Fluorescent**	**Incandescent**
19:00	24.0	20.0	0	0
20:00	23.5	20.0	0	0
21:00	23.0	20.0	0	0
22:00	22.0	20.0	0	0
23:00	22.0	20.0	0	0
23:59	22.0	20.0	0	0

Appendix B. Copyright Permission



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February 16th, 2013

Hope Hollocher, Ph.D. Editor
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Dear Dr. Hollocher:

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Stephens, Elizabeth L., Castro-Morales, Luz, & Quintana-Ascencio, Pedro F. (2012). Post-Dispersal Seed Predation, Germination, and Seedling Survival of Five Rare Florida Scrub Species in Intact and Degraded Habitats. *The American Midland Naturalist*, 167(2), 223-239. doi: 10.1674/0003-0031-167.2.223

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CHAPTER THREE: EFFECTS OF HABITAT, MICROSITE AND SEED DENSITY ON SEED PREDATION, GERMINATION, AND ESTABLISHMENT OF TWO NATIVE SCRUB HERBS

Abstract

Early life-history stages disproportionally influence population dynamics of short-lived species; understanding factors affecting variation in emergence and seedling survival is fundamental to assessing persistence. I evaluated the role of habitat (disturbed and intact), microsite (bare sand, leaf litter, shrubs), and seed density on seed dynamics of two native herbaceous species in Florida scrub. I did not find evidence of differences in individual seed production of *Chamaecrista fasciculata* (partridge pea) and *Balduina angustifolia* (coastalplain honeycombhead) between habitats. Invertebrates were primarily responsible for seed removal of both species, although peak season of removal and the effects of microsite varied with species; *C. fasciculata* had the most removal in spring from bare sand, *B. angustifolia* had the most in winter from litter. Removal of seeds, emergence, and establishment increased with seed density. Establishment of *C. fasciculata* may benefit from decreased below-ground competition in degraded scrub where nitrogen-fixation may be an advantage, while *B. angustifolia* emerged and established more successfully in bare sand away from shrub roots. Results emphasize that ecological drivers can have different degrees of influence at different life-history stages of individual species.

Introduction

Early life-history stages are critical to many plant species, which rely for persistence on dormant seeds until conditions are favorable for germination and establishment (Auld et al. 2000; Quintana-Ascencio and Menges 2000; Holmes and Newton 2004). Seed bank dynamics can be particularly important for short lived herbs (Navarra et al. 2011, Silvertown et al. 1993), semelparous species (Silvertown and Smith 1989; Silvertown et al. 1996), early successional species (Cipollini et al. 1993, Silvertown and Franco 1993) or those in open microsites (Perez-Ramos et al. 2012), and for species that live in conditions of unpredictable drought (van Groenendael and Slim 1988).

A deeper understanding of ecological factors influencing seed and seedling dynamics will help to identify demographic drivers of plant species with seed banks. Variation in habitat (Tallmon et al. 2003; Ronnenberg et al. 2008) and microsite characteristics (Oswald and Neuenschwander 1993; Bisigato and Bertiller 1999; Jones and del Moral 2005; Parent et al. 2006) affect transitions between early life-history stages. These environmental factors regulate the abiotic (resource availability, e.g., Coop and Givnish 2008, Ronnenberg et al. 2008, Badgery et al. 2008) and biotic conditions (competition, e.g., Liu et al. 2008; facilitation, e.g., Kellman and Kading 1992, Pihlgen and Lennartsson 2008; seed predation, e.g., Tallmon et al. 2003) for germination and seedling establishment.

In addition to environmental characteristics, the number of seeds available for germination and establishment in a given location determines seed dynamics. Seed predation may be density-dependent; relatively larger groups of seeds may attract more seed predators (Brewer and Webb 2001; Montesinos et al. 2006), which may proportionally increase the chance of individual seed mortality. Larger groups of seeds may also increase the chance of germination compared to smaller groups (e.g., Poulsen et al. 2007), which may proportionally increase or decrease the chance of individual germination. Seed availability may ultimately affect population persistence (Kirchner et al. 2006), community structure (Ostfeld et al. 1997; Howe and Brown 1999; Nathan and Muller-Landau 2000) and composition (Primack and Miao 1992; Clark et al. 1999; Turnbull et al. 2000; Martin and Wilsey 2006).

Florida Rosemary scrub is of particular interest to ecologists due to the large number of endemic herb species, many of which recruit from the seedbank (Quintana-Ascencio and Menges 2000; Navarra et al. 2012). Florida Rosemary scrub is characterized by short shrubs interspersed with bare sand gaps that historically were maintained by lightning-induced fires (Fernald and Purdum 1992). This ecosystem is threatened by fragmentation, fire suppression, and degradation (e.g., roller chopping) due to commercial and agricultural use (Weekley et al. 2008a). Intact and degraded scrub differ in habitat structure, and abundance and distribution of microsites; degraded scrub has more isolated patches of overgrown shrubs and continuous bare sand areas. Despite an overall negative effect of degradation on scrub ecosystems, the increased open habitat and reduction in shrub cover may result, at least transiently, in greater herb recruitment.

The opportunistic herbs *Chamaecrista fasciculata* (partridge pea) and *Balduina angustifolia* (coastalplain honeycombhead) occur in variable densities in degraded and intact scrub where they may have contrasting demography. I predicted that both species would produce more seeds per plant and have more seedlings emerge in degraded scrub because the more open structure of this habitat may reduce competition for resources and seed predation. Seed production and emergence of opportunistic species generally increases with disturbance (Hobbs and Mooney 1985; Schupp and Fuentes 1995; Pugnaire and Lozano 1997; Cole et al. 2004). I expected greater seed predation in intact than in degraded scrub because greater cover of low shrubs in intact scrub may protect seed predators from carnivores (Restrepo and Vargas 1999; Weekley et al. 2008b). I anticipated greatest seed production and seedling emergence in bare sand microsites where there is less belowground competition for resources (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernández 1997; Schafer et al. 2010; Petrů and Menges 2003). Greater deposited seed densities were expected to attract more seed predators and increase seed removal (Montesinos et al. 2006; Brewer and Webb 2001; Vargas-Mendoza and Gonzalez-Espinosa 1992, Casper 1987), as well as increase seedling emergence (Poulsen et al. 2007), relative to smaller seed densities. Seedling emergence at the population level can be relatively greater if the predator community becomes saturated.

The main goals of this study were to evaluate variation in seed production and estimate the effects of seed density, habitat (intact vs. degraded), and microsite (under shrubs, in litter, bare sand) on seed removal and emergence of *C. fasciculata* and *B. angustifolia*. A priori, relationships between ecological factors and seed dynamics were expected to be comparable between such co-existing species with similar life-history characteristics. I aimed to elucidate requirements for conservation and reestablishing populations in degraded habitat, such as shrub height reduction or providing ground cover to mirror intact habitat and microsite structure, or supplemental measures such as animal exclosures to protect seeds. This information will identify concerns about population persistence and management requirements in the two land types.

Methods

Study Species and Sites

Chamaecrista fasciculata (Michx.) Greene is an annual legume with relatively sizeable and abundant seeds, and a fast growth rate. Seeds of *C. fasciculata* are produced in late summer to early fall, and are eaten by birds and deer (Gee et al. 1994; Yarrow and Yarrow 1999, Jones et al. 2010*). C. fasciculata* is found throughout eastern North America (USDA 2012); it has been described as self-compatible but predominately outcrossing (Fenster 1991a, 1995), and dispersal limited (both via pollen and seeds, Fenster 1991a) with a short lived seed bank (Baskin and Baskin 1988; Fenster 1991b). *Balduina angustifolia* (Pursh) B. L. Rob. is a biennial dicot and widespread gap specialist. Its seeds are collected in quantity and primarily eaten by ants (*Pogonomyrmex badius*; M. Deyrup pers. comm.), but birds were observed eating seeds directly from the plant (C. Weekley pers. comm.). *B. angustifolia* is found in the southeastern United States (USDA 2012).

I conducted this study in the southern end of the Lake Wales Ridge in south-central Florida, a region characterized by some of the best remaining intact Florida scrub (Weekley et al. 2008a). This ecosystem occurs on well drained, nutrient-poor soils. Community composition and habitat structure depend on periodic fires (Abrahamson et al. 1984; Fernald and Purdum 1992). Many Florida scrub plant species recover from fire and other disturbances by seedling recruitment, although shrubs primarily resprout (Menges and Kohfeldt 1995). The study was performed in intact Florida Rosemary scrub in Archbold Biological Station (ABS; 2,104 ha) and degraded scrub in the neighboring Archbold Reserve (Reserve; 1,476 ha), Highlands County (Township 38S, Range 30E, sections 5-8, 18, 19, 29-32), Florida. All sites were managed by Archbold Expeditions. Yearly temperatures ranged from 8.33 ° C (January mean-minimum) to 34.05 ° C (July mean-maximum), with mean annual rainfall of 136.4 cm (Archbold Biological Station weather data). All sites had Satellite soils and locally high elevation (~45 m).

Florida rosemary scrub is dominated by Florida rosemary (*Ceratiola ericoides*), oaks (*Quercus* spp.), palmettos (*Serenoa repens* and *Sabal etonia*), *Lyonia* spp., and tough buckthorn

(*Sideroxylon tenax*) (Abrahamson et al. 1984). Herbaceous species, many of them rare and endemic, and lichens grow in gaps of bare sand (balds) between shrubs (Abrahamson et al. 1984; Christman and Judd 1990; Turner et al. 2006; Menges et al. 2008). Frequency of fires in Florida rosemary is moderate to low (15-40 years) (Menges and Kohfeldt 1995; Menges 1999). I chose balds burned between 8 and 27 years before study initiation.

The degraded scrub of the Reserve was subjected to roller chopping and light cattle grazing, with cattle on site until 2002. Fire frequency prior to management by Archbold Expeditions is unknown (ABS, unpublished data). Species composition in the degraded scrub was similar to rosemary scrub sites, aside from the presence of invasive nonnative grasses (*Digitaria eriantha* and *Rhynchelytrum repens*). However, vegetation structure, microsite and species distributions often differed between the two land types (David and Menges 2011; Navarra and Quintana-Ascencio 2012). In degraded scrub, patches of shrubs were overgrown, while the same shrub species in rosemary scrub are typically were 2-5 m high (Menges and Rickey 2005). Microsites differed in that bare sand areas surrounding shrubs were more extensive in degraded scrub (Menges and Rickey 2005), which also altered proximity to shrubs for some microsites (David and Menges 2011), and affected litter distribution. Percent organic matter was significantly greater in intact scrub versus degraded scrub but phosphorus and nitrogen were slightly greater in the degraded scrub (S. Hamman and P. Bohlen, unpublished data; ABS unpublished data).

Seed Production

In 2008 (August-November for *C. fasciculata*, November-December for *B. angustifolia*), I estimated seed production of each species in multiple sites per habitat. Sampling plots were either entire balds within intact habitat; N = 5 for *C. fasciculata* (6527 ± 3383 m^2); N = 4 for *B. angustifolia* (7888 ± 3998 m^2) or circular areas of 20 m radius within degraded habitat; N = 3 for each species. Plots in degraded habitat were centered on patches of study species, and were haphazardly selected if more than one patch occurred per site. More intact sites were used than degraded sites to compensate for smaller population sizes in the intact habitat; I studied all known populations of *C. fasciculata* in balds at the time of the study. In 2009, I only used three intact sites per species (4948 ± 3832 m^2) because study species were no longer present in some of the 2008 plots, or were present but not reproductive. I assessed multiple sampling plots in each degraded site to provide a comparable number of reproductive individuals: for two sites I used one 12.5 m and one 25 m radius plot and for the other site I used one 12.5 m and two 25 m radius plots.

Within each sampling plot, every individual of the focal species was marked with a wire stake flag and unique metal tag. Total seed pods or heads were counted per plant. I harvested three individuals adjacent to each plot and counted the number of seeds in each pod or head (visibly viable and inviable). I used mean values for seeds per pod or head from these plants as estimates of seeds per pod or head for each site. I also divided the number of reproductive individuals per site and total pods produced per site by the combined area of each site's plots to estimate density of reproductive individuals and density of pods or heads produced / m^2. While seed production is not equivalent to seeds available for secondary dispersal (movement of seeds to final deposit site after initial dispersal from plant), relative seed production at the different sites enabled comparisons between reproductive effort in intact and degraded scrub, as well as maximum seed availability in each habitat.

Seed Collection

I collected seeds for all experiments at ABS and the Reserve during the September to October reproductive season immediately prior to each experiment. Intact, fully pigmented seeds were separated under a dissecting microscope; these were pooled to randomize seed source. Seeds were sorted into groups with forceps and sealed in foil packets for efficient field deployment (number of seeds per group varied with experimental treatment). Seeds were stored in a refrigerator (4^o C) before use in the field and growth chamber.

Seed Removal

I assessed the effects of habitat, microsite, and seed density on seed removal in February to March of 2009 (Winter Trial) and May 2010 (Spring Trial). I assumed that seed removal was representative of post-dispersal seed predation in this system because seeds of the two study species do not have eliasomes (lipid attachments) or fleshy fruit, giving animals little incentive to move them without consumption. The experiment had a 6 x 3 x 4 x 3 replicated factorial design, where treatments were all possible combinations of site, microsite, seed density, and seed access treatment. I used 234 total units, including an additional 3 control treatments per microsite in each site, and 2,070 seeds. Locations of treatment units were assigned using random coordinates generated in ArcMap, and were located using a Trimble Global Positioning System with sub-meter accuracy (GPS).

I randomly selected three intact and three degraded sites among the sites used for the seed production study. Within each site I used the following microsites: “shrub” with experimental units placed under shrubs with leaf litter, “litter” with units placed in leaf litter without shrub cover, and “bare sand” with no shrub cover or leaf litter. I used seed densities of 1, 4, 8, and 24 seeds, which corresponded to approximately 122, 490, 980, and 2939 seeds per m^2. These densities were chosen in an attempt to capture natural variation, from a minimum possible number, to some number beyond those observed in field (pers. obs. E. Stephens). Petri dishes of seeds were retrieved after forty-eight hours to count remaining seeds. This time period was based on my preliminary experiments with commercially available seeds and previous seed removal studies (Fedriani et al. 2004). I observed that shorter trials did not provide sufficient time for animals to encounter seeds, and longer trials resulted in decreased effectiveness of Tangle-Trap Sticky Coating (Tanglefoot, for invertebrate exclusion) due to adhesion and accumulation of litter and dead insects.

I created the following treatments to filter animal access to seeds: 1) a no-access control comprised of a wire mesh cage covered with clear plastic, rimmed with sticky non-toxic Tanglefoot, with a PVC ring; no animals could access seeds, 2) a limited-access treatment comprised of a wire mesh cage with no plastic or Tanglefoot, with a PVC ring; only invertebrates could access seeds, 3) an all-access treatment with no cage, only a PVC ring; invertebrates and vertebrates could access seeds, and 4) an unmanipulated treatment with no cage or PVC ring; invertebrates and vertebrates could access seeds. PVC rings were 10.2 cm in diameter and 7.6 cm depth, buried approximately 3.5 cm, and were used to reduce the effects of wind / water displacement. I used removal from the limited-access treatment as an estimate of invertebrate-mediated seed removal, and the difference between removal from the all-access treatment and removal from the limited-access treatment as an estimate of vertebrate-mediated seed removal.

Emergence and Establishment

I assessed the effects of habitat and microsite on emergence and establishment in two trials, from April 2009 to April 2012, and from May 2010 to May 2012. The experiment had a 6 x 3 x 4 replicated factorial design where treatments were all possible combinations of site, microsite, and seed density. I used 234 total units with 1,998 seeds. Locations of treatment units were assigned using random coordinates generated in ArcMap, and were located using a Trimble Global Positioning System with sub-meter accuracy (GPS).

I planted seeds of both study species in three intact and three degraded sites for each trial. I replicated units in the aforementioned three microsites (shrub, litter, bare sand). Controls with no planted seeds were used to assess emergence from outside sources (Turnbull et al. 2000). Seeds were deposited within PVC rings of 10.2 cm diameter and 7.6 cm depth, which were partially buried (approximately 3.5 cm) in sand to keep the seeds in place. I sprinkled sand on the seeds in each ring until they were just covered; rings were each protected with wire mesh vertebrate exclosures to reduce removal, and marked with wire-stake flags. Invertebrates were not excluded due to anticipated effects of plastic covering (see seed removal study) on light levels and humidity for seedlings. I monitored for seedlings and recorded individual plant survival, height, and reproductive status once every week for the first month and monthly thereafter. Plants were considered established if they grew to a height of at least 30 cm or were reproductive. Background germination rates were monitored in a growth chamber (CONVIRON CMP 4030) set to seasonal temperatures for Venus, FL (Appendix C1-3; ABS weather data), and considered an upper boundary for expected germination of seeds in the field. I used Petri plates with moistened filter paper for 6 plates of 10 seeds per plate; filter papers were moistened with ambient water as needed, and germinants were counted daily.

Statistical Analysis

I conducted analyses in R (2.7.2). I transformed data using natural logarithm as appropriate to meet test assumptions. I used sites as replicates for all analyses. I conducted a nested Analysis of Variance to determine whether seed pod or head production per individual was significantly different between habitats. I used two-way Analysis of Variance to compare differences between habitats and between sampling years in average numbers of seeds per pod or head, reproductive individuals per square meter, and total pods or heads produced per square meter.

I conducted logistic regression analyses to determine whether habitat, microsite, exclosure treatment, and trial season / year influenced seed removal. Habitat (2 levels), microsite (3 levels), exclosure treatment (4 levels), and trial season / year (2 levels) were categorical predictor variables and seed density was a continuous predictor variable. The response variable was presence (1) or absence (0) of seed removal per treatment unit. I used Akaike's Information Criterion (AIC) to select the most informative model. For the seedling data, I also conducted logistic regression analyses using habitat (2 levels), microsite (3 levels), and trial year (2 levels) as categorical predictor variables and seed density as a continuous predictor variable. Treatment units were coded for the presence (1) or absence (0) of emerged seedlings and established plants. Plants were considered established if they grew to ≥ 30 cm or had reproductive structures. Microsites were compared in two tests to examine all microsite pairs (shrub vs. litter, shrub vs.

bare sand, litter vs. bare sand). Significance levels for microsite comparisons were adjusted using Bonferroni correction (α = 0.025). Monte Carlo analyses were conducted to determine whether shrub species significantly affected emergence or establishment. Overall combined probabilities of early establishment were obtained by multiplying probabilities of seed removal and seedling emergence in each combination of habitat, microsite, and seed density treatment.

Results

Seed Production

Mean seed pod production per individual of *C. fasciculata* did not differ significantly between habitats (2008: degraded: 37.4 ± 14.6 pods, intact 30.0 ± 5.4, P = 0.740, DF = 1; 2009: degraded: 20.3 ± 4.0, intact: 9.8 ± 3.9; P = 0.407, DF = 1), but differed significantly among sites (2008: P = 0.002, DF = 6; 2009: P < 0.001, DF = 4) (Figure 4a). There was no significant difference in number of seeds per pod between habitats (P = 0.078, DF = 1), or between years (P = 0.767, DF = 1), but there was a significant interaction between habitat and year (P = 0.017, DF = 1) with fewer seeds per pod in degraded than in intact scrub in 2009 (10.7 ± 1.1 seeds per pod, intact: 6.4 ± 0.3, P = 0.038, DF = 1), but not in 2008 (8.8 ± 0.5 seeds per pod, intact: 8.4 ± 0.6) (Figure 4b). Mean density of reproductive plants was significantly greater in degraded than in intact habitat (2008: degraded: 0.04 ± 0.01 individuals per m^2, intact: 0.01 ± < 0.01, 2009: degraded: 0.03 ± 0.01, intact: 0.01 ± < 0.01; P = 0.001, DF = 1), but not significantly different between years (P = 0.654, DF = 1), and there was no significant interaction between habitat and year (P = 0.398, DF = 1). Mean density of pods produced was also significantly greater in degraded than in intact habitat (2008: degraded: 1.8 ± 0.9 pods per m^2, intact: 0.2 ± 0.1, 2009: degraded: 0.1 ± 0.02 pods, intact: 0.6 ± 0.3; P = 0.002, DF = 1), but not between years (P =

0.211, DF = 1); there was no significant interaction between habitat and year (P = 0.447, DF = 1).

Mean number of seed heads per individual of *B. angustifolia* was significantly greater in degraded habitat in 2008 (degraded: 25.7 ± 6.2 heads, intact: 21.6 ± 2.9**,** P=0.003, DF = 1) but not in 2009 (degraded mean: 17.9 ± 3.6, intact mean: 19.2 ± 4.0, P = 0.910, DF = 1); there was a significant difference among sites in both years (P < 0.001 in 2008, P < 0.001 in 2009) (Figure 5a). Mean number of seeds per head did not differ significantly between habitats (P = 0.820, DF = 1), years (P = 0.191, DF = 1), or with the habitat x year interaction (2008: degraded: 18.4 ± 7.0 seeds, intact: 15.5 ± 3.0; 2009: degraded: 24.1 ± 5.3 seeds, intact: 21.8 ± 3.1; (P = 0.905, DF = 1)) (Figure 5b). There was no significant difference in mean density of reproductive plants between habitats, between years, or with the habitat x year interaction (2008: degraded: 0.04 ± 0.01, intact: 0.05 ± 0.04; 2009: degraded: 0.03 ±0.02, intact: 0.01 ± 0.01). There was no significant difference in mean density of heads produced between habitats, between years, or with the habitat x year interaction (2008: degraded 1.03 ± 0.42 heads per m^2, intact 0.77 ± 0.54; 2009: degraded 0.17 ± 0.09 heads per m^2, intact 0.44 ± 0.24).

Seed Removal

Seed removal of *C. fasciculata* was best explained by the additive model of all factors: habitat, microsite, exclosure treatment, deposited seed density, and trial season / year (Table 5, Figure 6, Appendix D1). Seed density had a significant positive effect on seed removal in both trials (Table 5; model estimate = 0.091; SE = 0.013; Z = 7.001; P < 0.001); number of units with at least one seed removed increased with increasing seed density. Significantly fewer seeds were removed in the Winter Trial (4.8%) than in the Spring Trial (14.7%; Table 5: model estimate =

1.275; SE = 0.247; Z = 5.166; P < 0.001). The unmanipulated treatment (Table 5; model estimate = 2.552; SE = 1.041; P = 0.014, Z = 2.451) and all-access treatment (model estimate: 2.189, SE = 1.043, Z = 2.098, P = 0.036) had significantly more removal than the no access control. Estimated invertebrate-mediated seed removal (limited-access treatment) was greater than estimated vertebrate-mediated seed removal (all-access treatment – limited-access treatment) (Figure 6, Table 6). There were no significant differences in seed removal among the three microsites (litter vs. bare sand: model estimate: 0.13, SE = 0.28, Z = 0.44, P = 0.657; litter vs. shrub: model estimate: 0.33, SE = 0.29, Z = 1.14, P = 0.26; bare sand vs. shrub: model estimate: 0.20, SE = 0.29, Z = 0.70, P = 0.49); the two seasons / years did not exhibit the most removal in the same microsite (Winter: 17 units with removal in litter, 15 units in shrub, 8 units in bare sand; Spring: 35 units in bare sand, 29 units in litter, 26 units in shrub).

