

**MICROHABITAT DISTRIBUTION AND DEMOGRAPHY OF TWO FLORIDA
SCRUB ENDEMIC PLANTS WITH COMPARISONS TO THEIR HABITAT-
GENERALIST CONGENERS**

A Dissertation

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ABSTRACT

I evaluated hypotheses regarding the nature of habitat specialization by comparing the microhabitat distribution and demography of *L. cernua* and *P. basiramia*, two Florida rosemary scrub habitat specialist species, with their habitat generalist congeners, *L. deckertii* and *P. robusta*. Specifically, I addressed the following two hypotheses: (1) that habitat specialist species may occur in a narrower range of microhabitat conditions than habitat generalist species, and (2) that demographic parameters of habitat specialist species may be more variable than those of their habitat generalist congeners. For each pair of congeners, I compared the microhabitat distributions, variation in vital rates and population growth rates, and extinction probabilities under different climate regimes to evaluate these hypotheses. Both rosemary scrub specialist species occurred in a narrower range of bare sand microhabitat conditions than their habitat generalist congeners. Rosemary scrub specialists were significantly more likely to occur in sites with high percentage bare sand, whereas microhabitats of generalists were more variable with respect to percentage bare sand. Recruitment and survival rates of both rosemary scrub specialist species were more temporally variable than those of their habitat generalist congeners; however, plant growth rates of rosemary scrub specialist species were less variable than those of their generalist congeners. Rosemary scrub specialist species also exhibited greater temporal variation in population growth rates than their habitat generalist congeners. Both rosemary scrub specialist species had higher probabilities of quasi-extinction than their generalist congeners under every climate modeling scenario. The narrower microhabitat requirements and greater temporal variability of demographic parameters of *L. cernua* and *P. basiramia* distinguish them from their habitat generalist

congeners. The restriction of *P. basiramia* and *L. cernua* to microhabitats with high percentage bare sand may limit their distribution to rosemary scrub habitat. Greater temporal variability in recruitment, survival, and population growth rates in *L. cernua* and *P. basiramia* may be associated with specialization on a narrower range of environmental conditions in these rosemary scrub specialist species. Greater temporal variability of demographic parameters in these rosemary scrub specialist species may make them more vulnerable to extinction than could be predicted solely from availability of suitable rosemary scrub habitat.

CHAPTER 1. INTRODUCTION

Ecologists have long recognized the phenomenon of rarity (Darwin 1872). Rare species are less abundant than other species; however, it is often not known why particular species are rare and others are common. Understanding rarity has become increasingly important in the context of the current rates of extinctions (Pimm *et al.* 1995, Pitman *et al.* 2002, Thomas *et al.* 2004b), especially because rarity is often a precursor to extinction (Darwin 1872). However, despite the recognized importance of understanding rarity, the mechanisms that regulate the relative abundance of species are often poorly understood (May 1999). In my dissertation, I address the following question, “do rare species have general ecological and demographic characteristics that may be linked to their rarity?” I approach this question by comparing the ecology and demography of two rare plant species with their more common congeners at sites where they co-occur in south-central Florida.

Rabinowitz *et al.* (1981) described seven different types of rarity, with respect to regional abundance, local population size, and habitat specificity. Regionally rare species have limited geographic distributions. Locally rare species have locally small population sizes and are never dominant members of any community in which they are found. Habitat specialist species can only persist in a small subset of habitat types. Different processes may regulate different forms of rarity. For example, biogeographic and evolutionary history may be most relevant to explaining patterns of global abundance; whereas ecological processes may be most important in determining patterns of local abundance and habitat specialization.

Habitat specialization is the most frequent type of rarity (Rabinowitz *et al.* 1986), and a variety of different mechanisms have been proposed to account for habitat specialization.

Regeneration niche specialization (Hubbell and Foster 1986), narrow physiological tolerance (Robson and Maze 1995), and poor competitive ability (Griggs 1940) are among the leading suggested causes of habitat specialization. Each instance of specialization may be caused by any of these factors alone, or in combination. Furthermore, specialization on a narrow set of environmental conditions can affect the variability of demographic parameters in response to variation in environment, although this relationship has been little studied.

Habitat specialization is a relative trait, and should be measured relative to other related species (Futuyma and Moreno 1988). Such ecological characteristics of species are best understood in the context of the evolutionary comparative method. Species cannot be treated as independent observations because they are related hierarchically according to a bifurcating phylogeny. One method of controlling for phylogenetic effects is to draw contrasts between pairs of species for which the most recent common ancestor is exclusive of all other pairs included in the study (Felsenstein 1985). Pairs of closely related species are ideal because they minimize spurious differences that could obscure the ecological pattern of interest (Moller and Birkhead 1992, Grafen and Ridley 1996). Finally, consideration of ecological criteria is also important in selecting appropriate species-pairs for comparison. For example, comparing species that co-occur in the same habitat minimizes the potentially misleading effects of contrasting ecological forces on differences in life history (Bevill and Louda 1999).

In my dissertation, I compared the microhabitat distribution and demography of two pairs of congeners, in the genera *Lechea* and *Polygonella*, which differ in their degree of habitat specialization. Each pair belongs to a unique family of plants, Cistaceae and Polygonaceae, respectively, thus the pairs are phylogenetically independent from one another. Additionally, the species in each pair are members of the same genus, thus they meet the criterion of close

phylogenetic relationship as described by Moller and Birkhead (1992). Finally, all four study species can be studied in the same ecological context, because they co-occur in the habitat of the specialist species.

Using this comparative method with a detailed demographic approach is a promising method to accelerate progress in the understanding of rarity (Bevill and Louda 1999). Schemske *et al.* (1994) advocate a comprehensive, demographic framework for individual rare plant species recovery efforts consisting of three steps: first collect detailed demographic data on all life history stages in order to generate population projection matrices, then identify the life history stages critical to population growth, and finally determine the underlying ecological causes of variation in critical life history stages. Using this detailed demographic approach in a comparative framework should promote not only a better understanding of why particular species are rare, but also may elucidate general ecological and demographic features of rarity.

In my dissertation, I compare some of the ecological and demographic characteristics of two habitat specialist species with those of their habitat generalist congeners to evaluate hypotheses regarding the nature of habitat specialization. Specifically, I address the hypothesis that habitat specialist species have narrower niche breadths than habitat generalist species by comparing their microhabitat distributions in habitat patches where they co-occur. Habitat refers to strong environmental discontinuities at large scales, greater than 10 m³ (Svenning 1999), whereas microhabitat is defined as the environmental conditions surrounding an individual (Menges *et al.* 1999). In addition, I evaluate the hypothesis that demographic parameters of habitat specialist species are more variable than those of their habitat generalist congeners. The importance of this type of comparative study to the understanding of habitat specialization has been widely recognized (Futuyma and Moreno 1988, Bevill and Louda 1999). To illuminate the

links between habitat specialization, niche breadth, and variability of demographic parameters, I compared the behavior of multiple pairs of related species that differ in their degree of habitat specialization using microhabitat distribution data and detailed demographic data collected over two years.

STUDY SYSTEM

I compared the ecology and demography of two congeneric pairs of species. All four species are short-lived, perennial, suffrutescent herbs (Wunderlin 1982). One member of each congeneric pair is a Florida scrub endemic. *Polygonella basiramia* (Small) Nesom and Bates is endemic to the Lake Wales Ridge and the Avon Park Bombing Range Ridge (Christman and Judd 1990). *Lechea cernua* Small occurs patchily throughout the Lake Wales Ridge and the scrubs of peninsular Florida (Christman and Judd 1990). Both of these endemic species are restricted predominantly to large white-sand gaps in Florida rosemary scrub (Christman and Judd 1990, Hawkes and Menges 1995, USFWS 1999). The other member of each pair is more widespread. *P. robusta* (Small) Nesom and Bates occurs in sandy habitats throughout Florida, and *L. deckertii* Small occurs in sandy habitats throughout Florida and southern Georgia (Wunderlin 1982). Both of these more widespread species also have more general habitat requirements, occurring in other sandy habitats such as scrubby flatwoods and sandhills, in addition to co-occurring in Florida rosemary scrub (Wunderlin 1982, Abrahamson *et al.* 1984, Menges and Salzman 1992).