Across trials, seed removal of *B. angustifolia* from individual treatment units was best explained by the additive model of all main factors: (habitat, microsite, exclosure treatment, deposited seed density, and trial season / year, plus the habitat x microsite interaction (Table 7, Figure 7, Appendix D2). Deposited seed density had a significant positive effect on removal (model estimate = 0.091, SE = 0.013, Z = 7.053, P < 0.001); number of units with seed removal increased with increasing seed density. Significantly more units in litter microsites exhibited removal than in shrubs (model estimate = 0.862, SE = 0.383, Z = 2.250, P = 0.024). Across trial seasons / years, intact habitat had more removal in litter than in shrub, and a tendency for more removal in bare sand than in shrub (35 units in intact / litter, 32 in intact / bare sand, 23 in intact / shrub), while degraded habitat had more removal in shrub than in litter, and a tendency for more removal in bare sand than in litter (33 units in degraded / shrub, 34 units in degraded / bare sand, 29 in degraded/litter) (shrub vs. litter: model estimate = -1.14, SE = 0.54, Z = -2.14, P = 0.03;

bare sand vs. litter: model estimate = -0.56, SE = 0.52, Z = -1.07, P = 0.29; bare sand vs. shrub: model estimate = 0.58, SE = 0.53, Z = 1.10, P = 0.27). Significantly fewer seeds were removed in Spring (18.32%) than in Winter (28.60%) (Table 7; model estimate = -0.531; SE = 0.217; Z = -2.446; P = 0.014). The unmanipulated treatment (Table 7; model estimate = 2.814, SE = 0.754, Z = 3.731, P < 0.001) and all-access treatment (model estimate = 2.123, SE = 0.756, Z = 2.809, P = 0.005) had significantly more units with seed removal than the no-access control. Estimated invertebrate-mediated seed removal was greater than estimated vertebrate-mediated seed removal (Figure 7). In Winter, the most seeds were removed from the all-access treatment, followed by the unmanipulated treatment (Table 8). In the Spring, the most seeds were removed from the unmanipulated trial (Table 8).

Emergence and Establishment

Cumulative emergence of *C. fasciculata* during the first two years post seeding (2009-2011 and 2010-2012) was best explained by the model including all main factors and their interactions: habitat, microsite, planted seed density, and trial year (Table 9a, Figures 8a, b, Appendix D3). Number of units with emergence increased with increasing seed density (model estimate = 0.091, SE = 0.013, Z = 7.053, P < 0.001). There were fewer units with emergence and fewer emerged seedlings for all densities in the 2010 trial than in the 2009 trial (Appendix E1), except for observations of the smallest density. Establishment of *C. fasciculata* (cumulative three years post seeding, 2009 - 2012) was explained by an additive model of all factors studied (habitat, microsite, seed density) (Table 9b, Figure 8c). There were significantly more established plants in degraded scrub than in intact (degraded: 24 plants, 3 units; intact: 3 plants, 2 units; model estimate = 2.341, SE = 0.768, Z = 3.048, P = 0.002) (Table 9b, Figure 8c). Seed density had a significant effect on establishment; number of established plants increased with seed density (Table 9b, Figure 8c, Appendix D5). Overall, I observed more total emerged seedlings in intact scrub, but more established plants in degraded scrub (Figure 9). Shrub species did not have a significant effect on emergence (presence of *C. ericoides*: P = 0.590; *Quercus* spp.: P = 0.823; *S. repens*: P = 0.940) or establishment (presence of *C. ericoides*: P = 0.131; *Quercus* spp.: P = 0.286; *S. repens*: P = 0.437). I observed 41.67% germination in the growth chamber germination study. Combined probability of survival and emergence was similar between habitats, but slightly greater in degraded bare sand treatments (Appendix F1). Early individual survival in this treatment combination was most likely at the moderate and greatest seed densities (8 seeds: 50.5% chance; 24 seeds: 46.4% chance; Appendix F1).

Emergence of *B. angustifolia* was best explained by an additive model of habitat, microsite, and planted seed density (sampling year did not significantly improve the model) (Appendix D4). There were significantly fewer planting locations with *B. angustifolia* seedlings in the degraded habitat (80 rings, 109 emerged seedlings (years combined)) than in the intact habitat (in 207 rings, 321 emerged seedlings (years combined)) (model estimate = -0.662, SE = 0.214, Z = -3.091, P = 0.002, Table 10a, Figure 10a). Emergence increased with planted seed density (mean estimate = 0.096, SE = 0.012, Z = 7.672, P < 0.001; Appendix E2). There were significantly more emerged seedlings in bare sand microsites than in shrub microsites (model estimate = 1.353, SE = 0.264, Z = 5.121, P < 0.001) or in litter microsites (model estimate = -1.084, SE = 0.258, Z = -4.197, P < 0.001) (bare sand: 88 rings, 299 seedlings; litter: 53 rings, 123 seedlings; shrub: 48 rings, 106 seedlings (years combined); Table 10a, Figure 10a). Establishment of *B. angustifolia* was best explained by an additive model of all factors: habitat, microsite, and planted seed density (Table 10b, Figure 10b, Appendix D6). There was an overall significant effect of seed density; presence of established plants increased with increases in planted seed density (model estimate = 0.048, SE = 0.020, Z = 2.446, $P < 0.014$). There were significantly more established plants in bare sand than in shrub microsites (model estimate = 2.282, SE = 0.527, Z = 4.333, $P < 0.001$) or in litter microsites (model estimate = -1.761, SE = 0.449, Z = -3.918, $P < 0.001$) (30 total rings, 45 established plants with establishment in bare sand microsites vs. 8 rings, 12 plants in shrub, and 5 rings, 6 plants in litter). Overall, there were more emerged seedlings in intact scrub, but there was less of a distinction between habitats for established plants. Bare sand microsites, on the other hand, had the most emerged seedlings and established plants (Figure 11). Shrub species did not have a significant effect on emergence (presence of *C. ericoides*: P = 0.259; *Quercus* spp.: P = 0.875; *S. repens*: P = 0.191) or establishment (presence of *C. ericoides*: P = 1.000; *Quercus* spp.: P = 0.504; *S. repens*: P = 0.605). I observed 38.33% germination of *B. angustifolia* seeds in the growth chamber germination study. Seeds planted in bare sand microsites in either habitat had the greatest combined probability of survival and emergence, although these values were slightly greater in intact habitat (greatest value for seed density of 1 in intact habitat: 30.9%, Appendix F2).

Discussion

Seed density, microsite, and habitat affected early stages of the population dynamics of the focal herbaceous species in different ways. In contrast, there was little habitat-associated variation in individual seed production. Similar, coexisting species can have very different competitive abilities and biological tradeoffs in contrasting environmental conditions. The effects of such conditions can also vary seasonally or temporally for individual species.

Seed production per plant in *C. fasciculata* and *B. angustifolia* was not greater in degraded scrub than in intact scrub. Substantial variation within each habitat and microsite in number of seeds produced per individual may explain the lack of habitat-specific trends. Indirect effects of habitat on seed production, such as differences in maximum local density of reproductive individuals, may still provide support for the role of habitat in population growth and community composition. A spatial analysis of the relationship between individual seed production and local density of reproductive adults (Houle et al. 2001) may further elucidate patterns observed in this study.

Seed removal increased with seed density but was not greater in intact scrub than in degraded scrub as expected. Increased likelihood of predators perceiving seeds in relatively larger piles (Brewer and Webb 2001), and the increased efficiency (reward for time and energy expended) of concentrating seed removal efforts on more plentiful seed sources may explain these observations (Bülow-Olsen 1984; Bullock 1989; Gorb and Gorb 2000; Montesinos et al. 2006; Pol et al. 2012). The significant difference in seed removal among microsites for *B. angustifolia*, but not for *C. fasciculata*, suggests that microsite may be more important for population dynamics of *B. angustifolia*. Habitat-associated microsite trends in *B. angustifolia* (degraded: greatest removal in bare sand, intact: greatest in litter) also indicate that habitat degradation may alter the abundances or distributions of seed predators (see also Restrepo and Vargas 1999).

Invertebrates (likely ants, E. Stephens pers. obs., M. Deyrup, pers. comm.) were primarily responsible for removal of *C. fasciculata* and *B. angustifolia* seeds in both Winter and Spring. Invertebrates are important seed predators in other xeric, nutrient-poor systems (Pirk and De Casenave 2010; Arnan et al. 2011; Pol et al. 2011). However, considering that the two species differed in the season of peak seed removal (Winter for *B. angustifolia*, Spring for *C. fasciculata*), it is possible that different invertebrates were responsible for seed removal of each study species.

Emergence and establishment of both species increased with increased density of seeds. Increased number of seeds enhances the chance of at least one emerged seedling in a given location (Poulsen et al. 2007). This result, together with the finding that seed removal also increased with deposited seed density, may have important implications for *C. fasciculata* and *B. angustifolia*. Positive density-dependent effects of increasing seed availability (more seedling emergence and establishment) must outweigh the negative density-dependent effects of increasing seed availability (more seed predation) for the population to grow. *Chamaecrista fasciculata* had the greatest combined probability of early individual survival at the greatest seed densities. The relationship between seed density, seed survival, and emergence may be more complex for *B. angustifolia*, which had the greatest chance of survival through emergence at moderate seed densities and the smallest chance of survival at the greatest seed density. Consequently, it may be relatively more advantageous for individuals in *C. fasciculata* populations to invest heavily in seed production compared to *B. angustifolia*.

Early life-history stages of *C. fasciculata* provided some support for habitat as a driver of population dynamics, but contrary to predictions, it tended to have greater emergence in intact habitat. This trend may be somewhat obscured by the combined likelihood of seeds surviving from predators and emerging as seedlings, which was slightly greater in degraded scrub. These patterns evoke the “seed-seedling conflict” documented in previous studies (Schupp 1995, Smit et al. 2006). At later life-history stages, the role of habitat type as an ecological driver became clearer as there was significantly greater establishment in degraded habitat. Differing trends for emergence and establishment suggest that conditions favorable for germination were not optimal for establishment. Intact scrub may provide more favorable conditions for emergence of *C. fasciculata* due to increased organic matter or more abundant, beneficial microorganisms in top soil layers (Hawkes 2000). In contrast, intact scrub may be less hospitable than degraded scrub for establishment of *C. fasciculata* because of greater belowground competition for resources (space, nutrients, water).

Intact Florida scrub contains most of its vegetative biomass below ground (Guerin 1993; Schmalzer et al. 2002; Hawkes and Casper 2002; Saha et al. 2010). Previous studies documented greater recruitment in anthropogenically disturbed scrub or scrub-like sites than in comparable intact sites, attributing results to release from below ground competition. For example, complete gaps (cleared above and belowground) had greater seedling numbers and colonization than natural gaps (open aboveground only) (Petrů and Menges 2003). Areas along firelanes adjacent to intact scrub supported greater occupancy and densities of the herb *Paronychia chartacea* var. *chartacea* than in rosemary scrub, and within rosemary balds, densities of *P. chartacea* were greatest in the center of large gaps (Schafer et al. 2010). Both of these site types have reduced belowground root structure compared to small gaps, which have shorter distances to shrubs. As trends in *C. fasciculata* emergence and establishment were similar to those in these previous studies, it seems possible that observed differences between habitats were correlated with degree of belowground competition.

Furthermore, *C. fasciculata* may have different biochemical relationships with the soil in each habitat. As a legume, *C. fasciculata* could have a competitive advantage conferred by an ability to fix nitrogen over co-occuring species in degraded scrub (Singer et al. 2009). Adult *C. fasciculata* plants may also be less dependent on soil microbes (e.g., soil crusts, Hawkes 2000) than neighboring species, which would be an advantage in degraded habitats where such microbes may be less abundant. These features of *C. fasciculata* may not be advantageous in intact habitat, where other plants have strong relationships with soil crusts that can facilitate nitrogen uptake and may increase survival. *C. fasciculata* may also establish more easily in degraded scrub if root exudates and leaf leachates from allelopathic plants occur at lower concentrations (Weekly et al. 2008; Hewitt and Menges 2008). However, this later possibility seems unlikely, as there was no relationship between shrub species and emergence and establishment in either habitat.

Early life-history stages of *B. angustifolia* provided support for habitat and microsite as drivers of population dynamics. Contrary to predictions, emergence was significantly greater in intact than in degraded habitat. The combined likelihood of seeds surviving from predators and emerging as seedlings reinforced this pattern, as early individual survival was greatest in bare sand in both habitats but slightly greater in intact habitat. Unlike *C. fasciculata*, the role of habitat type as an ecological driver became less clear at later life-history stages of *B. angustifolia*. Evidence for microsite type as a driver remained strong with greatest emergence and establishment in bare sand.

Considering that *B. angustifolia* emergence was greater in intact scrub than degraded scrub, but establishment was not greater in intact scrub, it appears that there was relatively more seedling mortality in the intact habitat. This pattern may be due to increasing belowground competition in the intact habitat as seedlings became adults (as proposed for *C. fasciculata*). Furthermore, *B. angustifolia* seedlings may emerge and establish most easily in bare sand because of an increased distance from the resource-dominating root networks of shrubs. Seedling herbivory can also greatly affect establishment (Clark et al. 2012); herbivores of *B. angustifolia* seedlings may be more ubiquitous in the intact scrub, and under shrubs and in litter.

These results indicate that habitat and microsite effects on seed production, seed removal, and seedling emergence influence population dynamics of *C. fasciculata* and *B. angustifolia*. These conclusions are also relevant to other scrub herbs, including those that are endemic or endangered, as these species all tolerate infertile, xeric conditions, and benefit from gap-generating disturbances. However, as evidenced by differences between *C. fasciculata* and *B. angustifolia,* environmental characteristics can affect species within the same ecosystem differently. This study suggests the need for considering multiple life-history stages in different settings for population studies (Ticktin et al. 2012) and restoration efforts. Land managers and restoration biologists should expect differing environmental conditions to affect some life-history stages of target species more than others. In the case of these two species, managers should plant *B. angustifolia* seeds in bare sand microsites and *C. fasciculata* seeds in a variety of microsites to maximize emergence and establishment. *B. angustifolia* may need to be planted at relatively greater seed densities with animal exclosures to compensate for the significantly reduced emergence in degraded habitat. It is advisable to conduct preliminary studies of habitat-altering plans in an attempt to identify negative synergistic repercussions of management decisions (e.g., population decline or extinction, invasion by exotics).

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Tables and Figures

Table 5. Logistic regression model of seed removal of *C. fasciculata* across trials (seed removal ~ habitat + microsite + exclosure treatment + seed density + season / year). Degrees of freedom = 9.

Coefficients	Estimate	Std. Error	Z value	Pr (>|Z|)
Intercept	-4.79	1.06	-4.52	< 0.001
Habitat (degraded)	-0.25	0.24	-1.08	0.28
Microsite (litter) †	0.33	0.29	1.14	0.26
Microsite (bare sand) †	0.20	0.29	0.70	0.49
Treatment (limited access)	1.79	1.05	1.71	0.09
Treatment (all access)	2.19	1.04	2.10	0.04
Treatment (unmanipulated)	2.55	1.04	2.45	0.01
Seed density	0.09	0.01	7.00	< 0.001
Season/year (Spr 2010)	1.27	0.25	5.17	< 0.001

† Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction (α = 0.025); litter vs. bare sand microsites: model estimate: 0.13, SE = 0.28, Z = 0.44, P = 0.66.

Table 6. Seed removal of *C. fasciculata* (units with removal and seeds removed) in seed predation study. Unmanipulated treatment provided seed access to vertebrates and invertebrates (72 units, 666 seeds per trial); all-access provided access to vertebrates and invertebrates but reduced wind / water displacement (72 units, 666 seeds); limited access gave seed access to invertebrates only (72 units, 666 seeds); no-access did not provide seed access to vertebrates or invertebrates (18 units, 72 seeds).

	Winter Trial (2009)		Spring Trial (2010)	
Treatment	Units with removal	Total seeds removed	Units with removal	Total seeds removed
Unmanipulated	17	51	34	144
All-access	16	31	26	80
Limited-access	7	17	26	79
No-access (control)	0	0	1	1

Table 7. Logistic regression model of seed removal of *B. angustifolia* across trials (seed removal ~ habitat + microsite + exclosure treatment + seed density + trial season / year + habitat*microsite). Degrees of freedom = 11.

Coefficients	Estimate	Std. Error	Z value	Pr(>|Z|)
Intercept	-3.58	0.79	-4.55	<0.001
Habitat (degraded)	0.72	0.38	1.88	0.06
Microsite (litter) †	0.86	0.38	2.25	0.02
Microsite (bare sand) †	0.65	0.38	1.70	0.09
Treatment (limited access)	1.28	0.76	1.67	0.10
Treatment (all access)	2.12	0.76	2.81	0.01
Treatment (unmanipulated)	2.81	0.75	3.73	<0.001
Seed density	0.09	0.01	6.99	<0.001
Season / year (Spr 2010)	-0.51	0.22	-2.35	0.02
Habitat X microsite (degraded, litter) †	-1.14	0.54	-2.14	0.03
Habitat X microsite (degraded, bare sand) †	-0.58	0.53	-1.10	0.27

† Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter vs. bare sand (model estimate = 0.21, SE = 0.37, Z = 0.57, P = 0.57); degraded with litter vs. degraded with bare sand microsites: model estimate = -0.56, SE = 0.52, Z = -1.07, P = 0.29.

Table 8. Seed removal of *B. angustifolia* (units with removal and seeds removed) in seed predation study. Unmanipulated treatment provided seed access to vertebrates and invertebrates (72 units, 666 seeds per trial); all-access provided access to vertebrates and invertebrates but reduced wind / water displacement (72 units, 666 seeds); limited access gave seed access to invertebrates only (72 units, 666 seeds); no-access did not provide seed access to vertebrates or invertebrates (18 units, 72 seeds).

	Winter Trial (2009)		Spring Trial (2010)	
Treatment	Units with removal	Total seeds removed	Units with removal	Total seeds removed
Unmanipulated	41	218	42	266
All-access	39	229	23	80
Limited-access	23	144	16	32
No-access (control)	1	1	1	1

Table 9. Models of seedling emergence (A) and seedling establishment (B) of *C. fasciculata* from logistic regression analysis. Presence of emerged seedlings ~ habitat + microsite + seed density +habitat:microsite + habitat:seed density + microsite:seed density; degrees of freedom = 24. Presence of established plants ~ habitat + microsite + seed density; degrees of freedom = 5. Plants were considered to be established if they grew to a height of at least 30 cm or were reproductive.

A) Coefficients	Estimate	Std. error	Z value	Pr(>|Z|)
Intercept	-3.30	1.23	-2.68	0.007
Habitat (degraded)	2.55	1.39	1.83	0.067
Microsite (litter) †	-0.34	1.81	-0.19	0.849
Microsite (bare sand) †	-18.53	942.51	-0.02	0.984
seed density	0.58	0.20	2.96	0.003
season/year (2010)	1.68	1.35	1.25	0.213
Habitat X microsite (degraded, litter) †	-0.75	2.04	-0.37	0.713
Habitat X microsite (degraded, bare sand) †	16.66	942.51	0.02	0.986
Habitat X density (degraded)	-0.35	0.23	-1.54	0.124
Microsite X density (litter) †	0.55	0.43	1.29	0.196
Microsite X density (bare sand) †	4.70	235.63	0.02	0.984
Habitat X season / year (2010)	-2.81	1.61	-1.75	0.080.
Microsite X season / year (litter, 2010) †	0.86	1.95	0.44	0.659

Coefficients	Estimate	Std. error	Z-value	Pr(>|Z|)
Microsite X season / year (bare sand, 2010) †	18.12	942.51	0.02	0.985
Density X season / year (Spr 2010)	-0.46	0.20	-2.26	0.024
Habitat X microsite X density (degraded, litter) †	-0.39	0.47	-0.83	0.405
Habitat X microsite X density (degraded, bare sand) †	-4.46	235.63	-0.02	0.985
Habitat X microsite X season / year (degraded, litter) †	0.02	2.33	0.01	0.994
Habitat X microsite X season / year (degraded, bare sand) †	-16.81	942.51	-0.02	0.986
Habitat X density X season / year (degraded, litter) †	0.32	0.23	1.35	0.175
Microsite X density X season / year (bare sand) †	-0.57	0.43	-1.31	0.191
Microsite X density X season / year (litter) †	-4.64	235.63	-0.020	0.984
Habitat X microsite X density X season / year (litter, bare sand) †	0.41	0.48	0.86	0.392
Habitat X microsite X density X season / year (degraded, bare sand) †	4.62	235.63	0.02	0.984

†Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction (α = 0.025); none of the microsite comparisons were significant.

B) Coefficients	Estimate	Std. Error	Z value	Pr (>|Z|)
Intercept	-4.25	0.86	-4.93	<0.001
Habitat (degraded)	2.34	0.77	3.05	0.002
Microsite (litter) †	-0.90	0.65	-1.40	0.163
Microsite (bare sand) †	-0.55	0.61	-0.90	0.366
Seed density	0.06	0.03	2.08	0.038

†Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); none of the microsite comparisons were significant.

Table 10. Models of emergence (A) and seedling establishment (B) of *B. angustifolia* from logistic regression analyses. Presence of emerged seedlings ~ habitat + microsite + seed density; degrees of freedom = 5. Presence of established plants ~ habitat + microsite + seed density; degrees of freedom = 5. Plants were considered to be established if they survived to a height of ≥ 2 cm.

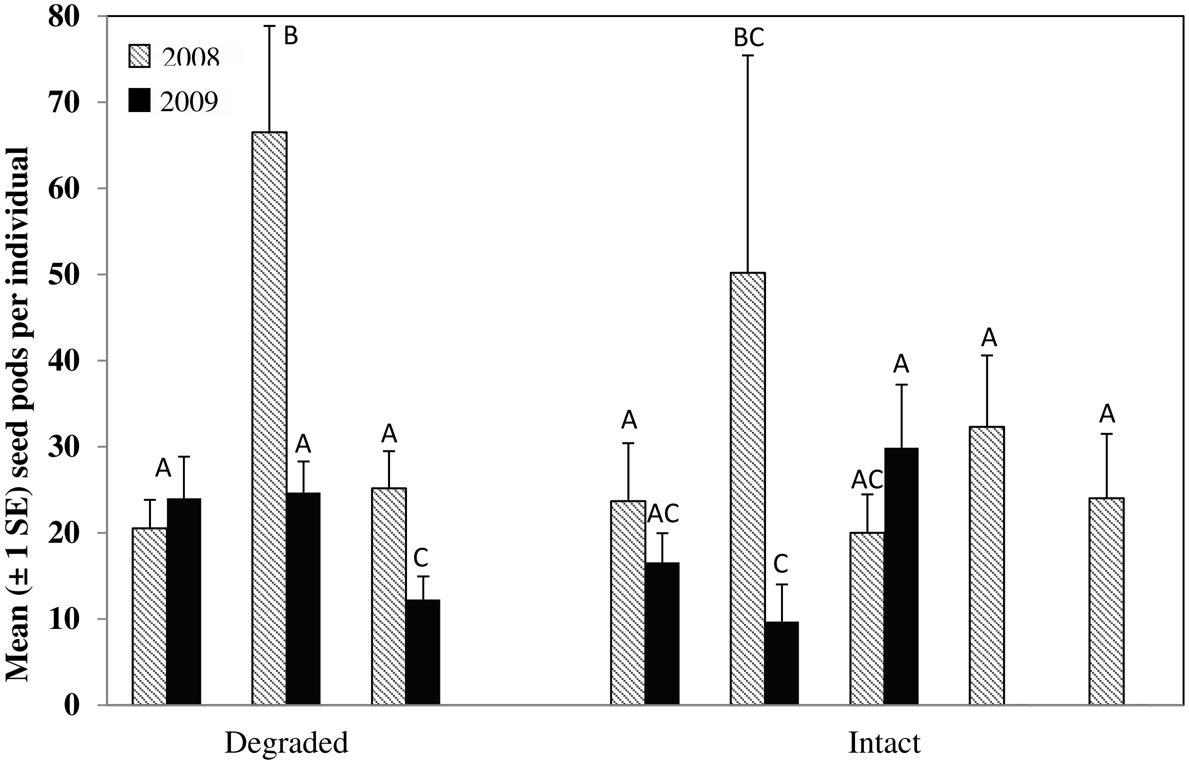
A) Coefficients	Estimate	Std. Error	Z value	Pr (>|Z |)
Intercept	-1.47	0.24	-6.05	<0.001
Habitat (degraded)	-0.66	0.21	-3.09	0.002
Microsite (litter) †	0.27	0.27	1.01	0.310
Microsite (bare sand) †	1.35	0.26	5.12	<0.001
Seed density	0.10	0.01	7.67	<0.001

†Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter vs. bare sand microsites: model estimate = -1.08, SE = 0.26, Z = -4.20, P < 0.001.