Rosemary-phase sand pine scrub, or “Florida rosemary scrub,” is the preferred habitat of the habitat-specialist species in our study (Abrahamson *et al.* 1984, Myers 1990). Florida rosemary scrub is dominated by the shrub Florida rosemary, *Ceratiola ericoides*, which occurs in pure stands or intermixed with scrub oaks (*Quercus inopina*, *Q. chapmannii*, and *Q. geminata*)

and sand pines (*Pinus clausa*) (Abrahamson *et al.* 1984). This low-productivity ecosystem is located on nutrient-poor, excessively-drained, xeric white sands— Entisols of the St. Lucie or Archbold series (Abrahamson *et al.* 1984, Carter 1999). Rosemary scrub is patchily distributed throughout the surrounding landscape that contains habitats with less well-drained soils and greater shrub and herb cover (Abrahamson *et al.* 1984). Fire-return intervals in rosemary scrub average between 15-60 years (Menges 1999). *Ceratiola ericoides* is killed by fire and recovers via seedling establishment (Johnson and Abrahamson 1990). Most other shrubs in rosemary scrub, predominantly *Quercus* spp., recover rapidly from fire by resprouting (Abrahamson 1984b, Menges and Kohfeldt 1995, Schmalzer 2003). *Ceratiola ericoides* and *Quercus* spp. form the boundaries of bare sand gaps in rosemary scrub (Menges 1999). Periodic fires aid in maintaining open-structured habitat with large bare sand gaps that are distinguished from the surrounding shrub matrix by the lack of large *Ceratiola* shrubs, and lower levels of leaf litter and ground lichens (Menges 1999).

The species pairs and study system chosen for this dissertation are ideal for this type of comparative study. All four species occur sympatrically, in the same habitat patches, thus I can evaluate how the same forces affect their distribution and demography. Rosemary scrub habitat is discretely defined (Hermanson *et al.* in prep) from surrounding habitat patches, thus measurement of habitat attributes is straightforward. Additionally, the patchy nature of rosemary scrub habitat means that multiple populations of each species that are spatially separated from each other can be easily located and defined.

DISSERTATION STRUCTURE

In chapter two, I addressed the hypothesis that habitat-specialist species may be restricted to a narrower range of microhabitat conditions than habitat-generalist species. I compared the

microhabitat distributions of two rosemary scrub habitat specialists, *L. cernua* and *P. basiramia*, with those of their habitat generalist congeners, *L. deckertii* and *P. robusta*. I also analyzed microhabitats of all species in comparison to random points in rosemary scrub habitat to evaluate the importance of various microhabitat variables to the distribution of both specialist and generalist species in rosemary scrub habitat. Furthermore, I investigated the potential mechanisms behind differences in microhabitat utilization of habitat specialists and generalists with a series of experimental and observational studies. I compared seedling survival and growth of habitat specialists and generalists in contrasting microhabitats to determine whether the differences in seedling survival among contrasting microhabitats may explain the narrower microhabitat requirements of the rosemary scrub specialist species. I also characterized the abiotic properties of microhabitats, to determine whether soil temperature, soil nutrients, or soil moisture differed consistently across contrasting microhabitats in a way that could explain the restriction of the rosemary scrub specialists to particular microhabitat conditions.

In chapter three, I addressed the hypothesis that the vital rates and population growth rates of habitat specialist species are more variable than those of habitat generalist species. I compared the variation in vital rates and population growth rates of populations of two rosemary scrub specialist species, *L. cernua* and *P. basiramia* with their habitat-generalist congeners, *L. deckertii* and *P. robusta*. Annually over five years, I measured survival, growth, seed production, and recruitment in six populations of all four study species, including two populations in each of three time-since-fire categories. I evaluated the relative importance of time-since-fire and rainfall on various demographic parameters for each study species. Using these demographic data, I conducted matrix population analyses to estimate population growth rates for each population in each year and the mean and variance of stochastic population growth

rates for each species. In addition, I conducted population viability analyses under varying probabilistic weather and fire scenarios, to determine whether these habitat-specialist species are consistently more vulnerable to extinction than the generalist species.

CHAPTER 2. MICROHABITAT DISTRIBUTION OF TWO FLORIDA SCRUB ENDEMIC PLANTS IN COMPARISON TO THEIR HABITAT-GENERALIST CONGENERS*

INTRODUCTION

Habitat specialization is widely cited as a potential cause of rarity (Vivian 1967, Kruckeberg and Rabinowitz 1985, Hodgson 1986, Hubbell and Foster 1986, Buchele *et al.* 1989, Prober and Austin 1990) and species coexistence (Bazzaz 1991, Clark *et al.* 1993, Debski *et al.* 2002); however, the mechanistic basis of habitat specificity is often not well understood. Species that persist in only a small subset of habitat types within a given geographic area are considered habitat-specialists. Strong and consistent selection imposed by environmental conditions characteristic of the preferred habitat(s) is predicted to cause habitat specialization (Bazzaz 1991).

The key to understanding ecological phenomena such as habitat specialization depends on clarification of mechanisms behind observed distributions and identification of the scale at which these mechanisms function (Levin 1992). The definition of commonness and rarity is scale dependent (Schoener 1987); there are several different types of rarity defined by geographic regional abundance, local abundance, and habitat specificity (Rabinowitz 1981). Seemingly contradictory models describing patterns of abundance are compatible when the scales referred to in each model are considered (Collins and Glenn 1991). In certain cases, studies that focus on large spatial scales may be hampered by neglecting smaller scales, which often may be more relevant to mechanisms causing observed distributional patterns (Huston 1999).

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The difference between habitat and microhabitat is a difference of scale, and I argue that this distinction is critical to the elucidation of the mechanisms underlying the restriction of rare, habitat-specialist plants. Habitat generally refers to strong environmental discontinuities at large scales, greater than 10^3 m (Svenning 1999) and is usually characterized by the dominant plant forms or physical characteristics of the habitat (Ricklefs 1990). Microhabitat refers to environmental conditions that vary at small scales (Svenning 1999), and can be defined as the environmental conditions surrounding an individual (Menges *et al.* 1999).

Habitat generalists and habitat specialists are expected to differ in their response to variation in microhabitat. Generalists that can occupy several habitat types are predicted to exhibit little difference in performance among habitat types (Seamon and Adler 1996) and little specificity for particular microhabitats within a single habitat type (Brown and Pavlovic 1992). Conversely, the performance of specialists that are restricted to a single habitat may be dependent on particular microhabitat conditions that are characteristic of their preferred habitat (Rosenzweig 1981). Thus, the performance of habitat specialists may be differentially affected by contrasting microhabitat types within a habitat (Griffith 1996, Hilton and Boyd 1996, Menges and Kimmich 1996, Kephart and Paladino 1997, Dinsdale *et al.* 2000, Wolf 2001, Bruno 2002, Colling *et al.* 2002).

A variety of mechanisms have been proposed as causes of habitat specialization. Regeneration niche specialization (Hubbell and Foster 1986), narrow physiological tolerance (Robson and Maze 1995), and poor competitive ability (Griggs 1940) are among the leading suggested causes of habitat specialization. Each instance of specialization may be caused by any of these factors alone, or in combination; however, specialization should be measured relative to other related species (Futuyma and Moreno 1988).

Comparison of congeneric rare and common species can be a useful approach to understanding rarity (Bevill and Louda 1999) and ecological specialization (Futuyma and Moreno 1988). Such comparisons may provide insights into the relative importance of various ecological factors that affect population persistence (Fiedler 1987, Prober 1992, Byers and Meagher 1997, Menges *et al.* 1999). The comparison of close relatives minimizes the chance that observed differences may be artifacts of phylogenetic inertia. However, consideration of ecological criteria, such as preferred habitat types of each species, is also important in selecting appropriate species-pairs for comparison because it minimizes the potentially misleading effects of contrasting ecological forces on differences in life history (Bevill and Louda 1999). In this study, I compare congeners that occur sympatrically, in at least some of the same habitat patches. Specifically, I compare the microhabitat utilization of two habitat-specialist species with their habitat-generalist congeners, in the habitat where they co-occur.