B) Coefficients	Estimate	Std. Error	Z value	Pr (>|Z |)
Intercept	-3.21	0.56	-5.76	<0.001
Habitat (degraded)	0.07	0.37	0.19	0.853
Microsite (litter) †	0.52	0.60	0.87	0.384
Microsite (bare sand) †	2.28	0.53	4.33	<0.001
Seed density	0.05	0.02	2.45	0.014

†Microsites were compared in two tests to examine all microsite pairs. Significance levels for microsite comparisons were adjusted using Bonferroni correction ($\alpha = 0.025$); litter vs. bare sand microsites: model estimate = -1.761, SE = 0.449, Z = -3.918, P < 0.001.

A)



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Mean (± 1 SE) seed pods per individual
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Degraded
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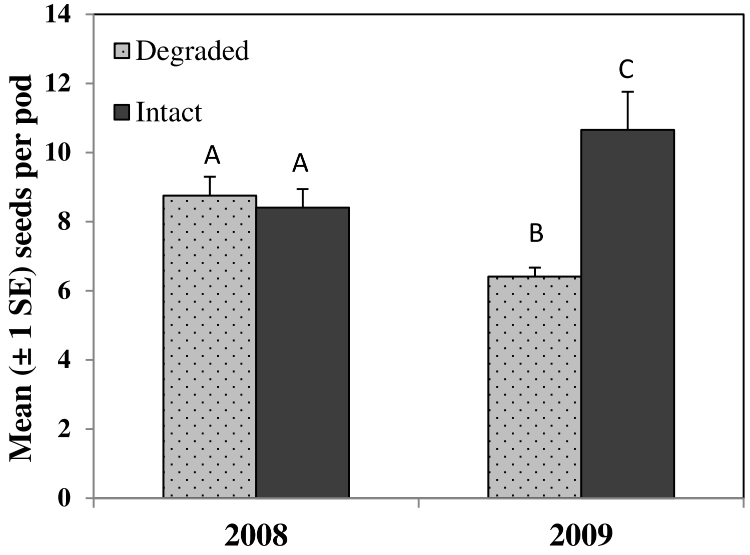
B)



14
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Mean (± 1 SE) seeds per pod
▨ Degraded
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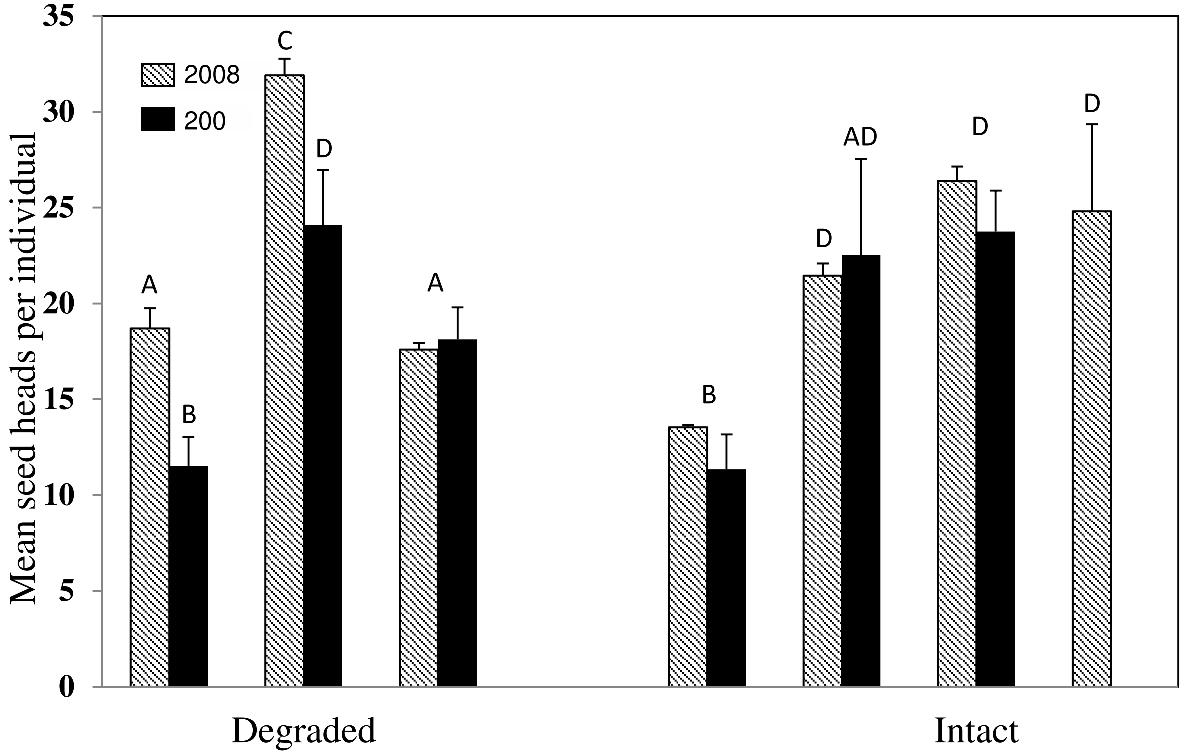
Figure 4. Seed production of *C. fasciculata* in degraded and intact scrub sites in the Lake Wales Ridge, Florida. (A) Individual bars represent mean seed pod production per individual for one site, in one trial (2008 or 2009). (B) Individual bars represent mean seeds per pod for one habitat, in one trial (2008 or 2009). Error bars represent SE values, different letters represent significant differences.

A)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Mean seed heads per individual
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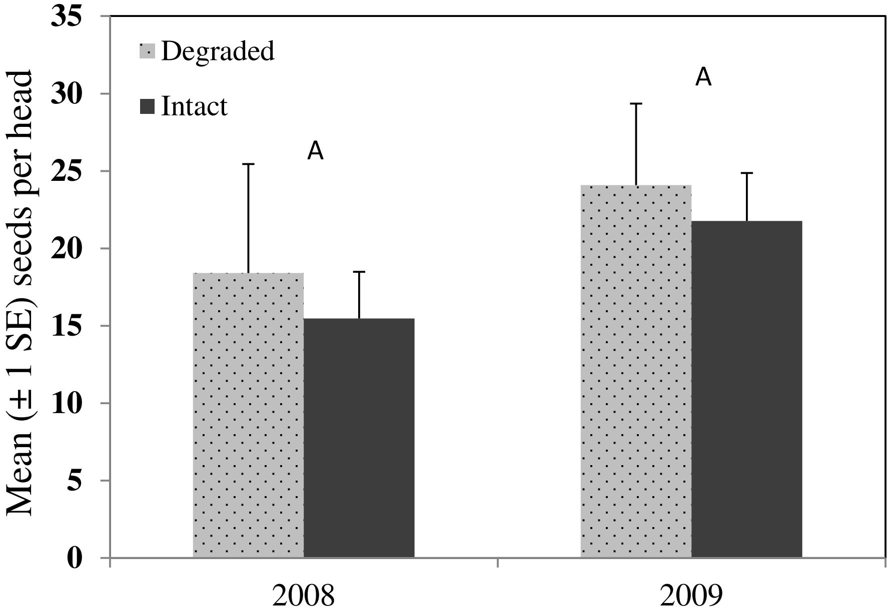
Degraded
Intact

B)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Mean (± 1 SE) seeds per head
Degraded
Intact
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2009

Figure 5. Seed production of *B. angustifolia* in intact and degraded scrub in the Lake Wales Ridge, Florida. (A) Each bar represents mean seed head production per individual for one site, in one trial (2008 or 2009). (B) Individual bars represent mean seeds per head for one habitat, in one trial (2008 or 2009). Error bars represent SE values, different letters represent significant differences.

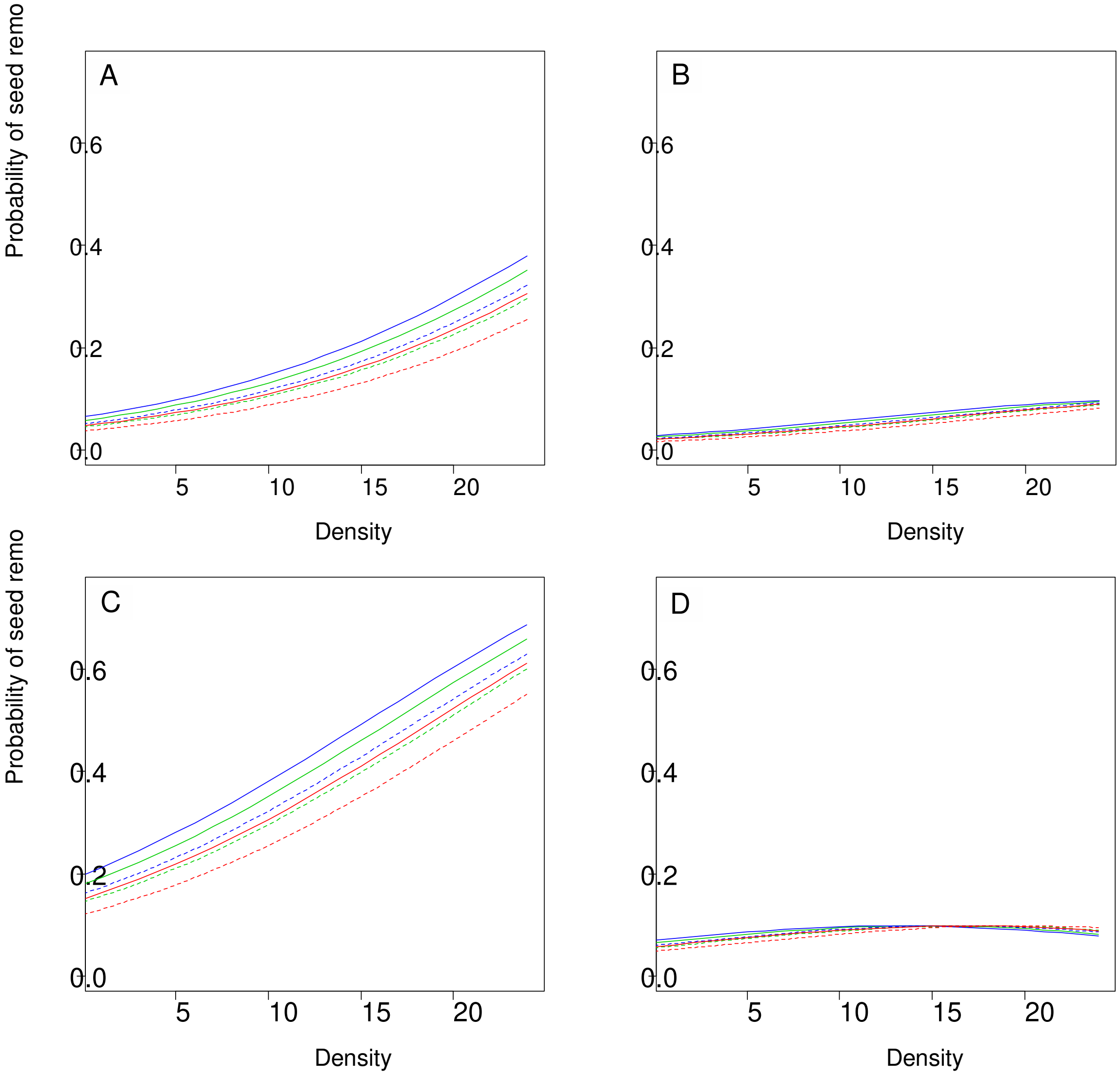

Figure 6. Predicted seed removal of *C. fasciculata* by invertebrates in Winter Trial, 2009 (A), vertebrates in Winter Trial, 2009 (B), invertebrates in Spring Trial, 2010 (C), and vertebrates in Spring Trial, 2010 (D). Density = deposited seed density. Red lines represent shrub microsites, blue lines represent litter microsites, and green lines represent bare sand microsites. Solid lines represent intact scrub, and broken lines represent degraded scrub. Models were selected with AIC.

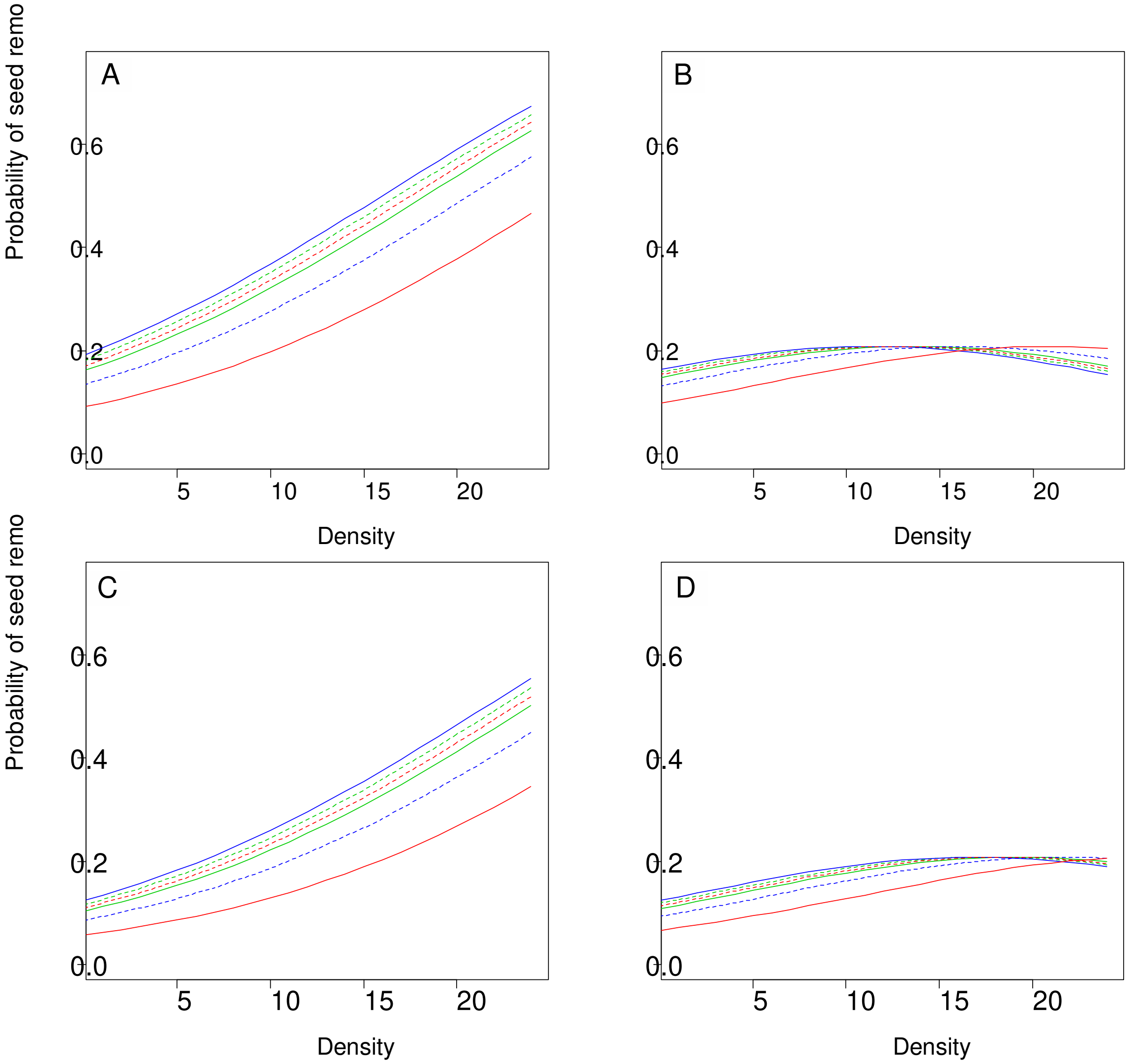

Figure 7. Predicted seed removal of *B. angustifolia* by (A) invertebrates in Winter Trial, 2009, (B) vertebrates in Winter Trial, 2009, (C) invertebrates in Spring Trial, 2010, and (D) vertebrates in Spring Trial, 2010. Density = deposited seed density. Red lines represent shrub microsites, blue lines represent litter microsites, and green lines represent bare sand microsites. Solid lines represent intact scrub, and broken lines represent degraded scrub. Models were selected with AIC.

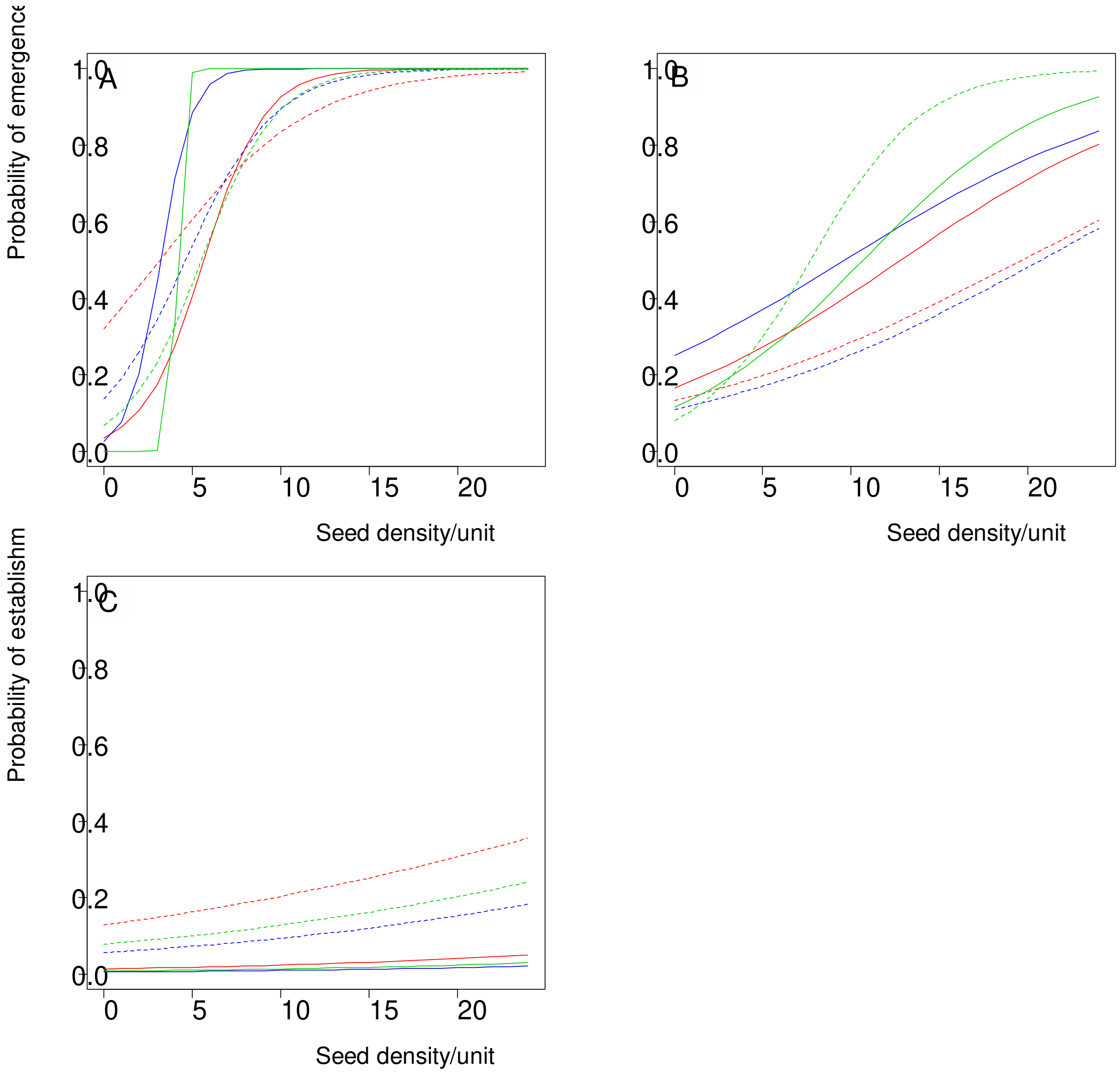

Figure 8. Predicted emergence and establishment of *C. fasciculata* in intact (solid lines) and degraded scrub (broken lines). (A) Emergence from trial initiated 2009; (B) emergence from trial initiated 2010; (C) establishment from trial initiated 2009. Red lines represent shrub microsites, blue lines represent litter microsites, and green lines represent bare sand microsites. Seed density / unit = planted seed density. Models were selected with AIC.

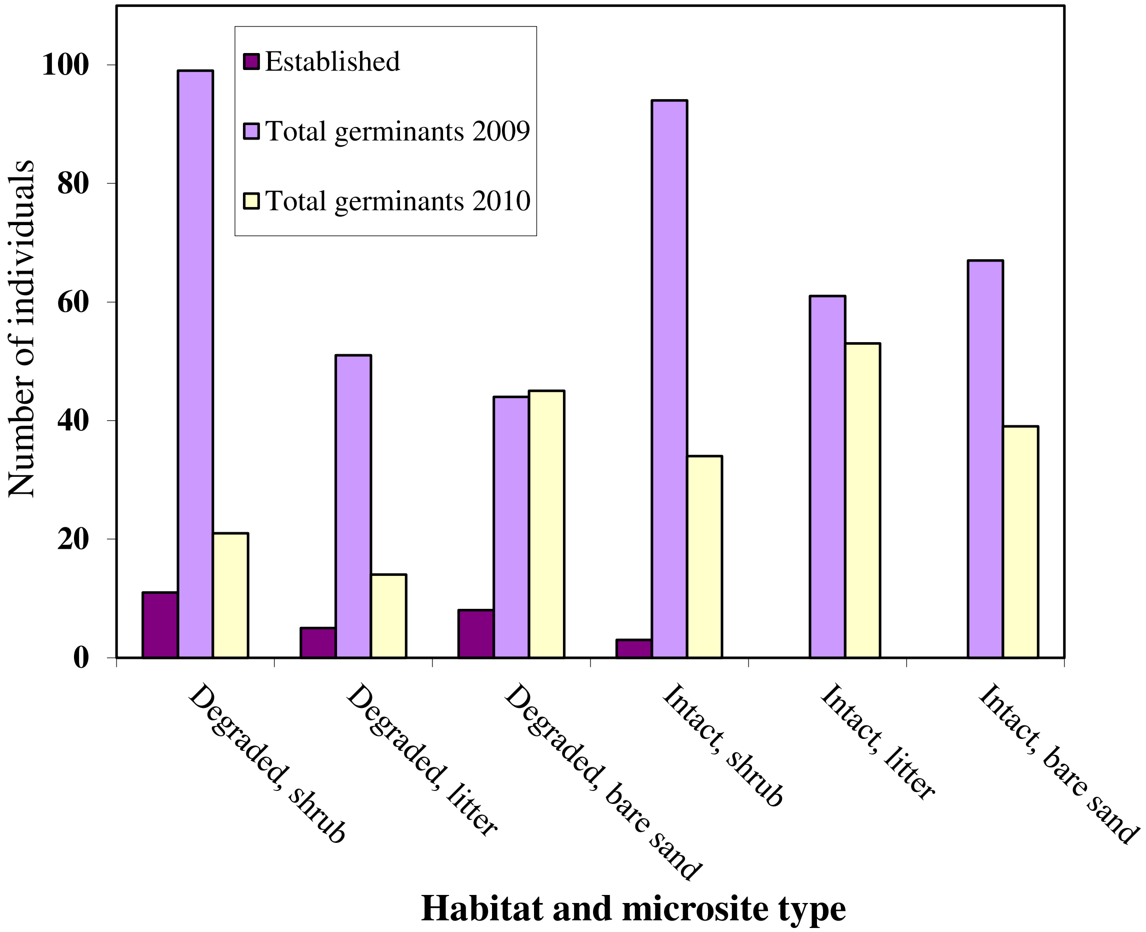

Figure 9. Emerged seedlings (2009, 2010 trials) and established individuals (2009 trial) per habitat and microsite for *C. fasciculata*. Plants were considered established if they grew to ≥ 30 cm, or had reproductive structures (flowers, buds, seed pods).