I tested the hypothesis that habitat-specialists occur in a narrower range of microhabitat conditions within a habitat than species that occur in a larger number of habitats. I compared microhabitats of two rare species that are restricted predominantly to Florida rosemary scrub habitat with congeners that co-occur in rosemary scrub but also commonly occur in other habitats. I also analyzed microhabitats of all species in comparison to random points in rosemary scrub habitat to evaluate the importance of various microhabitat variables to the distribution of both specialist and generalist species in rosemary scrub habitat. In addition, I investigated the potential mechanisms behind differences in microhabitat utilization of habitat specialists and generalists with a series of experimental and observational studies. I compared seedling survival and growth of habitat specialists and generalists in contrasting microhabitats, testing the hypothesis habitat specialists have a more narrow regeneration niche than habitat generalists. I

also characterized the abiotic properties of microhabitats, to determine whether soil temperature, soil nutrients, and soil moisture differed consistently across contrasting microhabitats in a way that could explain narrower physiological tolerance of habitat specialists to particular microhabitat conditions than habitat generalists.

MATERIALS AND METHODS

Study Species

I characterized the microhabitat preferences of two congeneric pairs of species. All four species are short-lived, perennial, suffrutescent herbs (Wunderlin 1982). One member of each congeneric pair is a Florida scrub endemic. *Polygonella basiramia* (Small) Nesom and Bates is endemic to the Lake Wales Ridge and the Avon Park Bombing Range Ridge (Christman and Judd 1990). *Lechea cernua* Small occurs patchily throughout the Lake Wales Ridge and the scrubs of peninsular Florida (Christman and Judd 1990). Both of these endemic species are restricted predominantly to large white-sand gaps in Florida rosemary scrub (Christman and Judd 1990, Hawkes and Menges 1995, Anonymous 1999). The other member of each pair is more widespread. *P. robusta* (Small) Nesom and Bates occurs in sandy habitats throughout Florida, and *L. deckertii* Small occurs in sandy habitats throughout Florida and southern Georgia (Wunderlin 1982). Both of these more widespread species also have more general habitat requirements, occurring in other sandy habitats, such as scrubby flatwoods and sandhills, in addition to co-occurring in Florida rosemary scrub (Wunderlin 1982, Abrahamson *et al.* 1984).

Study Site

This study was conducted at Archbold Biological Station (ABS), a 2000-ha private biological station located in Highlands County, Florida. Annual rainfall exceeds 1200 mm, with the majority falling June through September due to convective thunderstorms and tropical storm

systems (Abrahamson *et al.* 1984, Menges 1999). A variety of habitats are found at ABS, including approximately 36 ha of rosemary-phase sand pine scrub, or “Florida rosemary scrub,” the preferred habitat of the habitat-specialist species in our study (Abrahamson *et al.* 1984). Florida rosemary scrub is dominated by the shrub Florida rosemary, *Ceratiola ericoides*, which occurs in pure stands or intermixed with scrub oaks (*Quercus inopina*, *Q. chapmannii*, and *Q. geminata*) and sand pines (*Pinus clausa*) (Abrahamson *et al.* 1984). This low-productivity ecosystem is located on nutrient-poor, excessively-drained, xeric white sands— Entisols of the St. Lucie or Archbold series (Abrahamson *et al.* 1984, Carter 1999). Fire-return intervals in rosemary scrub average between 15-60 years (Menges 1999). *Ceratiola ericoides* is killed by fire and recovers via seedling establishment (Johnson and Abrahamson 1990). Most other shrubs in rosemary scrub, predominantly *Quercus* spp., recover rapidly from fire by resprouting (Abrahamson 1984b, Schmalzer 2003). *Ceratiola ericoides* and *Quercus* spp. form the boundaries of bare sand gaps in rosemary scrub (Menges 1999). Periodic fires aid in maintaining open-structured habitat with large bare sand gaps that are distinguished from the surrounding shrub matrix by the lack of large *Ceratiola* shrubs, and lower levels of leaf litter and ground lichens (Menges 1999). Several herbaceous plants are specialized on these bare sand gaps (Menges and Kimmich 1996, Quintana-Ascencio and Morales-Hernandez 1997, Menges and Hawkes 1998, Petru and Menges 2003).