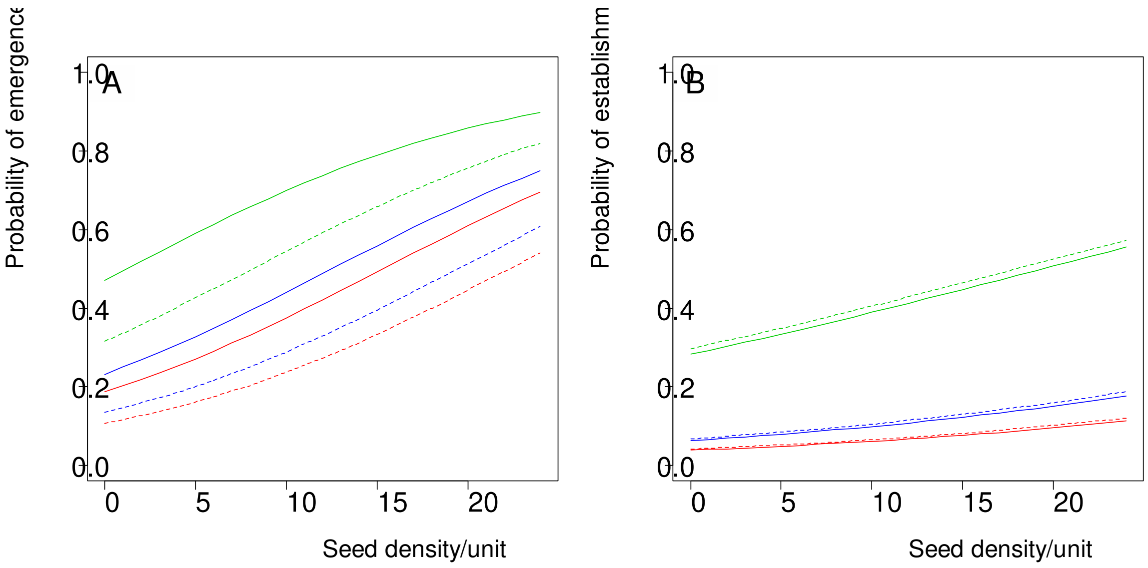

Figure 10. Predicted emergence (A) and establishment (B) of *B. angustifolia* in intact (solid lines) and degraded scrub (broken lines). Red lines represent shrub microsites, blue lines represent litter microsites, and green lines represent bare sand microsites. Seed density / unit = planted seed density. Models selected with AIC.

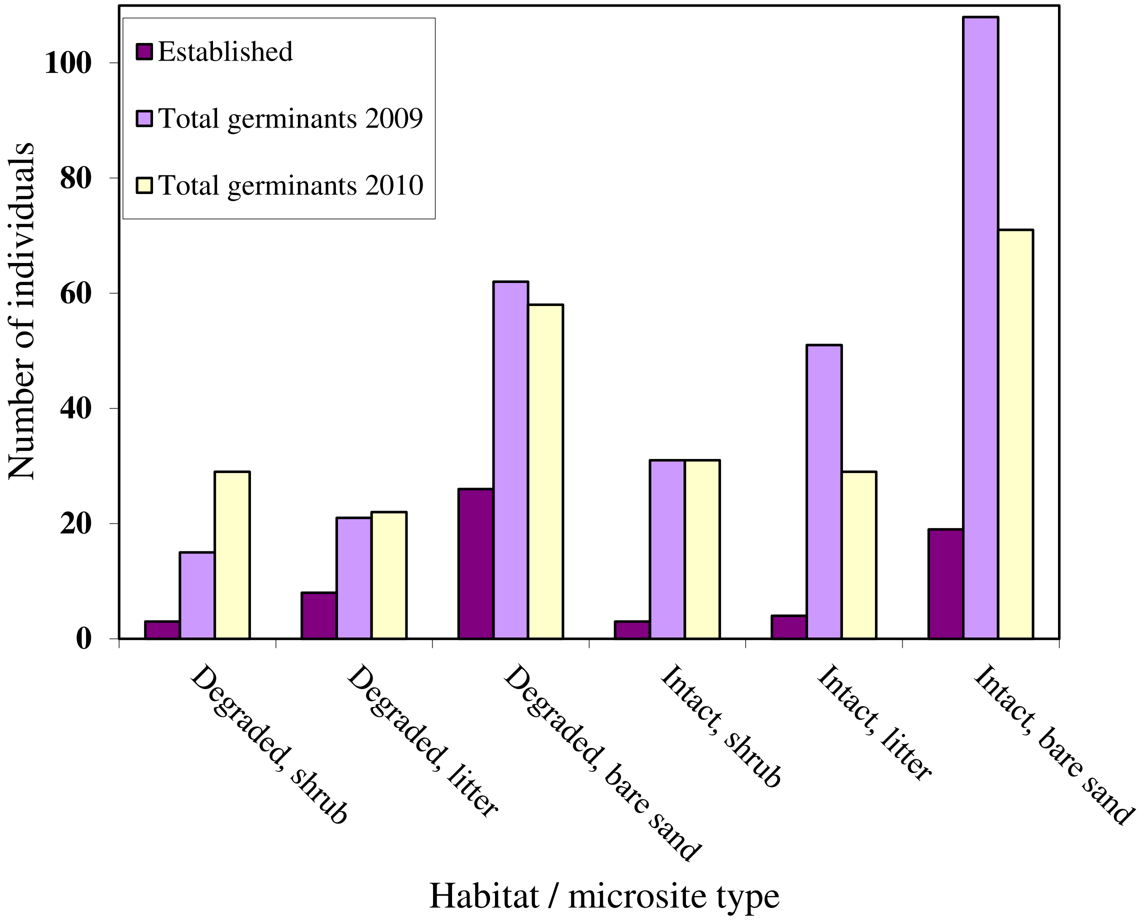

Figure 11. Emerged seedlings (2009, 2010 trials) and established individuals (2009 trial) per habitat and microsite for *B. angustifolia*. Plants were considered established if they grew to ≥ 30 cm, or had reproductive structures (flowers, buds, seed heads).

Appendix C1. Temperature and light schedule for germination study in growth chamber from April 6th, 2009 to June 16th, 2009 (late spring conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour.

Time	**Degrees C**	**Fluorescent**	**Incandescent**
0:00	14	0	0
1:00	14	0	0
2:00	14	0	0
3:00	14	0	0
4:00	14	0	0
5:00	14.5	0	0
6:00	15	0	1
7:00	16	1	1
8:00	17	1	1
9:00	18	1	2
10:00	20	2	2
11:00	25	2	2
12:00	29	2	2
13:00	31	2	2
14:00	32	2	2
15:00	31	2	2
16:00	30	2	2
17:00	27	2	2
18:00	22	2	1
19:00	20	2	1

Time	**Degrees C**	**Fluorescent**	**Incandescent**
20:00	18	1	1
21:00	16	1	0
22:00	15	0	0
23:00	14	0	0
23:59	14	0	0

Appendix C2. Temperature and light schedule for germination study in growth chamber from June 16th, 2009 to November 3rd, 2009 (summer / fall conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour.

Time	**Degrees C**	**Fluorescent**	**Incandescent**
0:00	21	0	0
1:00	22	0	0
2:00	23	0	0
3:00	24	0	0
4:00	25	0	0
5:00	26	0	0
6:00	27	0	1
7:00	28	1	1
8:00	29	1	1
9:00	30	1	2
10:00	31	2	2
11:00	33	2	2
12:00	34	2	2
13:00	35	2	2
14:00	34	2	2
15:00	33	2	2
16:00	31	2	2

Time	Degrees C	Fluorescent	Incandescent
17:00	30	2	2
18:00	29	2	1
19:00	27	2	1
20:00	25	1	1
21:00	24	1	0
22:00	23	0	0
23:00	22	0	0
23:59	21	0	0

Appendix C3. Temperature and light schedule for germination study in growth chamber from November 4th, 2009 to January 21st, 2010 (fall / winter conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour.

Time	Degrees C	Fluorescent	Incandescent
0:00	14.3	0	0
1:00	15	0	0
2:00	16	0	0
3:00	17	0	0
4:00	18	0	0
5:00	19	0	0
6:00	20	0	1
7:00	21	1	1
8:00	22	1	1
9:00	23	1	2
10:00	24	2	2
11:00	25	2	2
12:00	26	2	2
13:00	27	2	2
14:00	26	2	2
15:00	25	2	2
16:00	24	2	2
17:00	23	2	2
18:00	22	2	1
19:00	21	2	1

Time	**Degrees C**	**Fluorescent**	**Incandescent**
20:00	20	1	1
21:00	18	1	0
22:00	16	0	0
23:00	15	0	0
23:59	14.3	0	0

Appendix D1. Logistric regression model selection for seed removal of *C. fasciculata*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	Factors	DF	AIC
1	Habitat * microsite * treatment * density * year	85	511.31
2	Habitat + microsite + treatment + density	8	489.41
2a	**Habitat + microsite + treatment + density + year**	**9**	**462.30**
3	Habitat	2	550.32
3a	Habitat + year	3	527.96
4	Microsite	3	552.22
4a	Microsite + year	4	529.82
5	Treatment	4	533.01
5a	Treatment + year	5	509.81
6	Density	2	494.70
6a	Density + year	3	468.48
7	Habitat + microsite + treatment + density + habitat:microsite	10	492.01
7a	Habitat + microsite + treatment + density + year + habitat:microsite	11	464.78
8	Habitat + microsite + treatment + density + habitat:treatment	11	493.70
8a	Habitat + microsite + treatment + density + year + habitat:treatment	12	466.54

Model	Factors	DF	AIC
9	Habitat + microsite + treatment + density + habitat:density	9	483.32
9a*	**Habitat + microsite + treatment + density + year + habitat:density**	**10**	**455.34**
10	Habitat + microsite + treatment + density + microsite:treatment	14	492.44
10a	Habitat + microsite + treatment + density + year + microsite:treatment	15	464.70
11	Habitat + microsite + treatment + density + microsite:density	10	489.31
11a	**Habitat + microsite + treatment + density + year + microsite:density**	**11**	**461.77**
12	Habitat + microsite + treatment + density + treatment:density	11	494.84
12a	Habitat + microsite + treatment + density + year + treatment:density	12	467.68

Appendix D2. Logistric regression model selection for seed removal of *B. angustifolia*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	Factors	DF	AIC
1	Habitat * microsite * treatment * density * year	84	568.76
2	Habitat + microsite + treatment + density	8	536.27
2a	**Habitat + microsite + treatment + density + year**	**9**	**532.76**
3	Habitat	2	632.63
3a	Habitat + year	3	630.30
4	Microsite	3	633.45
4a	Microsite + year	4	631.11
5	Treatment	4	584.76
5a	Treatment + year	5	581.94
6	Density	2	573.06
6a	Density + year	3	570.10
7	Habitat + microsite + treatment + density + habitat:microsite	10	535.71
7a*	**Habitat + microsite + treatment + density + year + habitat:microsite**	**11**	**532.14**
8	Habitat + microsite + treatment + density + habitat:treatment	11	539.16
8a	Habitat + microsite + treatment + density + year + habitat:treatment	12	535.62

Model	**Factors**	**DF**	**AIC**
9	Habitat + microsite + treatment + density + habitat:density	9	538.20
9a	Habitat + microsite + treatment + density + year + habitat:density	10	534.69
10	Habitat + microsite + treatment + density + microsite:treatment	14	536.45
10a	**Habitat + microsite + treatment + density + year + microsite:treatment**	**15**	**532.79**
11	Habitat + microsite + treatment + density + microsite:density	10	539.43
11a	Habitat + microsite + treatment + density + year + microsite:density	11	535.92
12	Habitat + microsite + treatment + density + treatment:density	10	540.23
12a	Habitat + microsite + treatment + density + year + treatment:density	11	536.72

Appendix D3. Logistric regression model selection for germination of *C. fasciculata*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	**Factors**	**DF**	**AIC**
1	Habitat * microsite * density	12	493.34
1a*	**Habitat * microsite * density * year**	**24**	**439.60**
2	Habitat + microsite + density	5	496.60
2a	Habitat + microsite + density + year	6	473.24
3	Habitat	2	652.51
3a	Habitat + year	3	637.84
4	Microsite	3	654.44
4a	Microsite + year	4	639.90
5	Density	2	491.68
5a	**Density + year**	**3**	**468.39**
6	Habitat + microsite + density + habitat:microsite	7	497.48
6a	Habitat + microsite + density + year + habitat:microsite	8	473.90
7	Habitat + microsite + density + habitat:density	6	496.67
7a	**Habitat + microsite + density + year +habitat:density**	**7**	**473.18**
8	Habitat + microsite + density + microsite:density	7	488.34
8a	Habitat + microsite + density + year + microsite:density	8	463.94

Appendix D4. Logistric regression model selection for germination of *B. angustifolia*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	Factors	DF	AIC
1	Habitat * microsite * density	12	544.61
1a	Habitat * microsite * density * year	24	550.13
2	**Habitat + microsite + density**	**5**	**537.99**
2a	**Habitat + microsite + density + year**	**6**	**537.72**
3	Habitat	2	627.88
3a	Habitat + year	3	627.85
4	Microsite	3	610.21
4a	Microsite + year	4	610.25
5	Density	2	572.31
5a	Density + year	3	572.00
6	Habitat + microsite + density + habitat:microsite	7	539.67
6a	Habitat + microsite + density + year + habitat:microsite	8	539.43
7	Habitat + microsite + density + habitat:density	6	539.85
7a	Habitat + microsite + density + year + habitat:density	7	539.59
8	Habitat + microsite + density + microsite:density	7	538.52
8a	**Habitat + microsite + density + year + microsite:density**	**8**	**538.24**

Appendix D5. Logistric regression model selection for establishment of *C. fasciculata*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	**Factors**	**DF**	**AIC**
1	Habitat * microsite * density	12	126.10
2*	**Habitat + microsite + density**	**5**	**119.41**
3	Habitat	2	121.23
4	Microsite	3	134.44
5	Density	2	130.56
6	**Habitat + microsite + density + habitat:microsite**	**7**	**120.46**
7	Habitat + microsite + density + habitat:density	6	121.30
8	**Habitat + microsite + density + microsite:density**	**7**	**119.76**

Appendix D6. Logistric regression model selection for establishment of *B. angustifolia*. AIC: Akaike's Information Criterion. Bold text indicates models with low AIC values; asterisk indicates chosen model.

Model	Factors	DF	AIC
1	Habitat * microsite * density	12	207.06
2*	**Habitat + microsite + density**	**5**	**196.70**
3	Habitat	2	227.23
4	**Microsite**	**3**	**198.67**
5	Density	2	222.20
6	Habitat + microsite + density + habitat:microsite	7	200.51
7	**Habitat + microsite + density + habitat:density**	**6**	**198.53**
8	Habitat + microsite + density + microsite:density	7	200.05

Appendix E1. Counts of *C. fasciculata* seedlings from emergence and establishment experiments; habitats and microsites are pooled.

Seed density	Emergence 2009 (units, seedlings)		Emergence 2010 (units, seedlings)		Establishment (units, seedlings)	
1	7	9	4	5	0	0
4	16	24	28	42	3	5
8	22	37	46	89	9	13
24	43	136	53	280	7	9

Appendix E2. Counts of *B. angustifolia* seedlings from emergence and establishment experiments; habitats and microsites are pooled.

Seed density	Emergence 2009 (units, seedlings)		Emergence 2010 (units, seedlings)		Establishment (units, seedlings)	
1	9	10	6	7	5	5
4	25	41	19	26	9	11
8	31	66	27	62	14	19
24	36	170	35	145	14	27

Appendix F1. Combined probability of seed removal and emergence for *C. fasciculata*. Greatest values appear in bold. ISHR = shrub microsite in intact habitat, ILIT = litter microsite in intact habitat, IBS=bare sand microsite in intact habitat, DSHR = shrub microsite in degraded habitat, ILIT = litter microsite in degraded habitat, IBS = bare sand microsite in degraded habitat.

Seed density	ISHR	ILIT	IBS	DSHR	DLIT	DBS
1	0.177	0.228	0.102	0.236	0.165	0.094
4	0.253	0.303	0.207	0.292	0.211	0.235
8	0.366	0.394	**0.402**	0.367	0.276	**0.504**
24	**0.426**	0.360	**0.405**	**0.435**	0.354	**0.464**

Appendix F2. Combined probability of seed removal and emergence for *B. angustifolia*. Greatest values appear in bold. ISHR = shrub microsite in intact habitat, ILIT = litter microsite in intact habitat, IBS=bare sand microsite in intact habitat, DSHR = shrub microsite in degraded habitat, ILIT = litter microsite in degraded habitat, IBS = bare sand microsite in degraded habitat.

Seed density	ISHR	ILIT	IBS	DSHR	DLIT	DBS
1	0.160	0.129	**0.305**	0.060	0.095	**0.238**
4	0.186	0.137	**0.309**	0.066	0.107	**0.259**
8	0.216	0.138	**0.293**	0.071	0.120	**0.273**
24	0.196	0.076	0.129	0.055	0.098	0.165

CHAPTER FOUR: HABITAT AND MICROSITE INFLUENCE DEMOGRAPHY OF TWO SHORT-LIVED SCRUB HERBS

Abstract

Identifying environmental factors associated with variation in vital rates is critical to predict population consequences of environmental perturbation. I used matrix models to explore the effect of habitat and microsite in demography of two Florida scrub herbs, *Chamaecrista fasciculata* (partridge pea) and *Balduina angustifolia* (coastalplain honeycombhead). I created models simulating population dynamics in intact and degraded scrub habitats; shrub, litter, and bare sand microsites within each habitat; habitat by microsite combinations; and an overall model that pooled all habitat and microsite combinations. Each model included four stages (seed bank, small vegetative plants, large vegetative plants, reproductive adults) and three vital rates (survival, growth, fecundity), summarized in sixteen transitions. I conducted life table response experiments (LTREs) to assess the contribution of each habitat and microsite to population growth. I evaluated scenarios concerning the effects of seed density and successional change in each habitat by microsite combination on population growth rate. *C. fasciculata* had the greatest population growth in degraded habitat and litter microsites. *B. angustifolia* had similar population growth between habitats and greatest in bare sand. Seed survival of *C. fasciculata* had the greatest elasticity on population growth in degraded habitat, shrub, and bare sand; seed production had the greatest elasticity in intact habitat, as did the transition from vegetative to reproductive stages in litter microsites. Seed production of *B. angustifolia* had the greatest elasticity on population growth in all habitats and microsites. In the successional models, seed survival had the greatest elasticity for *C. fasciculata*, decreasing in importance with increasing seed density. Seed production of *B. angustifolia*, with subsequent entry into the seedbank, had the greatest elasticity; it decreased only slightly in importance at the greatest seed density. For the study species, bare sand gaps in intact scrub were not equivalent to bare sand areas in degraded scrub. Nitrogen fixation and release from below-ground competition may facilitate greater population growth of *C. fasciculata* in degraded scrub, whereas *B. angustifolia* may be most affected by competition with shrubs. My study emphasizes that intact scrub is ecologically complex and critical to preserve.

Keywords: Periodic matrix models, LTREs, Florida scrub, germination, population dynamics, anthropogenic disturbance.

Introduction

Identifying environmental factors associated with variation in vital rates is critical to understanding population dynamics (Benton et al. 2006; Bakker et al. 2009; Crone et al. 2011), and the ability to predict consequences of environmental perturbation. Studies of population dynamics often collect environmental data, but either fail to examine the influence of these factors on vital rates (e.g., Munzbergova 2006), or do not use proper experimental controls, leaving the effects of particular environmental factors on vital rates ambiguous (Jongejans et al. 2006; Brown 2011). Other studies primarily evaluate environmental factors with projected data (Arribas et al. 2012).

Models evaluating environmental factors typically identified them as influential in population dynamics. In plants, decreased vegetation cover and increased light availability (Valvarde and Silvertown 1998; Jacquemyn et al. 2010), increased grazing (Bullock et al. 1994), relatively shorter time-since-fire intervals (Menges and Dolan 1998; Satterthwaite et al. 2002, Quintana-Ascencio et al. 2003; Liu et al. 2005), hurricane damage (Pascarella et al. 2007), and increased levels of gap-opening (Sletvold and Rydgren 2007) all affected population growth. Population growth in animals was affected by decreased predation and El Niño weather patterns (Bakker et al. 2009). Other models revealed only small effects of environmental factors on population growth of plants (Cipollini et al. 1993; Oostermeijer et al. 1996) and animals (Forbes et al. 2010). Only two studies of plants evaluated the effect of anthropogenic habitat degradation on vital rate variation: one found negative effects (Martinez et al. 2010), while the other found similar population growth between degraded and intact habitats (Bell et al. 2003).

I compared population dynamics of two herbs in degraded and intact habitats, using data from multiple sites per habitat, and examined the same three microsites (litter under shrubs (“shrub”), litter with no nearby shrub (“litter”), bare sand with no nearby shrub (“bare sand”)) in each site. In each combination of habitat and microsite conditions, I tracked individual emerged seedlings of the study species. I used stage-based periodic matrix models to explore how population growth and the relative importance of stage transitions were affected by successional changes in habitat availability and microsite abundance. I used both prospective (perturbation analyses) and retrospective (Life Table Response Experiments, LTRE) approaches to evaluate potential effects of habitat degradation and microsite on vital rate variation in these species.

I conducted this study in Florida scrub, an ecosystem recognized for its concentration of rare and endemic plants (Abrahamson et al. 1984). I focused on two common herbs that grow in degraded and intact scrub: *Balduina angustifolia* (coastalplain honeycombhead; semelparous, typically biennial), and *Chamaecrista fasciculata* (partridge pea; primarily semelparous, annual / biennial). I predicted (1) greater population growth in degraded than in intact scrub because more isolated shrubs and extensive bare sand areas in degraded scrub (Menges and Rickey 2005) may reduce herb competition and promote emergence and seedling establishment as has been demonstrated for other herbs in bare sand gaps in intact scrub (e. g. Menges and Kimmich 1996; Quintana-Ascencio and Morales-Hernández 1997; Petrů and Menges 2003; Schafer et al. 2010); (2) greater population growth of *B. angustifolia* and *C. fasciculata* in bare sand microsites than in microsites with shrubs or litter; and (3) greater effects of individual growth and fecundity of *C. fasciculata* and *B. angustifolia* on population growth than survival. Individual growth was critical for many plants in early successional habitats (Silvertown and Franco 1993) and those in gaps (Cipollini et al. 1993); fecundity was important as disturbance intensity increased (Bullock et al. 1994) and during early stages of colonization (Silvertown et al. 1996). These conditions mirror those in scrub, particularly in degraded scrub, where I expected such trends to be most pronounced.

I explored the effects of post-disturbance successional changes in habitats and microsites on population dynamics. I used microsite by habitat models (two habitats x three microsites = six combinations) together with theoretical assumptions about the availability of each microsite and habitat to evaluate study species' probability of persistence. Immediately after an anthropogenic disturbance, I expected greatest abundance of bare sand, then litter microsites, and shrub microsites in the degraded habitat. With increased time-since-disturbance, I expected soil conditions to recover (bare sand microsites in intact habitat), litter to accumulate (litter microsites in intact habitat), and more shrubs to establish and increase in cover (shrub microsites in intact habitat). At longest time-since-disturbance, I expected the greatest proportion of shrub microsites in intact habitat. I predicted (4) more degraded habitat will increase population growth of each species due to reduced belowground competition compared to intact habitat; (5) dominance of bare sand microsites would increase population growth of each species due to greater availability of open area for recruitment. I anticipated that population growth would be mediated by increased germination from the seedbank and increased seed production because opportunistic species exhibit these tendencies in degraded conditions (Hobbs and Mooney 1985; Schupp and Fuentes 1995; Pugnaire and Lozano 1997; Cole et al. 2004).

I evaluated the effect of seed density on population growth. Prior data revealed that increased seed density of *C. fasciculata* and *B. angustifolia* was associated with greater seed removal by animals and greater emergence (Stephens *in preparation*). I evaluated whether increases in seed density would increase population growth, with the expectation that positive effects of increased germination would outweigh the potentially negative effects of greater seed removal from the seedbank. I based this expectation on my observations of dense populations of the study species in degraded habitats (Stephens *in preparation*). I predicted (6) early life-history stage transitions (seed survival, germination and emergence) would have great elasticity values throughout successional changes, regardless of seed density, because of the importance of a seedbank for population persistence of other plants in arid conditions (Brown et al. 1979; Freas and Kemp 1983).

My study contributes to an understanding of the consequences of habitat alteration on population dynamics by comparing vital rates in degraded and intact habitats. My results provide further insight into the way seed availability and habitat quality can influence population dynamics and community composition. My approach identifies threats to population persistence and can be used to propose management requirements in the two habitats.

Methods

Study Species and Sites

Balduina angustifolia (Pursh) B. L. Rob. is a dicot and a widespread gap specialist, described as having an annual or biennial life cycle (USDA, NRCS 2012). *Chamaecrista fasciculata* (Michx.) Greene is a dicot and a generalist, typically described as an annual (USDA, NRCS 2012). The two species coexist in Florida scrub and have overlapping reproductive seasons: seeds of *C. fasciculata* are available in fall, while seeds of *B. angustifolia* are primarily available in fall to early winter. Relative to other coexisting scrub species, *C. fasciculata* and *B. angustifolia* have sizeable and abundant seeds, fast growth rates, and widespread occurrence; these characteristics are favorable for addressing questions on seed and seedling dynamics in contrasting environments.

I conducted this study in the southern end of the Lake Wales Ridge in south-central Florida, a region characterized by some of the best remaining examples of intact Florida scrub (Weekley et al. 2008a). This ecosystem occurs on well drained, nutrient poor soils, and was historically maintained by lighting-induced fires (Fernald and Purdum 1992). Most Florida scrub herbs recover from fire and other disturbances by seedling recruitment, while shrubs primarily resprout (Menges and Kohfeldt 1995). I used intact scrub sites in Archbold Biological Station (ABS; 2,104 ha) and degraded scrub sites in the neighboring Archbold Reserve (Reserve; 1,476 ha), located in Highlands County. All sites shared Satellite soils and locally high elevations.

I chose intact scrub sites in rosemary scrub of ABS. Florida rosemary (*Ceratiola ericoides*) dominates the shrub layer of this open community, which is interspersed with patches of oaks (*Quercus* spp.), palmettos (*Serenoa repens* and *Sabal etonia*), *Lyonia* spp. and tough buckthorn (*Sideroxylon tenax*) (Abrahamson et al. 1984). Herbaceous species, many of them rare and endemic, and lichens grow in gaps of bare sand between shrubs (Abrahamson et al. 1984; Christman and Judd 1990; Turner, Wilcove and Swain 2006; Menges et al. 2008).

The degraded scrub of the Reserve was roller chopped (belowground disturbance) and grazed by cattle, with cattle on site until 2002. Species composition in degraded scrub was similar to rosemary scrub, aside from the presence of nonnative grasses (*Digitaria eriantha* and *Rhynchelytrum repens*) in degraded sites. However, vegetation structure, microsite abundance and species distributions differed between the two land types (Navarra and Quintana-Ascencio 2011). In degraded scrub, shrub patches were overgrown, while shrubs of rosemary scrub were typically only 2-5 m tall (Menges and Rickey 2005). Microsites differed in that bare sand areas surrounding shrubs were extensive in the degraded scrub (Menges and Rickey 2005). The degraded scrub sites are currently under treatments to restore native habitat structure.

Seed Collection and Germination

I collected seeds at ABS and the Reserve in September to October 2009, prior to the seedling emergence / establishment experiment and germination study. Intact, fully pigmented seeds were separated under a dissecting microscope; these were pooled to randomize seed source. Seeds were sorted into groups with forceps and sealed in foil packets for efficient field deployment. Seeds were stored in a refrigerator (4^{o} C) before use in the field and growth chamber. Background rates of germination were monitored in a growth chamber (Appendices G1 – G3) and considered as an upper boundary for expected germination of seeds in the field (Stephens *in preparation*).

Emergence and Establishment

Each species was planted into three native and three degraded sites in April 2009. I replicated experimental units in three microsites (litter under shrubs (“shrub”), litter with no nearby shrubs (units ≥ 1 m from shrubs, “litter”), bare sand with no nearby shrubs (“bare sand”). Controls with no planted seeds assessed emergence from natural sources (Turnbull, Crawley and Rees 2000). Experimental units consisted of PVC rings (10.2 cm diameter, 7.6 cm depth, buried approximately 3.5 cm to keep seeds in place), each protected with a wire mesh vertebrate exclosure to reduce removal, and marked with wire-stake flags. Each experimental unit was randomly assigned a seed density (1, 4, 8, 24; corresponded to approximately 122, 490, 980, and 2939 seeds per m^2). Random seed density assignments were stratified by habitat and microsite. Seeds were deposited within a given PVC ring and sprinkled with sand until they were just covered. I monitored for seedlings and recorded plant survival, height, and reproductive status once every week for the first month and monthly thereafter for three years. Treatment units were initially assigned locations based on coordinates of random points generated in ArcMap; coordinates were modified to correspond to the nearest (randomly) assigned microsite after each point was located using a Trimble Global Positioning System with sub-meter accuracy (GPS). Overall, there were 468 total units (4 densities x 3 microsites x 3 replicates x 6 sites x 2 species) with 3,996 seeds (Stephens *in preparation*).

Modeling Life Cycles of *C. fasciculata* and *B. angustifolia*

Demographic matrix models

I built periodic matrix models representing seasonal intervals (summer (U) = June, July, August; fall (F) = September, October, November; winter (W) = December, January, February; spring (S) = March, April, May) for each study species. Periodic models incorporate within-year data and examine between-year dynamics (Caswell 2001). These models included four stages (seed bank, small vegetative plants, large vegetative plants, reproductive adults) and three vital rates (survival, growth, fecundity), summarized in sixteen transitions (Appendix H).

I combined the four seasonal matrices into an annual matrix (Appendix I) using the fall to winter transition (B_{FW}) as the starting point in the cycle ($A = B_{UF}*B_{SU}*B_{WS}*B_{FW}$; B_{UF} = summer to fall, B_{SU} = spring to summer, B_{WS} = winter to spring). B_{FW} was the most biologically appropriate choice as it was the seasonal transition during which the study species produced seeds. The starting point in the cycle was mathematically arbitrary because population growth and associated sensitivity and elasticity values are not affected by this selection (Smith et al. 2005; Lesnoff, Ezanno and Caswell 2003). Due to the manner in which seasons are combined into an annual periodic matrix, a given transition represents strings of developmental steps occurring over multiple seasons. For example, depending on the number of seasons evaluated, a seedbank to seedbank transition (SBK, Appendix I) could represent a seed remaining viable in the seedbank (from one season to the next), or a seed that germinates, survives to reproduce as an adult, with seeds that subsequently enter the seedbank (may take up to five seasons). To test predictions 1 - 3, I constructed an overall matrix model (combining data pooled from all habitats and microsites), and matrices for habitat-specific models (intact, degraded scrub), microsite-specific models (bare sand, litter, shrub), and habitat by microsite models (intact with shrub, intact with litter, intact with bare sand, degraded with shrub, degraded with litter, degraded with bare sand).

Except as indicated, I built deterministic models with the following assumptions: (1) percent germination of seeds in the growth chamber represented initial viability of seeds produced by parent plants (V, Table 11); (2) all planted seeds were viable (Ss = 1, Table 11); (3) probability of survival in the seed bank in a given season was constant over time (Sb, Table 11; I fitted a survivorship curve to monthly emergence data from the field experiment and then extrapolated the likely number of seeds that survived in the seed bank each season after germination); and (4) individual seed production was estimated with the following equation: ph1*ph2*V*Ss, where ph1 = mean seeds per pod / head, ph2 = mean pods / heads per plant (Table 11).

Matrix stages were chosen based on biologically relevant morphological and life-history data. Seeds were considered part of the seed bank until emergence was recorded. New emerged plants ≤ 2 cm were considered small vegetative (non-reproductive) individuals, plants ≥ 2 cm without reproductive structures were considered large vegetative individuals, and plants displaying buds, flowers, or seed pods or heads were reproductive. These categories were appropriate because there was a notable transition between plants ≤ 2 cm, and those > 2 cm; individuals often remained ≤ 2 cm for many months, but grew more rapidly once they became > 2 cm in height.

I calculated population growth as the dominant eigenvalue for each matrix (deterministic lambda), and the stochastic lambda of successional simulated environments (Caswell 2000, 2001). I estimated deterministic and stochastic sensitivity and elasticity matrices (Caswell 2000, 2001) of population growth for each model. Sensitivity is the rate of change (or slope) of lambda with respect to a change in any given element of the matrix (Caswell 2000; Mills 2007). Sensitivity analyses identify the absolute effect of small perturbations in each stage transition probability on the overall population growth. Elasticity analyses provide proportional sensitivity values. These analyses were used to identify the transitions that had the greatest relative or proportional effect on population growth (de Kroon et al. 1986; Caswell 2000, 2001).

Bootstrapping

I used bootstrapping to estimate uncertainty in population growth of each matrix using sampling with replacement from the corresponding data subset (R 2.13.0; 1,000 iterations). Due to small sample size, values for fates of reproductive individuals were sampled from overall data for all matrices. I calculated mean and 95 % confidence intervals. Non-overlapping confidence intervals provided evidence of significantly different growth rates among some treatment combinations.

Life Table Response Experiments (LTRE)

I conducted LTREs in R (2.13.0, Popbio Package; Stubben and Milligan 2007) to further test predictions 1 - 3. These analyses enabled me to examine the effect of observed variation in vital rates by habitat, microsite, and habitat by microsite combinations on population growth variation of each species. I also examined summed contributions by habitat, microsite, and habitat by microsite to population growth. LTRE values are unitless, and represent the relative contribution of each treatment (habitat, microsite) or transition to population growth (Caswell 1996).

Models to evaluate successional change

To test predictions 4 - 6, I simulated the effects of successional changes in habitats and microhabitats associated with anthropogenic disturbance (using modified MATLAB code from Horvitz et al. 2010). I created an environmental matrix comprised of transition probabilities from each habitat by microsite combination to a recently disturbed environment and to all other habitat by microsite combinations (Appendix J). I used this environmental matrix in conjunction with the six habitat by microsite matrices, and a matrix representing a disturbance in which only seeds in the seedbank remained (using the SBK transition from the degraded model).

I considered the above environmental matrix as a reference model because it did not incorporate particular seed densities or changes in availability of habitat by microsite combinations. I compared with scenarios in which only one habitat or microsite type was available, and considered the effect of seed density on survival in seed bank and emergence (using data from *Stephens* in preparation). Baseline models for both species had 10 seeds per 0.03 m^2 area (PVC area, trial unit size) assuming a primary dispersal distance of 0.50 m (pers.

obs E. Stephens) and average seeds produced per individual. I then compared the effects of seed densities greater and smaller than the baseline density.

Results

Demographic Matrix Models of *C. fasciculata*

The overall demographic matrix model for *C. fasciculata* had a deterministic population growth (λ) of 1.65 (Figure 12, Appendix K1). Population growth was most affected by changes in advancing growth transitions, or those in which an individual moves from an earlier to a later developmental stage (in contrast to regressive transitions, such as returning to a vegetative state from a reproductive state, or shrinkage in height). Combined elasticity values for advancing growth transitions represented 40% of the total elasticity, and seed to reproductive adult survival (SBS2) had the greatest percentage in this group (Figure 13, Appendix K1).

The degraded habitat model had an increasing population growth (λ = 1.88), and intact habitat had a decreasing population growth (λ = 0.32) (Appendices K2 - 3). Population growth in each habitat was most affected by changes in advancing growth transitions (combined elasticity: 35% in degraded, 44% in intact, Figure 13), and was particularly affected by the seed survival transition (SBK) in degraded habitat (Appendix K2), and by production of dormant seeds (FSB) in intact habitat (Appendix K3).

Population growth was increasing in the shrub (λ = 1.14, Appendix K4) and litter models (λ = 1.52, Appendix K5), and decreasing in bare sand (λ = 0.62, Appendix K6). As with the overall and habitat models, the population growth of each microsite model was most affected by changes in advancing growth transitions (combined elasticity values: 38% in shrub, 39% in litter, 40% in bare sand; Figure 13). Population growth was particularly affected by survival of seeds in the seed bank (SBK) in the shrub model (Appendix K4), the survival of large vegetative plants to reproduction (G) in the litter (Appendix K5), and survival of seeds in the seed bank (SBK) in bare sand (Appendix K6).

Mean population growth rates from bootstrapped data were similar to those from observed data (Figure 14). Bootstrapped lambdas had mostly normal distributions, with some bimodal distributions (Appendix L, Figure 14). Confidence intervals in intact with bare sand and intact with litter combinations did not overlap each other or degraded with shrub, and those for intact with bare sand did not overlap degraded with bare sand. Those treatment combinations with the smallest deterministic population growth had the narrowest confidence intervals (intact with litter, intact with bare sand); degraded with litter and degraded with bare sand had the widest confidence intervals (Figure 14).

Demographic Matrix Models of *B. angustifolia*

The overall demographic matrix model for *B. angustifolia* had deterministic population growth (λ) of 1.75 (Figure 15, Appendix K7). This species was most affected by changes in positive growth transitions (combined elasticity: 48%) and reproductive transitions (36%), particularly for production of seeds that enter the seedbank (FSB) (Figure 16, Appendix K7).

Both habitat models had very similar, positively increasing population growth rates (degraded: $\lambda = 1.49$, Appendix K8; intact: $\lambda=1.43$, Appendix K9). Population growth in each habitat was most affected by changes in positive growth transitions (combined elasticity: 48 % in degraded, 47 % in intact, Figure 16), and was particularly affected by seed production by reproductive adults (FSB) in both habitats (Appendices K8 - 9).

The shrub microsite model had the smallest population growth ($\lambda = 0.56$, Appendix K10), followed by litter ($\lambda = 1.18$, Appendix K11), and bare sand ($\lambda = 1.71$, Appendix K12). The population growth of each microsite model was most affected by changes in positive growth transitions (combined elasticity: 44 % in shrub, 43 % in litter, 48 % in bare sand (Figure 16). Population growth was particularly affected by production of seeds (FSB) in all three microsite models (Appendices K10 - 12).

Mean population growth rates from bootstrapped data were similar to those for data without bootstrapping (Figure 17). Bootstrapped lambdas had mostly normal distributions, with some bimodal distributions (Appendix M, Figure 17). Only confidence intervals in intact habitat with bare sand and degraded with bare sand overlapped each other. Intact with shrub and degraded with litter treatment combinations had the smallest confidence intervals; intact with bare sand had the widest confidence intervals (Figure 17).

Life Table Response Experiments of *C. fasciculata*

For *C. fasciculata*, the degraded habitat had a positive contribution to overall population growth, whereas intact habitat had a negative but greater absolute contribution to population growth of the overall model (Figure 18a). Seed production (a14, Figure 18b) in intact habitat and germination from the seedbank in degraded habitat (a21) had the greatest absolute contributions to population growth, but this was positive in degraded and negative in intact habitat.

The shrub microsite had a small negative contribution to population growth. Litter was the only microsite with a positive contribution to overall population growth, and it had the greatest absolute contribution (Figure 18c). Bare sand had a negative contribution to population growth (Figure 18c). Survival of seeds in the seedbank (a11, Figure 18d) was the transition with the greatest contribution to population growth in all three microsites, but it was negative in shrub and bare sand, and positive for the litter.

All habitat by microsite treatment combinations in intact habitat were negative, and those in degraded scrub were positive (Figure 18e). The degraded with litter treatment had the greatest absolute contribution, while the degraded with shrub treatment had the smallest absolute contribution to overall population growth. The intact with shrub and degraded with litter had survival of seeds in the seedbank as the greatest individual contribution to population growth (a11, Figure 18f). Other important contributions were: production of seeds by reproductive adults in degraded with bare sand (a14), survival of seeds in seedbank through germination to large vegetative survival in degraded with shrub (a31), germination and survival to small vegetative in intact with litter (a21), and reproduction through germination and small vegetation survival in intact with bare sand (a24).

Life Table Response Experiments of *B. angustifolia*

For *B. angustifolia*, both intact and degraded habitats had small contributions to overall population growth. Unlike in *C. fasciculata*, degraded habitat had a negative contribution and intact habitat had a positive contribution (Figure 19a). Seed survival through germination and growth to reproductive adult was the transition with the greatest contribution in each habitat (a41, Figure 19b), but it was positive in the intact and negative in degraded (Figure 19b).

Shrub and litter microsites negatively contributed to population growth; bare sand positively contributed and represented the greatest absolute contribution to population growth (Figure 19c). Survival of seeds through the reproductive stage (a41, Figure 19d) was the transition with the greatest contribution to population growth for the litter and bare sand microsites but it was negative in the litter and positive for the bare sand. For the shrub microsite, seed production by reproductive adults (a14, Figure 19d) was the transition with the greatest contribution to population growth.

All of the habitat by microsite treatment combinations in the shrub and litter microsites were negative, and those in bare sand were positive (Figure 19e). Intact with bare sand had the greatest absolute contribution, while the intact with litter treatment had the smallest absolute contribution to overall population growth. The greatest contribution by an individual transition to population growth in intact with litter, intact with bare sand, degraded with litter, and degraded with bare sand was the survival of seeds in seedbank through germination to reproductive adults (a41, Figure 19f). In the intact with shrub treatment, the greatest contribution by a transition was in production of seeds by reproductive adults (a14), and for degraded with shrub it was small vegetative survival to reproduction (a42).

Models to Evaluate Successional Change in *C. fasciculata*

Population growth of *C. fasciculata* in simulated successional conditions was less than 1 ($\lambda = 0.58$; reference model). Population growth under continuously degraded habitat conditions was slightly greater than 1 ($\lambda = 1.04$), and that in continuously intact habitat conditions was less than 1 ($\lambda = 0.32$). Seed survival in the seedbank (SBK) had the greatest elasticity on stochastic lambda in all three models (Figure 20a, b, Appendix N), followed by small vegetative survival to reproduction with seeds entering seedbank (SFS) in the reference model, reproduction by flowering adults with seeds entering seedbank (FSB) in the continuously degraded model, and distantly followed by FSB in the continuously intact conditions model. Stochastic population growth in the successional environment decreased with increasing seed density (density of 5: λ =

0.55; density of 10: λ = 0.53; density of 20: λ = 0.45). Elasticity of SFS and FSB increased and the SBK transition decreased in importance with increasing seed density (Figure 20c, d, Appendix N).

Models to Evaluate Successional Change in *B. angustifolia*

Population growth of *B. angustifolia* in simulated successional conditions, continuously degraded habitat conditions, and continuously intact conditions was less than 1 (reference: λ = 0.58; degraded: λ = 0.46, intact: λ = 0.45). FSB had the greatest relative elasticity on stochastic population growth in the three models; FSD also had great elasticity values in the continuously intact and continuously degraded models (Figure 21a, b, Appendix O). Population growth decreased with increasing seed density (density of 5: λ = 0.58; density of 10: λ = 0.53; density of 20: λ = 0.37). The importance of SBK decreased as seed density increased. At the highest seed density FSB also decreased slightly (Figure 21c, d, Appendix O).

Discussion

The study of environmental factors associated with vital rate variation and demographic dynamics is essential to understanding the consequences of habitat change on species persistence (Crone et al. 2011). Comparative studies evaluating responses of different species to habitat degradation and associated microsite variation help evaluate the effects of management actions. Results from my study of two short-lived herbaceous species suggest that particular habitat and microsite conditions can affect population dynamics of coexisting species in distinct ways. While degraded habitat conditions increased population growth for *C. fasciculata* across all microsites, there was little direct effect of habitat on population growth of *B. angustifolia*, which benefited from open sand in both degraded and intact habitat compared to the other microsites.

Greater population growth of *C. fasciculata* in degraded habitats may be caused by reduced below-ground competition for resources resulting from mechanical disturbance of root systems (Petrů and Menges 2003; Calabrese and Menges 2008; Breininger and Schmalzer 1990). Furthermore, *C. fasciculata* may have a competitive advantage over co-occurring species in the degraded scrub, but not in the intact scrub. Because it is a legume, *C. fasciculata* may have increased survival and reproduction associated with nitrogen fixation. This benefit may be in direct contrast to intact scrub, where other scrub plants may have more extensive root systems, stronger relationships with soil microorganisms (e.g., soil crusts, Hawkes 2000), or greater tolerance of allelopathic shrub exudates (e.g., *Ceratiola ericoides*, Weekly et al. 2008; Hunter and Menges 2002; Hewitt and Menges 2008).

Variation in the relative importance of transitions in the elasticity matrices for *C. fasciculata* indicated demographic differences between habitats. Seed survival was the most influential transition for long-term population growth in degraded habitat. In intact habitat, production of seeds with subsequent entry into the seedbank was most influential. As there were significantly more established plants (large vegetative and reproductive plants) in degraded scrub, in denser patches (Stephens *In preparation*), it is likely that the number of reproductive plants and associated seeds entering the seedbank were limiting in intact scrub. Despite differences between habitats, I found that population dynamics of *C. fasciculata* are strongly influenced by seed dynamics. This pattern is common among plants in arid habitats (Pico et al. 2003; Salguero-Gómez et al. 2012), in which seeds are ecologically important to survival in harsh abiotic conditions (Brown et al. 1979; Freas and Kemp 1983).

Similar population growth rates for *B. angustifolia* in intact and degraded conditions were reinforced by my observations that adult density did not differ between habitats (*Stephens* in preparation). Populations in bare sand microsites exhibited the greatest population growth for *B. angustifolia*. In contrast, *C. fasciculata* had the poorest population growth in this microsite. *Balduina angustifolia* was most affected by shrub presence, which is also important for other scrub herb species (*Paronychia chartacea*, Schafer et al. 2010). Negative effects of shrubs on *B. angustifolia* population growth may include competition for nutrients, water, or light, which would be more intense with shrubs than with smaller herbs or grasses found in open areas. Other negative effects of shrubs may include an increased presence of herbivores or seed predators (Weekley et al. 2008). Herbivores or other factors may have a more pronounced effect on *B. angustifolia* than seed predators in shrub microsites, as seed predation was less intense under shrubs than in litter or bare sand microsites (Stephens *In preparation*). Positive effects of bare sand gaps on *B. angustifolia* population growth could include the presence of beneficial soil microorganisms such as soil crusts (Hawkes 2000) that may be absent or less abundant under shrubs.

Production of seeds and their subsequent entry into the seedbank was the most influential transition in all models of *B. angustifolia*. Populations of *B. angustifolia* are likely most limited by number of reproductive individuals and the initial fate of seeds. The significance of seed dynamics for population persistence of *B. angustifolia* is consistent with patterns for *C. fasciculata* and other plants that recruit from seeds in dry ecosystems (Brown et al. 1979; Frees and Kemp 1983; Pico et al. 2003; Salguero-Gómez et al. 2012).

The strong effect of habitat on *C. fasciculata*, but not *B. angustifolia*, suggests that only *C. fasciculata* is directly affected by time-since-disturbance. This difference between the focal species may again be related to competitive advantages conferred by nitrogen fixation in *C. fasciculata*, which is absent in *B. angustifolia*. In a successional trajectory from an anthropogenic (mechanical) disturbance event to relative restoration of intact scrub conditions, I expect that *C. fasciculata* would have an initially positive population growth rate that would gradually decline to a negative rate. I expect that the change in these rates would mirror the establishment of competing plant species or recovery of soil microbes. Periodic disturbance events (especially below-ground) would likely be required to maintain positive *C. fasciculata* population growth. In contrast, I expect very little direct effect of a transition from degraded to intact scrub for *B. angustifolia* within a given microsite. However, habitat type or quality may still affect *B. angustifolia* populations indirectly through microsite abundance or proportion within the habitat. The greater extent of bare sand gaps in degraded scrub may actually result in more *B. angustifolia* plants in degraded than in intact habitat. Also, the decreasing availability of bare sand gaps in intact scrub with increasing time-since-fire (Menges et al. 2008) would likely cause *B. angustifolia* populations to decline with fire suppression.

Habitat and microsite can influence population dynamics in conjunction with other factors, such as seed density. I observed that the most influential transition for each species (*C. fasciculata*: seed survival in seedbank; *B. angustifolia*: production of seeds with subsequent entry into seedbank) decreased in relative importance with increasing seed density. Considering that population growth decreased slightly as available seed density was increased, conditions may be less favorable for populations with greater densities of available seeds. This relationship between seed density and population growth may be explained by (1) a more than proportional increase in seed predation that reduces the number of seeds available for germination (Janzen 1971; Velho et al. 2012), or (2) greater competition resulting from an increasing number of germinants that suppresses (Clark et al. 2012) or delays (Hyatt and Evans 1998) subsequent vegetative survival. In addition, if seeds are abundant, the population is likely already large and additional germination and survival may be constrained by competition with established adults (Ellner 1986; Casper 1990).

My study links data from field experiments and matrix models in a way that clarifies the role of environmental factors in population growth and provides context for analyzing seed dynamics of the study species. I demonstrate how co-occurring species can be affected differently by habitat and microsite, and identify how available seed density may be relevant to the demography of these species. Species with similar morphology (height, seed size, flower color and abundance), distribution (intact and degraded scrub, roadsides), and life-history characteristics (fast growth rate, presence of seed bank, relatively great seed production), such as the focal species, may have unique relationships with their surroundings.

My results suggest that for some species bare sand gaps in intact scrub are not equivalent to the extensive bare sand areas in the degraded scrub. This conclusion is supported by the juxtaposition of a strong positive effect of degraded scrub and a negative effect of bare sand microsites on *C. fasciculata* population growth rates, as well as the lack of a specific effect of intact scrub vs. the strong positive effect of bare sand on *B. angustifolia* population growth rates. These trends further emphasize that intact scrub is ecologically complex and critical to preserve. Restoration efforts, while helpful in ameliorating some biotic and abiotic aspects of a habitat, may never achieve exact pre-degradation conditions (Schmalzer et al. 2002). Due to the intricate and often subtle ways that organisms are affected by their environments, it will be difficult to reestablish population dynamics of some species in habitat undergoing restoration. I strongly advocate for the protection of intact habitat whenever possible.

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Tables and Figures

Table 11. Vital rates and general seasonal matrix model of *C. fasciculat*a and *B. angustifolia*.

		Vegetative		
	Seedbank	Small	Large	Reproductive
Seedbank	(((ps*Ss)-g) *Sb)/ps	---	---	r*ph1*ph2*V*Ss
Small	(Ss*g)/ps	Sv1	Sv*G	Sr*ph1*ph2*((Ss*g)/ps)
Large	---	Sv*G	Sv2	Sr*G
Reproductive	---	Sv*G*F	Sv*F	Sr

ps	seeds in previous seasonal seedbank
g	number of germinants
G	probability of growth (positive or negative)
Ss	probability of seed survival in seedbank (before germination)
Sb	probability of seed survival in seedbank (after germinants leave)
Sd	probability of seedling survival
Sv1	probability of small vegetative survival
Sv2	probability of large vegetative survival
F	probability of becoming reproductive
ph1	average seeds per pod/head
ph2	average pods/heads per plant
r	number of reproductive individuals
V	probability of seed viability
---	structural zeros

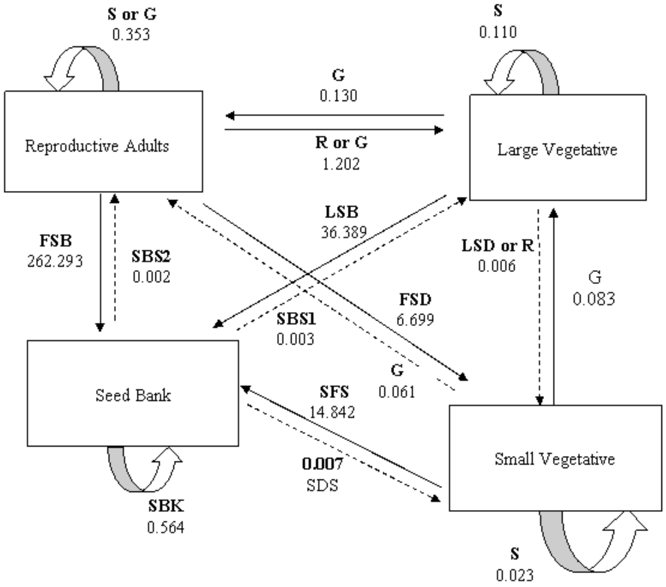


Figure 12. Life cycle of *C. fasciculata*. Values correspond to overall annual matrix model (pooled habitats, microsites); labels correspond to generalized annual matrix model (Appendix I). Discontinuous lines show transitions with values of less than 0.075.

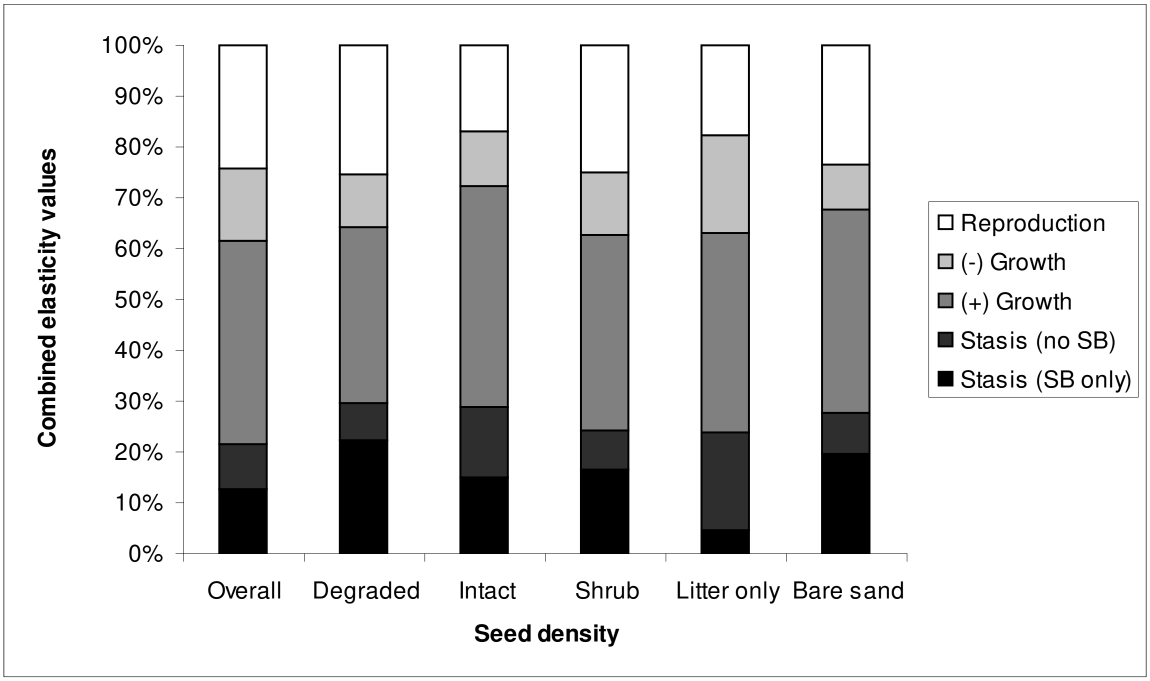


Figure 13. Combined elasticity values for the overall matrix model (overall), habitat models (degraded, intact), and microsite models (shrub, litter, bare sand) in *C. fasciculata*. Reproduction represents SFS, LSB, and FSB transitions; negative (-) growth represents R and FSD; positive (+, or advancing) growth represents SDS, SBS1, SBS2, and G; stasis (no SB) represents S; stasis (SB only) represents SBK. See Appendix I for definitions of transition abbreviations.

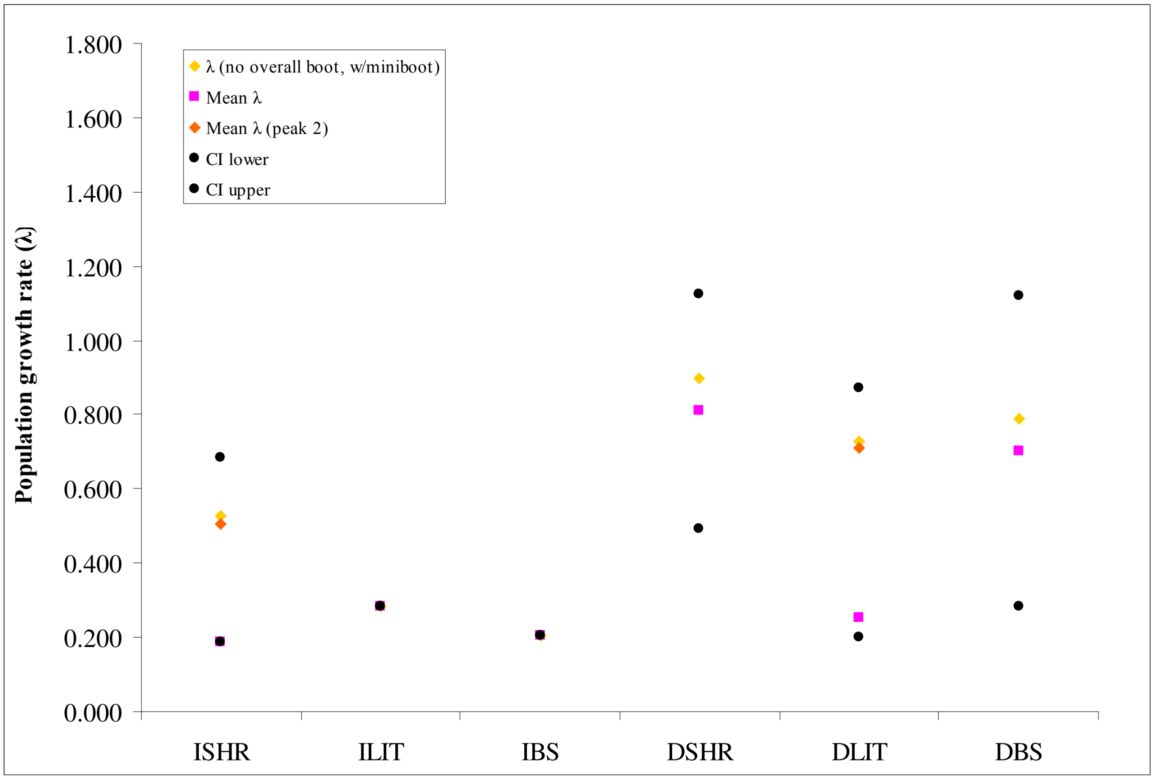


Figure 14. Population growth rates (λ) for *C. fasciculata* with and without boot strapping. Mean λ = result of 1000 bootstrap iterations. CI = confidence interval for mean λ. Normal distributions of bootstrapped λ are represented by one mean λ (pink square); bimodal distributions of bootstrapped λ values are represented by two mean λ values (pink square: greater λ of the two λ values, orange triangle: smaller λ). ISHR = shrub microsite in intact habitat, ILIT = litter microsite in intact habitat, IBS=bare sand microsite in intact habitat, DSHR = shrub microsite in degraded habitat, ILIT = litter microsite in degraded habitat, IBS = bare sand microsite in degraded habitat.

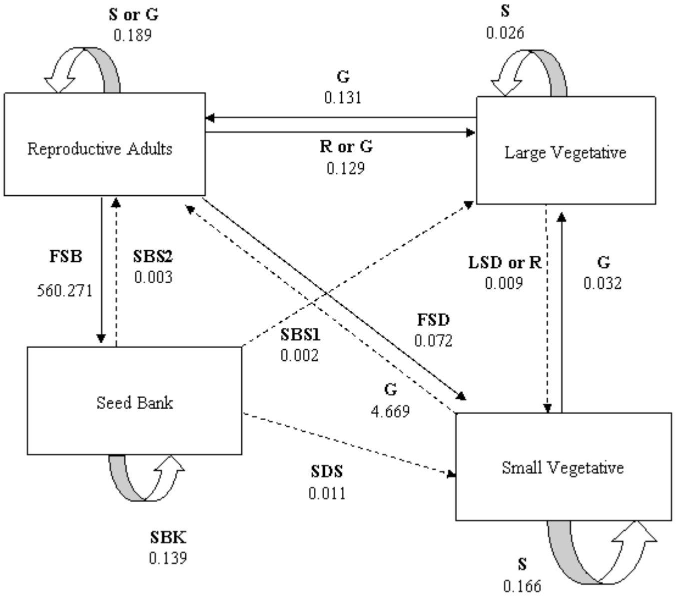


Figure 15. Life cycle of *B. angustifolia*. Values correspond to overall annual matrix model (pooled habitats, microsites); labels correspond to generalized annual matrix model (Appendix I). Discontinuous lines show transitions with values of less than 0.075. SFS and LSB = zero.

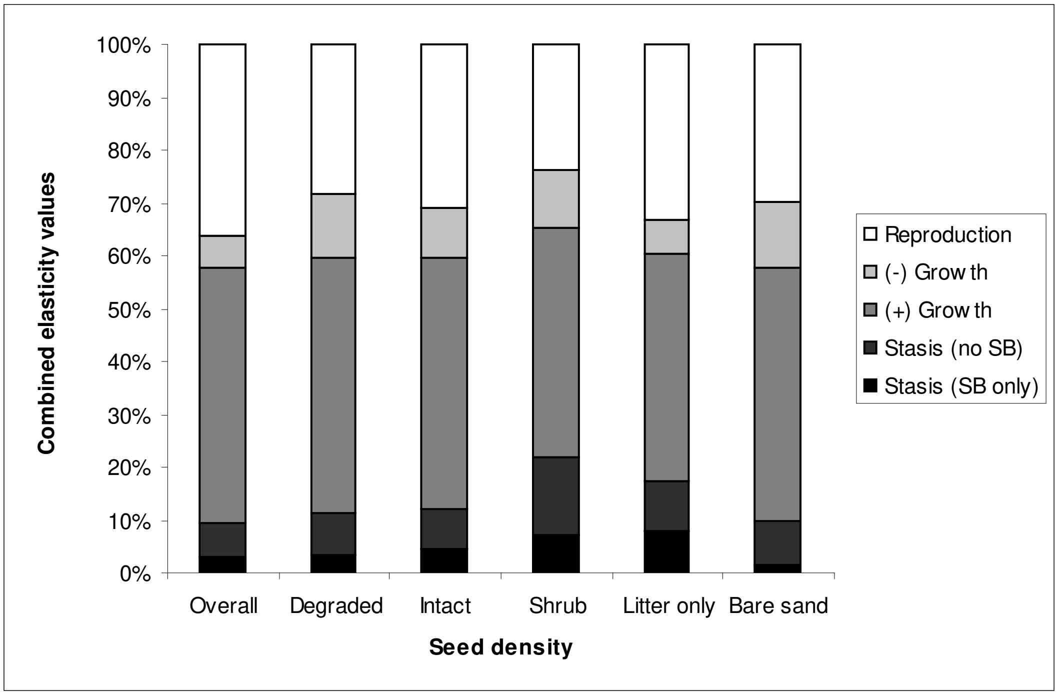


Figure 16. Combined elasticity values for the overall matrix model (overall), habitat models (degraded, intact), and microsite models (shrub, litter, bare sand) in *B. angustifolia*. Reproduction represents SFS, LSB, and FSB transitions; negative (-) growth represents R and FSD; positive (+) growth represents SDS, SBS1, SBS2, and G; stasis (no SB) represents S; stasis (SB only) represents SBK. See Appendix I for definitions of transition abbreviations.

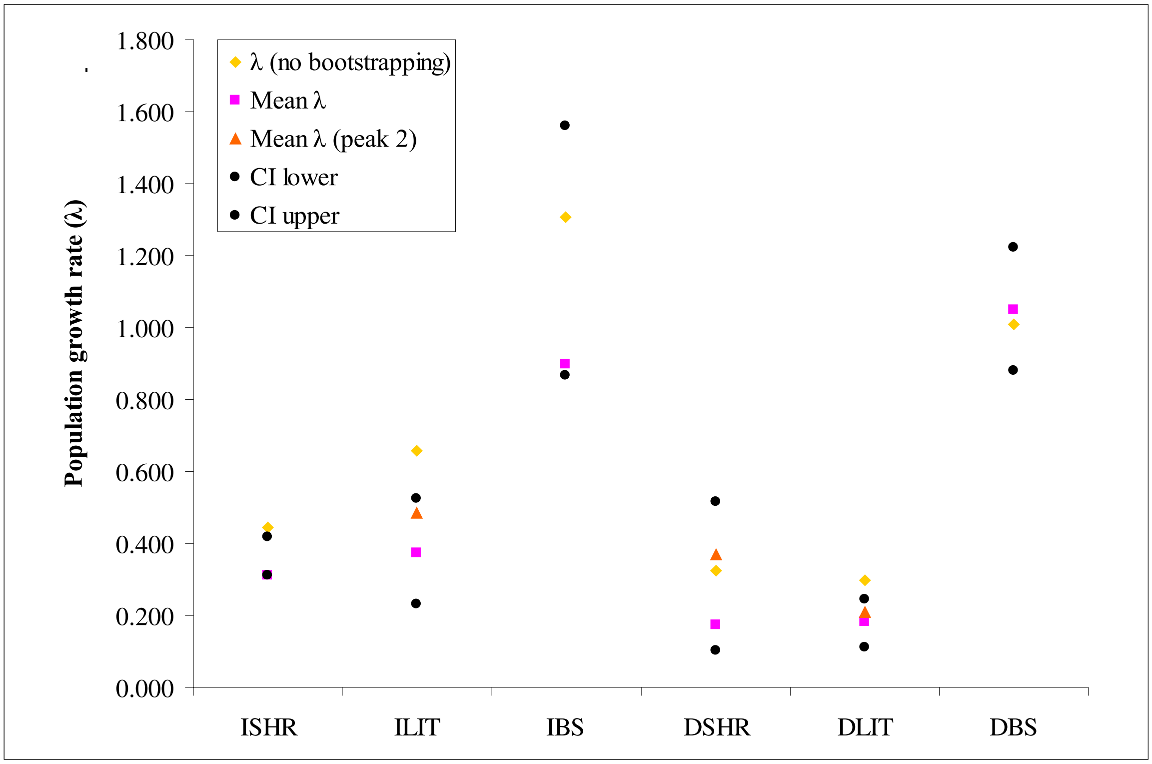


Figure 17. Population growth rates (λ) for *B. angustifolia* with and without boot strapping. Mean λ = result of 1000 bootstrap iterations. CI = confidence interval for mean λ. Normal distributions of bootstrapped λ are represented by one mean λ (pink square); bimodal distributions of bootstrapped λ values are represented by two mean λ values (pink square: greater λ of the two λ values, orange triangle: smaller λ). ISHR = shrub microsite in intact habitat, ILIT = litter microsite in intact habitat, IBS=bare sand microsite in intact habitat, DSHR = shrub microsite in degraded habitat, ILIT = litter microsite in degraded habitat, IBS = bare sand microsite in degraded habitat.

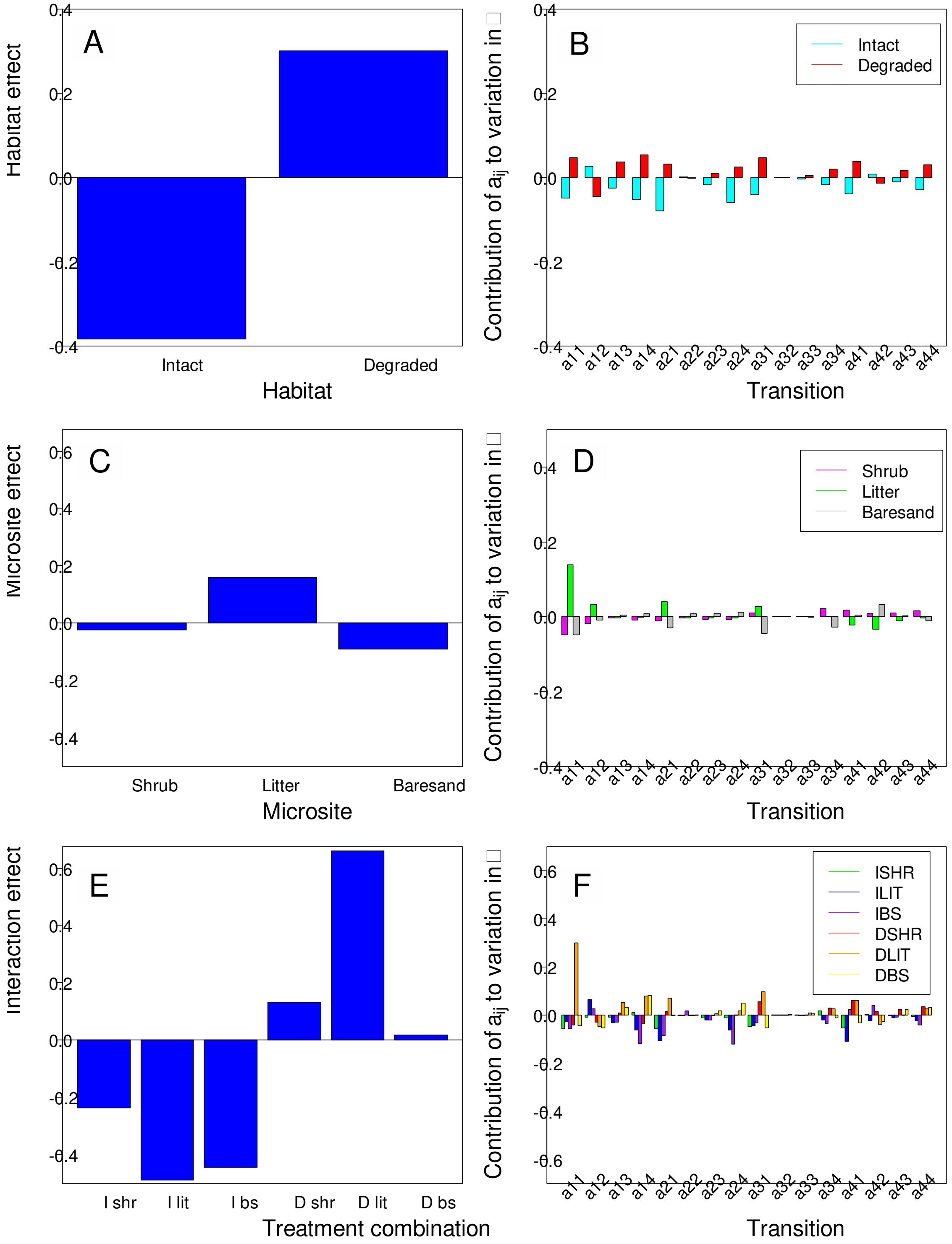
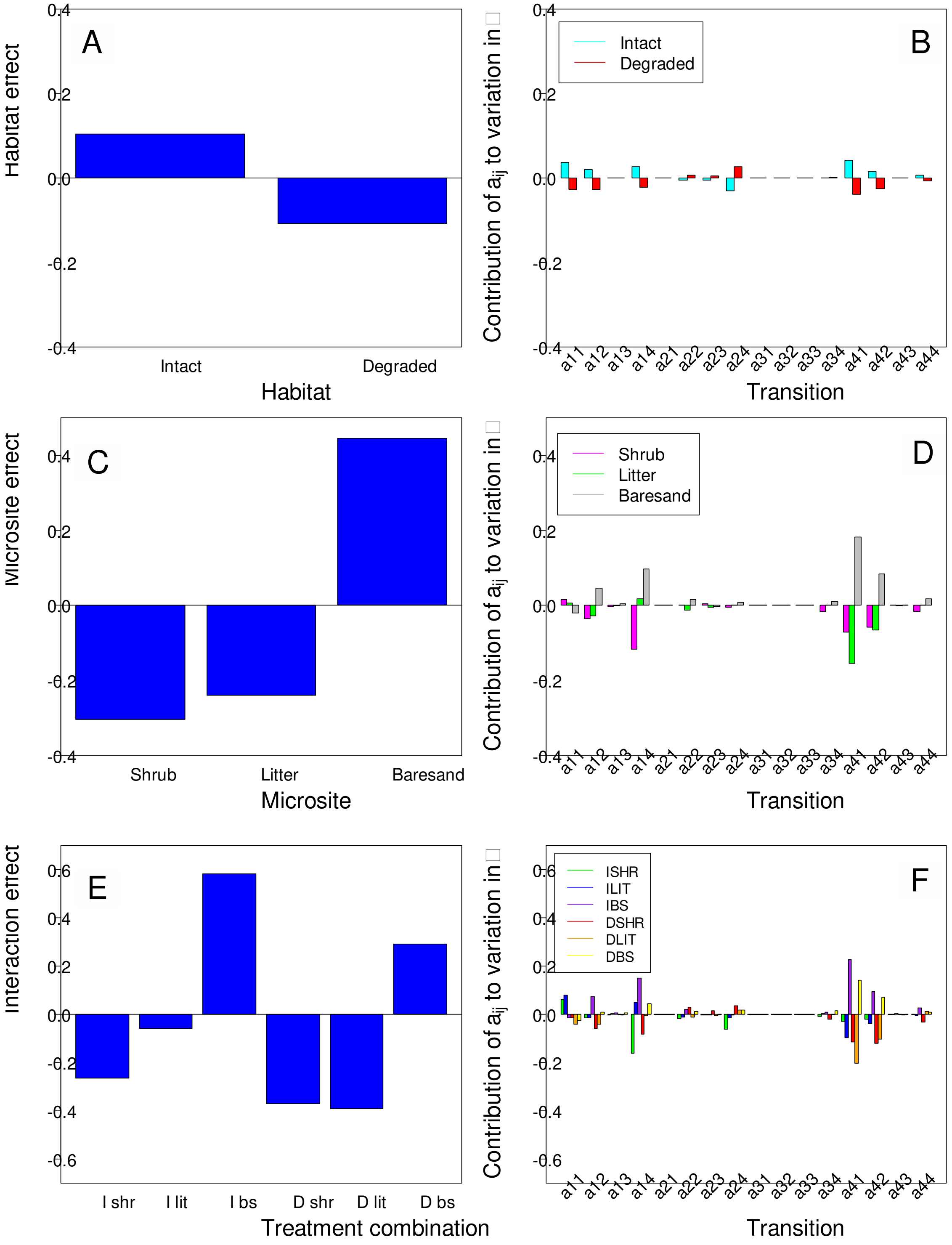

A
Habitat effect
0.4
0.2
0.0
-0.2
-0.4
Intact
Degraded
Habitat
B
Contribution of aij to variation in
Intact
Degraded
0.4
0.2
0.0
-0.2
-0.4
a11
a12
a13
a14
a21
a22
a23
a24
a31
a32
a33
a34
a41
a42
a43
a44
Transition
C
Microsite effect
0.6
0.4
0.2
0.0
-0.2
-0.4
Shrub
Litter
Baresand
Microsite
D
Contribution of aij to variation in
Shrub
Litter
Baresand
0.4
0.2
0.0
-0.2
-0.4
a11
a12
a13
a14
a21
a22
a23
a24
a31
a32
a33
a34
a41
a42
a43
a44
Transition
E
Interaction effect
0.6
0.4
0.2
0.0
-0.2
-0.4
I shr
I lit
I bs
D shr
D lit
D bs
Treatment combination
F
Contribution of aij to variation in
ISHR
ILIT
IBS
DSHR
DLIT
DBS
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
a11
a12
a13
a14
a21
a22
a23
a24
a31
a32
a33
a34
a41
a42
a43
a44
Transition

Figure 18. Results of LTRE for habitat of *C. fasciculata* (A, B), microsite (C, D), and habitat by microsite models (E, F). A, C, E: contribution of each treatment to mean population growth rate. B, D, F: contribution of each transition in each treatment to mean population growth rate; individual transitions represented by row, column numbers (i.e. a11 = seed survival in seedbank). For F: ISHR = intact habitat with shrub microsite, ILIT = intact habitat with litter microsite, IBS = intact habitat with bare sand microsite, DSHR = degraded habitat with shrub microsite, DLIT = degraded habitat with litter microsite, DBS = degraded habitat with bare sand microsite.



A
Habitat effect
0.4
0.2
0.0
-0.2
-0.4
Intact
Degraded
Habitat
B
Intact
Degraded
Contribution of a_{ij} to variation in
a11 a12 a13 a14 a21 a22 a23 a24 a31 a32 a33 a34 a41 a42 a43 a44
Transition
C
Microsite effect
Shrub
Litter
Baresand
Microsite
D
Shrub
Litter
Baresand
Contribution of a_{ij} to variation in
Transition
E
Interaction effect
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
I shr
I lit
I bs
D shr
D lit
D bs
Treatment combination
F
ISHR
ILIT
IBS
DSHR
DLIT
DBS
Contribution of a_{ij} to variation in
Transition

Figure 19. Results of LTRE for habitat of *B. angustifolia* (A, B), microsite (C, D), and habitat by microsite models (E, F). A, C, E: contribution of each treatment to mean population growth rate. B, D, F: contribution of each transition in each treatment to mean population growth rate; individual transitions represented by row, column numbers (i.e. a11 = seed survival in seedbank). For F: ISHR = intact habitat with shrub microsite, ILIT = intact habitat with litter microsite, IBS = intact habitat with bare sand microsite, DSHR = degraded habitat with shrub microsite, DLIT = degraded habitat with litter microsite, DBS = degraded habitat with bare sand microsite.

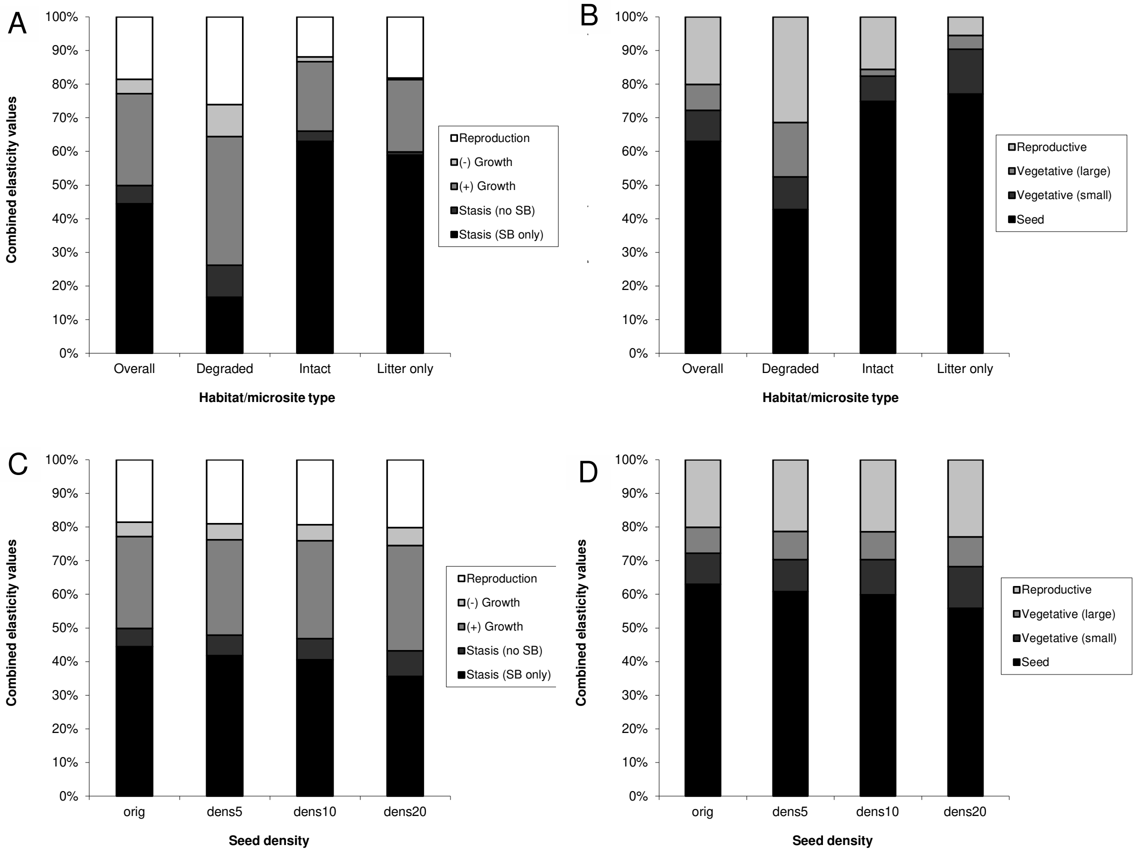


Figure 20. Combined elasticity values for successional models of *C. fasciculata*. Unmanipulated (Overall), individual habitat (Degraded, Intact), and microsite (Litter) scenarios with elasticity values combined by transition type (A), and combined by life-history stage (B); various initial seed density scenarios (unmanipulated (orig), 5, 10, and 20 seeds) with elasticity values combined by transition type (C), and combined by life-history stage (D). Reproduction represents SFS, LSB, and FSB transitions; negative (-) growth represents R and FSD; positive or advancing (+) growth represents SDS, SBS1, SBS2, and G; stasis (no SB) represents S; stasis (SB only) represents SBK. See Appendix I for definitions of transition abbreviations.

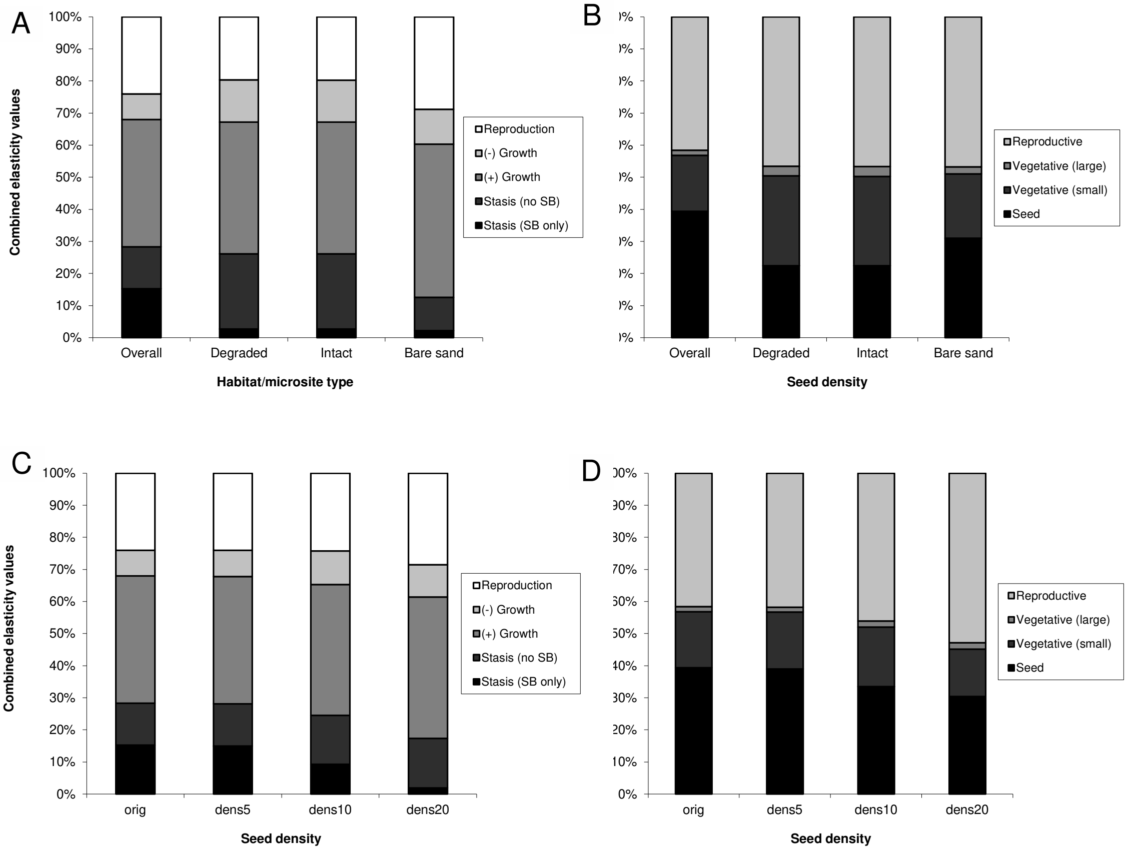


Figure 21. Combined elasticity values for successional models of *B. angustifolia*. Unmanipulated (Overall), individual habitat (Degraded, Intact), and microsite (Bare sand) scenarios with elasticity values combined by transition type (A), and combined by life-history stage (B); various initial seed density scenarios (unmanipulated (orig), 5, 10, and 20 seeds) with elasticity values combined by transition type (C), and combined by life-history stage (D). Reproduction represents SFS, LSB, and FSB transitions; negative (-) growth represents R and FSD; positive or advancing (+) growth represents SDS, SBS1, SBS2, and G; stasis (no SB) represents S; stasis (SB only) represents SBK. See Appendix I for definitions of transition abbreviations.

Appendix G1. Temperature and light schedule for germination study in growth chamber from April 6th, 2009 to June 16th, 2009 (late spring conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour

Time	**Degrees C**	**Fluorescent**	**Incandescent**
0:00	14	0	0
1:00	14	0	0
2:00	14	0	0
3:00	14	0	0
4:00	14	0	0
5:00	14.5	0	0
6:00	15	0	1
7:00	16	1	1
8:00	17	1	1
9:00	18	1	2
10:00	20	2	2
11:00	25	2	2
12:00	29	2	2
13:00	31	2	2
14:00	32	2	2
15:00	31	2	2
16:00	30	2	2
17:00	27	2	2
18:00	22	2	1
19:00	20	2	1

Time	**Degrees C**	**Fluorescent**	**Incandescent**
20:00	18	1	1
21:00	16	1	0
22:00	15	0	0
23:00	14	0	0
23:59	14	0	0

Appendix G2. Temperature and light schedule for germination study in growth chamber from June 16th, 2009 to November 3rd, 2009 (summer / fall conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour.

Time	Degrees C	Fluorescent	Incandescent
0:00	21	0	0
1:00	22	0	0
2:00	23	0	0
3:00	24	0	0
4:00	25	0	0
5:00	26	0	0
6:00	27	0	1
7:00	28	1	1
8:00	29	1	1
9:00	30	1	2
10:00	31	2	2
11:00	33	2	2
12:00	34	2	2
13:00	35	2	2
14:00	34	2	2
15:00	33	2	2
16:00	31	2	2
17:00	30	2	2
18:00	29	2	1
19:00	27	2	1

Time	Degrees C	Fluorescent	Incandescent
0:00	25	1	1
21:00	24	1	0
22:00	23	0	0
23:00	22	0	0
23:59	21	0	0

Appendix G3. Temperature and light schedule for germination study in growth chamber from November 4th, 2009 to January 21st, 2010 (fall / winter conditions). Fluorescent and Incandescent indicate number of bulbs of each type illuminated each hour.

Time	**Degrees C**	**Fluorescent**	**Incandescent**
0:00	14.3	0	0
1:00	15	0	0
2:00	16	0	0
3:00	17	0	0
4:00	18	0	0
5:00	19	0	0
6:00	20	0	1
7:00	21	1	1
8:00	22	1	1
9:00	23	1	2
10:00	24	2	2
11:00	25	2	2
12:00	26	2	2
13:00	27	2	2
14:00	26	2	2
15:00	25	2	2
16:00	24	2	2
17:00	23	2	2
18:00	22	2	1
19:00	21	2	1

Time	**Degrees C**	**Fluorescent**	**Incandescent**
21:00	18	1	0
22:00	16	0	0
23:00	15	0	0
23:59	14.3	0	0

Appendix H. Generalized seasonal matrix model for *C. fasciculata* and *B. angustifolia*

		Vegetative		
	Seedbank	Small	Large	Reproductive
Seedbank	SBK	---	---	FSB
Small	SDS	S	R	FSD
Large	---	G	S	R
Reproductive	---	G	G	S

SBK	seasonal seedbank survival
SDS	seedling recruitment from seedbank and early survival
FSB	flowering adult produces seeds, seeds enter seedbank
FSD	flowering adult produces seeds, seeds germinate, survive as seedlings
S	stasis
G	growth
R	regression
---	structural zeros

Appendix I. Generalized annual matrix model for *C. fasciculata* and *B. angustifolia*. Bold text indicates changes from generalized seasonal matrix

		Vegetative		
	Seedbank	Small	Large	Reproductive
Seedbank	SBK	**SFS**	**LSB**	FSB
Small	SDS	S	**R or LSD**	FSD
Large	**SBS1**	G	S	**R or G**
Reproductive	**SBS2**	G	G	**S or G**

SBK	annual seedbank survival
SDS	seedling recruitment from seedbank and early survival
SFS	small vegetative individual survives to become reproductive, produces seeds, seeds enter seedbank
FSB	flowering adult produces seeds, seeds enter seedbank
FSD	flowering adult produces seeds, seeds germinate, survive as seedlings
LSB	large vegetative adult becomes reproductive, produces seeds, seeds enter seedbank
LSD	large vegetative adult becomes reproductive, produces seeds, seeds germinate, survive as seedlings
SBS1	seedling recruitment from seedbank and survival to large vegetative adult
SBS2	seedling recruitment from seedbank and survival to reproductive adult
S	stasis
G	growth
R	regression

Appendix J. Environmental matrix comprised of estimated probabilities of each habitat and microsite combination transitioning to other combination types. DBS = degraded habitat with bare sand microsite, DLIT = degraded habitat with litter microsite, DSHR = degraded habitat with shrub microsite, IBS = intact habitat with bare sand microsite, ILIT = intact habitat with litter microsite, ISHR = intact habitat with shrub microsite

	DBS	DLIT	DSHR	IBS	ILIT	ISHR	DEG
DBS	0.30	0.25	0.05	0.05	0.05	0.05	0.50
DLIT	0.30	0.45	0.2	0.03	0.05	0.09	0.30
DSHR	0.15	0.10	0.5	0.01	0.04	0.09	0.10
IBS	0.10	0.09	0.01	0.50	0.31	0.11	0.01
ILIT	0.09	0.05	0.05	0.26	0.40	0.11	0.01
ISHR	0.01	0.01	0.14	0.10	0.10	0.55	0.03
DEG	0.05	0.05	0.05	0.05	0.05	0.05	0.05

Appendix K1. Annual demographic matrix model for *C. fasciculata* (pooled habitats, microsites) (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = summer-fall * spring-summer * winter-spring * fall-winter. Population growth rate for annual matrix: 1.65. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.564	14.842	36.389	262.293
Small	0.007	0.023	0.006	6.699
Large	0.003	0.083	0.110	1.202
Reproductive	0.002	0.061	0.130	0.353

B	Seedbank	Small	Large	Reproductive
Seedbank	0.369	0.006	0.002	0.001
Small	**9.942**	0.150	0.050	0.025
Large	**21.109**	0.319	0.107	0.054
Reproductive	**145.964**	2.208	0.740	0.374

C	Seedbank	Small	Large	Reproductive
Seedbank	**0.126**	0.050	0.041	**0.151**
Small	0.044	0.002	0.000	0.104
Large	0.044	0.016	0.007	0.040
Reproductive	**0.154**	0.082	0.058	0.080

Appendix K2. Annual demographic matrix model for *C. fasciculata* in degraded scrub (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.88. Greatest transition values in sensitivity and elasticity matrices appear in bold

	Seedbank	Small	Large	Reproductive
Seedbank	0.885	34.127	48.907	185.407
Small	0.004	0.009	0.003	2.352
Large	0.005	0.128	0.113	1.178
Reproductive	0.003	0.120	0.159	0.405

	Seedbank	Small	Large	Reproductive
Seedbank	0.476	0.003	0.002	0.001
Small	**16.939**	0.100	0.086	0.050
Large	**22.597**	0.134	0.115	0.067
Reproductive	**104.744**	0.619	0.534	0.309

	Seedbank	Small	Large	Reproductive
Seedbank	**0.224**	0.051	0.063	**0.138**
Small	0.037	0.000	0.000	0.062
Large	0.057	0.009	0.007	0.042
Reproductive	**0.158**	0.039	0.045	0.066

Appendix K3. Annual demographic matrix model for *C. fasciculata* in intact scrub (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 0.32. Greatest transition values in sensitivity and elasticity matrices appear in bold

	Seedbank	Small	Large	Reproductive
Seedbank	0.148	0.000	0.000	20.986
Small	0.008	0.036	0.003	0.934
Large	0.001	0.015	0.038	0.098
Reproductive	0.000	0.013	0.087	0.085

	Seedbank	Small	Large	Reproductive
Seedbank	0.318	0.018	0.003	0.003
Small	**2.971**	0.164	0.028	0.024
Large	**15.058**	0.832	0.140	0.120
Reproductive	**47.480**	2.624	0.443	0.377

	Seedbank	Small	Large	Reproductive
Seedbank	**0.149**	0.000	0.000	**0.168**
Small	0.075	0.019	0.000	0.070
Large	0.046	0.040	0.017	0.037
Reproductive	0.048	0.105	**0.123**	0.101

Appendix K4. Annual demographic matrix model for *C. fasciculata* in shrub microsites (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.14. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.448	11	24	111.306
Small	0.005	0.003	0.000	2.374
Large	0.003	0.045	0.058	0.663
Reproductive	0.002	0.064	0.126	0.238

B	Seedbank	Small	Large	Reproductive
Seedbank	0.415	0.005	0.002	0.002
Small	**9.984**	0.127	0.054	0.038
Large	**20.316**	0.258	0.109	0.076
Reproductive	**92.884**	1.181	0.498	0.349

C	Seedbank	Small	Large	Reproductive
Seedbank	**0.164**	0	0	**0.153**
Small	0.048	0.000	0.000	0.079
Large	0.049	0.010	0.006	0.045
Reproductive	**0.154**	0.066	0.056	0.073

Appendix K5. Annual demographic matrix model for *C. fasciculata* in litter (A), and corresponding (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.52. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.314	2	5	31.378
Small	0.011	0.001	0.001	1.054
Large	0.042	0.075	0.110	3.759
Reproductive	0.006	0.061	0.157	0.564

B	Seedbank	Small	Large	Reproductive
Seedbank	0.222	0.005	0.020	0.005
Small	1.290	0.029	0.116	0.029
Large	**3.158**	0.072	0.284	0.070
Reproductive	**21.050**	0.477	**1.890**	0.465

C	Seedbank	Small	Large	Reproductive
Seedbank	0.046	0	0	0.101
Small	0.009	0.000	0.000	0.020
Large	0.087	0.004	0.021	**0.172**
Reproductive	0.079	0.019	**0.194**	**0.172**

Appendix K6. Annual demographic matrix model for *C. fasciculata* in bare sand microsites (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 0.62. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.282	2	2	35.817
Small	0.010	0.069	0.023	1.138
Large	0.004	0.085	0.055	0.261
Reproductive	0.002	0.043	0.037	0.106

B	Seedbank	Small	Large	Reproductive
Seedbank	0.432	0.015	0.007	0.003
Small	**5.273**	0.181	0.083	0.039
Large	**4.218**	0.145	0.066	0.031
Reproductive	**43.827**	1.503	0.690	0.321

C	Seedbank	Small	Large	Reproductive
Seedbank	**0.196**	0	0	**0.182**
Small	0.087	0.020	0.003	0.071
Large	0.028	0.020	0.006	0.013
Reproductive	**0.121**	0.105	0.041	0.055

Appendix K7. Annual demographic matrix model for *B. angustifolia* (pooled habitats, microsites) (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = summer-fall* spring-summer * winter-spring * fall-winter. Population growth rate for annual matrix: 1.75. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.139	0	0	560.271
Small	0.011	0.166	0.009	4.669
Large	0.002	0.032	0.026	0.129
Reproductive	0.003	0.072	0.131	0.189

B	Seedbank	Small	Large	Reproductive
Seedbank	0.392	0.006	0.001	0.001
Small	**7.705**	0.117	0.011	0.022
Large	**12.558**	0.190	0.018	0.036
Reproductive	**164.530**	2.495	0.240	0.473

C	Seedbank	Small	Large	Reproductive
Seedbank	0.031	0	0	**0.360**
Small	0.047	0.011	<0.001	0.059
Large	0.012	0.003	<0.001	0.003
Reproductive	**0.302**	**0.102**	0.018	0.051

Appendix K8. Annual demographic matrix model for *B. angustifolia* in degraded scrub (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.49. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.152	0	0	353.960
Small	0.009	0.246	0.000	4.610
Large	0.002	0.054	0.024	0.039
Reproductive	0.003	0.100	0.128	0.152

B	Seedbank	Small	Large	Reproductive
Seedbank	0.316	0.007	0.001	0.001
Small	**10.091**	0.215	0.019	0.038
Large	**10.466**	0.223	0.020	0.039
Reproductive	**119.131**	2.533	0.229	0.449

C	Seedbank	Small	Large	Reproductive
Seedbank	0.032	0	0	**0.284**
Small	0.061	0.036	0.000	0.118
Large	0.011	0.008	<0.001	0.001
Reproductive	**0.212**	**0.171**	0.020	0.046

Appendix K9. Annual demographic matrix model for *B. angustifolia* in intact scrub (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.43. Greatest transition values in sensitivity and elasticity matrices appear in bold.

A	Seedbank	Small	Large	Reproductive
Seedbank	0.180	0	0	276.058
Small	0.016	0.131	0.011	6.159
Large	0.002	0.019	0.021	0.071
Reproductive	0.003	0.058	0.142	0.187

B	Seedbank	Small	Large	Reproductive
Seedbank	0.354	0.012	0.001	0.002
Small	**4.757**	0.162	0.008	0.022
Large	**10.393**	0.353	0.018	0.047
Reproductive	**102.990**	3.498	0.182	0.466

C	Seedbank	Small	Large	Reproductive
Seedbank	0.045	0	0	**0.310**
Small	0.054	0.015	<0.001	0.093
Large	0.011	0.005	<0.001	0.002
Reproductive	**0.245**	**0.142**	0.018	0.061

Appendix K10. Annual demographic matrix model for *B. angustifolia* in shrub microsites (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 0.56. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.128	0	0	50.646
Small	0.005	0.096	0.000	0.794
Large	0.001	0.031	0.019	0.049
Reproductive	0.002	0.072	0.056	0.135

B	Seedbank	Small	Large	Reproductive
Seedbank	0.307	0.008	0.001	0.003
Small	**8.737**	0.217	0.031	0.074
Large	**5.536**	0.138	0.020	0.047
Reproductive	**53.755**	1.336	0.193	0.457

C	Seedbank	Small	Large	Reproductive
Seedbank	0.070	0	0	**0.236**
Small	0.074	0.037	0.000	0.106
Large	0.007	0.008	0.001	0.004
Reproductive	**0.155**	**0.172**	0.019	0.110

Appendix K11. Annual demographic matrix model for *B. angustifolia* in litter (A), and corresponding (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.18. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.224	0	0	154.453
Small	0.004	0.014	0	2.250
Large	0.001	0.014	0.023	0.031
Reproductive	0.004	0.079	0.176	0.226

B	Seedbank	Small	Large	Reproductive
Seedbank	0.408	0.006	0.000	0.003
Small	**5.528**	0.087	0.006	0.034
Large	**12.054**	0.189	0.013	0.075
Reproductive	**79.480**	1.245	0.087	0.492

C	Seedbank	Small	Large	Reproductive
Seedbank	0.077	0	0	**0.331**
Small	0.020	0.001	0	0.065
Large	0.009	0.002	<0.001	0.002
Reproductive	**0.302**	0.083	0.013	**0.094**

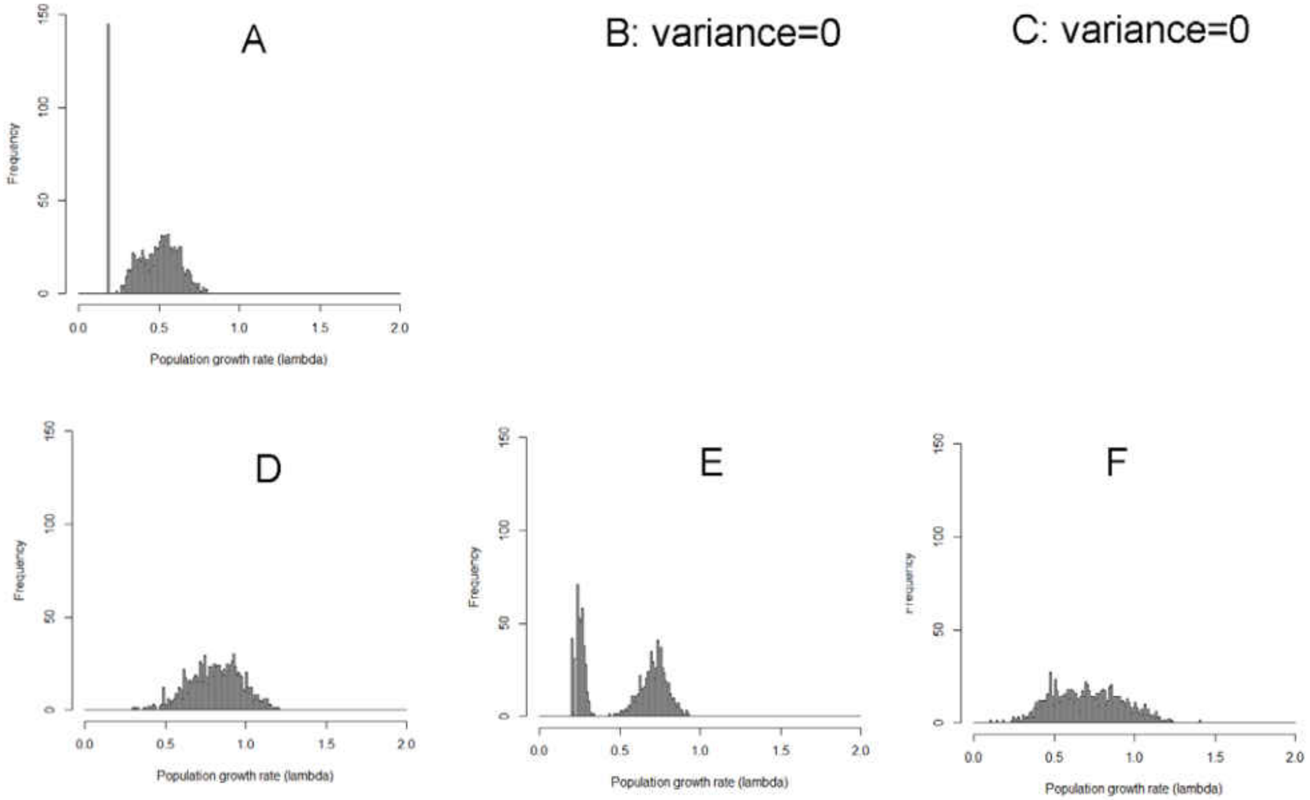
Appendix K12. Annual demographic matrix model for *B. angustifolia* in bare sand microsites (A), and corresponding sensitivity (B) and elasticity matrices (C). Annual = spring-summer * winter-spring * fall-winter * summer-fall. Population growth rate for annual matrix: 1.71. Greatest transition values in sensitivity and elasticity matrices appear in bold

A	Seedbank	Small	Large	Reproductive
Seedbank	0.073	0	0	250.337
Small	0.021	0.201	0.015	8.113
Large	0.003	0.031	0.021	0.212
Reproductive	0.006	0.074	0.119	0.223

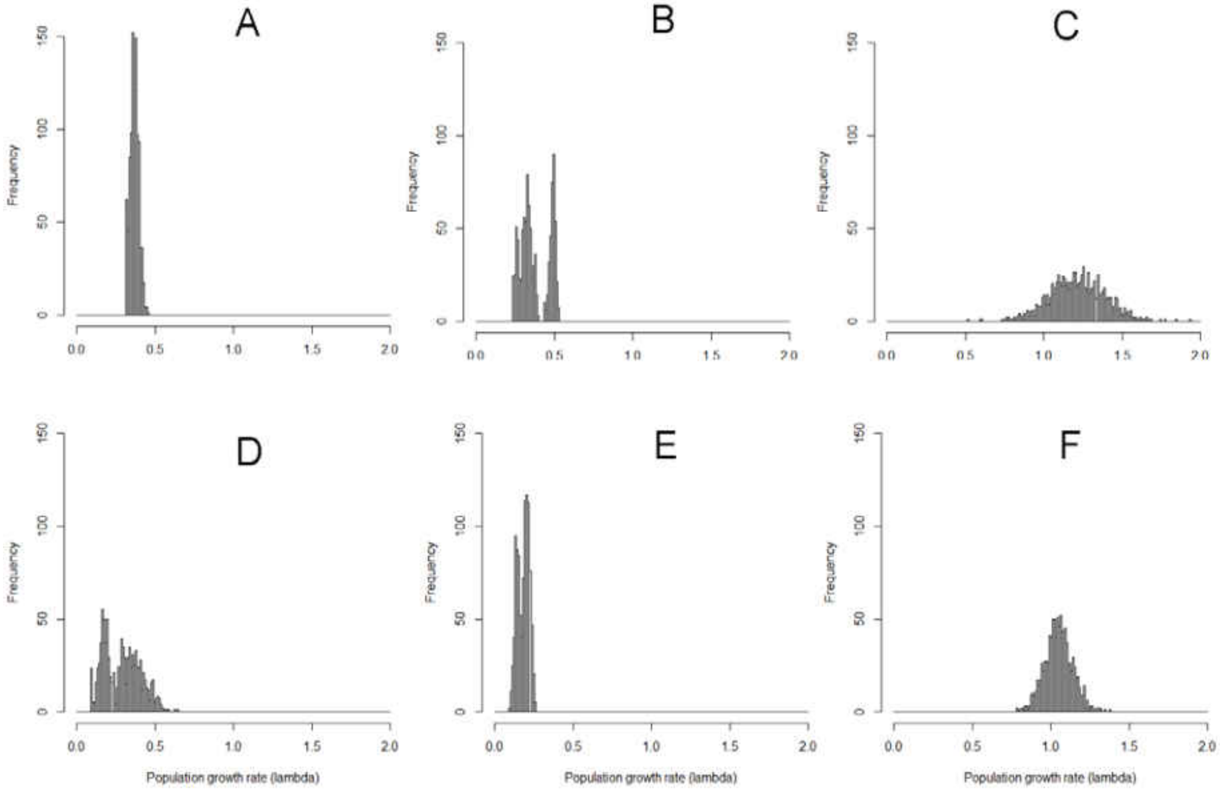
B	Seedbank	Small	Large	Reproductive
Seedbank	0.313	0.015	0.001	0.002
Small	**3.778**	0.185	0.013	0.025
Large	**5.276**	0.259	0.018	0.034
Reproductive	**74.304**	3.643	0.247	0.484

C	Seedbank	Small	Large	Reproductive
Seedbank	0.013	0	0	**0.299**
Small	0.046	0.022	<0.001	0.117
Large	0.008	0.005	<0.001	0.004
Reproductive	**0.245**	**0.159**	0.017	0.063

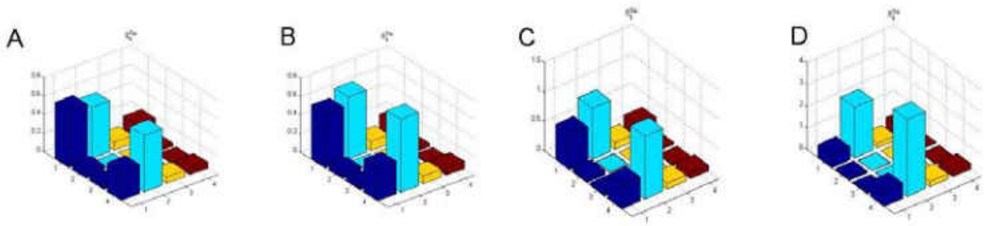
Appendix L. Population growth rate (λ) distributions from bootstrapped matrices (1000 iterations) for *C. fasciculata*. (A) intact habitat with shrub microsite, (B) intact habitat with litter microsite, (C) intact habitat with bare sand microsite, (D) degraded habitat with shrub microsite, (E) degraded habitat with litter microsite, (F) degraded habitat with bare sand microsite



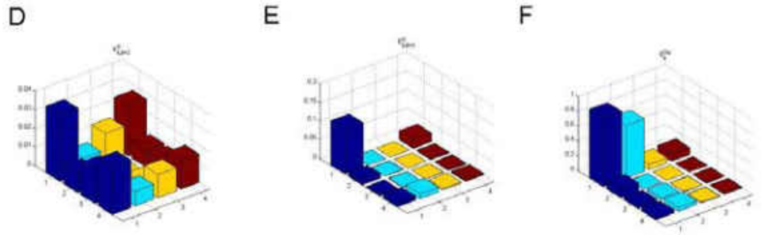
Appendix M. Population growth rate (λ) distributions from bootstrapped matrices (1000 iterations) for *B. angustifolia*. (A) intact habitat with shrub microsite, (B) intact habitat with litter microsite, (C) intact habitat with bare sand microsite, (D) degraded habitat with shrub microsite, (E) degraded habitat with litter microsite, (F) degraded habitat with bare sand microsite



Appendix N. Stochastic elasticity matrices for successional models of *C. fasciculata* using pooled habitat and microsite combinations with perturbation of each mean transition

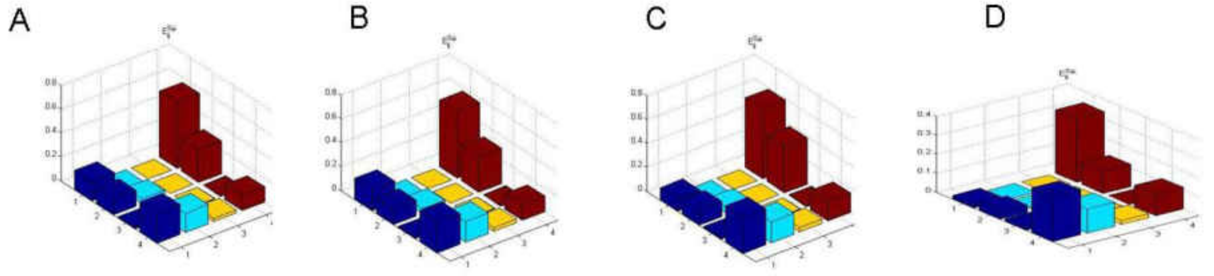


Null Seed density = 5 Seed density = 10 Seed density = 20



Degraded habitat Intact habitat Litter only microsite

Appendix O. Elasticity matrices for successional models of *B. angustifolia* using pooled habitat and microsite combinations with perturbation of each mean transition

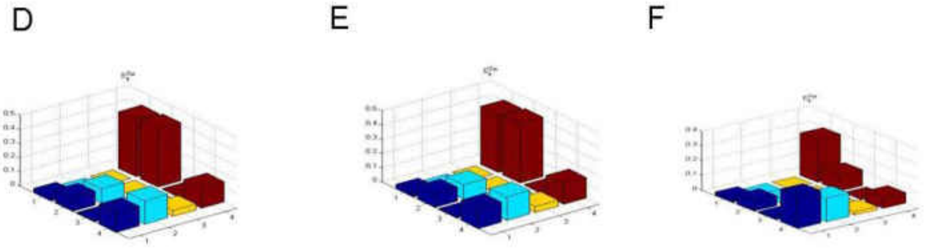


Null

Seed density = 5

Seed density = 10

Seed density = 20



Degraded habitat

Intact habitat

Bare sand microsite

CHAPTER FIVE: CONCLUSION

Contrasting responses to environmental factors provided insight into differing life-history patterns of co-existing species. In this dissertation, I provided evidence that habitat and microsite characteristics in Florida scrub influenced population dynamics of endemic and common native herbs through effects on seed removal, emergence, and establishment. I used manipulative (Chapters 2, 3), and observational demographic studies (Chapter 3), deterministic matrix modeling (Chapter 4), and stochastic models of hypothetical scenarios (Chapter 4) to explore these relationships. Idiosyncratic dynamics of target species in intact and degraded scrub revealed different ecological consequences of natural and anthropogenic disturbances. Studies of multiple habitat types (Ostfeld et al. 1997; Tallmon et al. 2003), along with a multi-species approach (Petrů and Menges 2003; Calabrese and Menges 2007; Menges 2007), should be used to generate well-founded predictions on potential success of introduced species assemblages in novel environments.

Chapters 2 and 3 offer information on variation of seed removal with habitat and microsite, as well as with species, seed predator, trial season, and seed density. Contrasting effects of disturbance on seed removal are likely related to which animal species consume the seeds, and how disturbance shapes their habitat conditions (Ostfeld et al. 1997; Tallmon et al. 2003; Schleuning et al. 2011; Torres et al. 2012). Invertebrate predators of small seeds (*Hypericum cumulicola*, *Paronychia chartacea*) may avoid open vegetation in degraded scrub, and may use low shrub cover and associated litter to hide from carnivorous predators (Restrepo and Vargas 1999; Weekley et al. 2008). Vertebrate seed predators of larger seeds may benefit from increased visibility in foraging due to decreased shrub cover in degraded scrub. Seed predator species may also frequent different microsites in different disturbance regimes, and may disproportionately forage in particular seasons (C. *fasciculata*, *B. angustifolia*). Habitats with more extensive degradation (Webb and Willson 1985), like abandoned pastures, may have a relatively greater effect on seed predators. Seed removal increased with seed density across all treatments (for seeds of *C. fasciculata* and *B. angustifolia*), which may be attributed to increased detection and foraging efficiency with more abundant seed sources (Bülow-Olsen 1984; Bullock 1989; Gorb and Gorb 2000; Brewer and Webb 2001; Montesinos et al. 2006; Pol et al. 2012).

Chapters 2, 3, and 4 present data indicating that emergence and establishment varied with habitat, microsite, and seed density. Some species had greater emergence or establishment in degraded habitat (*E. cuneifolium*, *C. fasciculata*), and others emerged more in intact habitat (*P. chartacea*). Particular species characteristics, such as the ability to fix nitrogen, may confer a competitive advantage over co-occurring species in the degraded scrub. Traits such as extensive root systems, strong relationships with soil microorganisms (e.g. soil crusts, Hawkes 2000), or great tolerance of allelopathic shrub exudates (e.g. *Ceratiola ericoides*, Weekly et al. 2008; Hunter and Menges 2002; Hewitt and Menges 2008) may enable other plants to compete better in intact scrub. Scrub herbs emerged and established most easily in bare sand away from shrubs (especially *P. chartacea*, *H. cumulicola*, *B. angustifolia*). Negative effects of shrubs on herb population growth may include competition for nutrients, water, or light, which would be more intense with shrubs than with smaller herbs or grasses found in open areas (Miller and Gorchov 2003; Schafer et al. 2010). Shrubs may attract herbivores or seed predators with shelter and protection (Weekley et al. 2008); however, my results show that seed predation is less under shrubs than in microsites without shrubs for some species. Positive effects of bare sand gaps on herbaceous population growth could include the presence of beneficial soil microorganisms that may be absent or less abundant under shrubs. Emergence and establishment increased with seed density for *C. fasciculata* and *B. angustifolia*.

Although certain types of anthropogenic disturbance may increase population growth of some herbs in the short term, such results must be interpreted with caution. Herb populations along firelanes can have shorter-lived individuals (Schafer et al. 2010) and greater population instability (Quintana-Ascencio et al. 2007). Longer term studies, as in the herb *Dicerandra frutescens* (13 years), have found negative population growth rates along firelanes and positive population growth rates in oak-hickory scrub (Menges et al. 2006). In areas undergoing restoration, it should be an ultimate goal to reestablish native species, not only in composition and abundance, but in population dynamics of individual species. Demographic studies of target species in both intact and degraded habitats can reveal relative contributions of individual life-history stages in different habitats. Species native to the target habitat with greater population growth rates in degraded conditions confer an advantage to restoration projects; they should require less time and resources to reintroduce. Herbs such as *C. fasciculata* that are easy to remove can be planted early in the restoration process to help exclude invasive grasses and herbs. Plantings of *C. fasciculata* could contribute to organic carbon accumulation in the soil and homogenize phosphorous distribution (depleting it in areas with many roots), as in other native pioneer legumes used in land restoration (Boldt et al. 2012). Then, as above and below ground structure is restored, the density of *C. fasciculata* plants would be reduced to levels in intact scrub.

My dissertation reveals that natural disturbances such as fire are not equivalent to anthropogenic disturbances such as roller chopping (Breininger and Schmalzer 1990; Schmalzer et al. 2002), which can severely disrupt below-ground root systems. Such disturbances can alter the composition and distribution of native species (Navarra and Quintana-Ascencio 2012), which may have serious ecological implications (David and Menges 2011; reviewed in Menges and Gordon 2010). Palmettos (*S. repens*, *S. etonia*), for example, are extremely restricted in their ability to recolonize scrub after mechanical disturbance (Breininger and Schmalzer 1990; Schmalzer et al. 2002). Therefore, anthropogenic degradation of scrub should not be rationalized by potential for transient herb population growth.

Microsite-specific demographic information about species used in restoration efforts is invaluable for determining where and when individual species should be introduced (either as seeds, or as transplants), and any other remedial measures that may be necessary to ensure establishment success (Dhillion 1999; Renison et al. 2005; Donath et al. 2007). Vertebrate exclosures are best employed for species with relatively larger seeds that are most vulnerable during the seed to germinant transition (*L. ohlingerae*, *E. cuneifolium*, *P. basiramia*). For those species most limited in emergence and seedling survival (*P. basiramia*, *H. cumulicola*), it could be more beneficial to transplant adult individuals reared in greenhouse or nursery conditions than to plant seeds (Dunn 1998; Koyama and Tsuyuzaki 2012). Finally, as each species is differently influenced by habitat and microsite conditions, efforts to increase environmental variation in areas slated for restoration will likely promote the establishment of multiple target species (Ruiz-Benito et al. 2012). Establishing patchy populations of native species with different life histories and growth habits (e.g. shrubs, herbs) should maximize structural heterogeneity and lead to greater biodiversity (Lindenmayer et al. 2012).

Experimental and observational data must be combined with ecological theory in both the planning and assessment of restoration activities (Maschinski and Wright 2006). Incorporating demographic and environmental variation into projections of introduced populations will decrease likelihood of restoration failure due to unexpected biological conditions. Proper foresight in conservation efforts minimizes loss of time and resources; this is particularly important for rare species with dwindling populations that have few propagules available for experiments. As human development continues to expand into new natural areas, the effects of anthropogenic disturbance will undoubtedly have an increasingly negative effect on native populations (Torres et al. 2011). Restoration of abandoned lands, such as those used for agriculture, ranching, and mining, can mitigate some negative consequences of human use and create conditions for reestablishment of certain native species (Martin and Wilsey 2006; DeFalco et al. 2012, Navarra and Quintana-Ascencio 2012; Scott and Morgan 2012). Comparative life-history and environmental data for these species will provide invaluable information for biologists and stewards of land acquired for conservation.

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