Microhabitat Characterization

I characterized the microhabitats surrounding individual plants of each species relative to randomly chosen points within rosemary scrub. I measured microhabitat variables for randomly selected plants from each of six populations of *L. cernua* (n=551), *L. deckertii* (n=536), and *P. basiramia* (n=523), and each of five populations of *P. robusta* (n=369). For *L. cernua*, *L.*

deckertii, and *P. basiramia*, two populations were selected from rosemary scrub patches in each of three time-since-fire classes: recently burned (<5 years), intermediate-aged (12-15 years), and long-unburned (>25 years). For *P. robusta*, two populations were selected in each of the intermediate-aged and long-unburned time-since-fire classes, but only one population in the recently-burned class was included in this study. In most cases the same rosemary scrub patch contained all or most of the study species. Nine sites were used in this study— three sites in each of the three time-since-fire classes. At each of these nine sites, I also randomly selected 50 points within regions of the rosemary scrub patch that contained plants of at least one of the study species. I compared the microhabitats of random points in rosemary scrub habitat of the three time-since-fire classes to determine how microhabitat characteristics change with time-since-fire.

Microhabitat was defined as the area within a circular quadrat of 27 cm radius (area of 0.229 m²) centered on the randomly selected plant or point. For each plant or point, I visually estimated the percent cover of open sand to the nearest 10 percent and measured the maximum height to the nearest 10 cm of the nearest shrub greater than 50 cm in height. I also measured the distance to the nearest 10 cm from the nearest *Ceratiola* and *Quercus* spp. greater than 50 cm in height.

Seedling Experiment

I conducted an experiment in which I manipulated the lichen and litter microhabitats of naturally established seedlings of all four species. I located naturally established seedlings of all four study species in two rosemary scrub habitat patches; *L. cernua* and *L. deckertii* seedlings were found together in one patch, and *P. basiramia* and *P. robusta* were found together in the other. In the first week of June 2002, I randomly selected 50 seedlings of each species, and measured

initial height for each seedling. Initial heights of seedlings ranged from 2-5 cm. I then randomly assigned 25 seedlings of each species to each of two different microhabitat treatments. A bare sand treatment was applied by removing all lichens and litter in a 25 cm radius around a target seedling, and a lichen and litter treatment was applied by adding lichens and litter to attain 100 % coverage and 1-2 cm depth in a 25 cm radius around a target seedling. At the beginning of November 2002, I measured final height, crown diameter, and crown width (the horizontal distance perpendicular to crown diameter). I estimated final size by calculating volume of an inverted cone (tapering from maximum diameter at the top of plant to a point) using these measured variables.

Physical Characterization of Microhabitats

I characterized the physical properties of contrasting microhabitats with a series of both experimental and observational studies. I conducted a soil temperature experiment to determine the effect of lichen and litter cover and distance from nearest *Ceratiola* on soil temperature. I also conducted soil nutrient and soil moisture studies to determine how levels of soil carbon, soil nitrogen, and soil moisture differed with respect to microhabitat and time-since-fire.

During a seven-day period in the end of October 2002, I measured soil temperature at fifteen-minute intervals in four different microhabitat treatments within rosemary scrub habitat using portable HOBO dataloggers with internal temperature sensors (ONSET Computer Corporation, Pocasset, Massachusetts, USA). I designed microhabitat treatments as a factorial combination of the lichen and litter treatment and distance from *Ceratiola*. I created two levels of the lichen and litter treatment (lichens and litter added in 100 % coverage and 1-2 cm depth vs. lichens and litter removed to expose 100% bare sand), and two levels of distance to nearest *Ceratiola* (under the dripline on the N side of a *Ceratiola* >50 cm tall vs. greater than 2 m from

any *Ceratiola* >50 cm tall). For each of the four different microhabitat treatments, I used one datalogger in each of five replicate microhabitat treatment locations to measure soil temperatures. I placed sensors 0.5 cm below the soil surface, and replaced lichens and litter to 100% cover on top of the buried sensors for those treatments with lichen and litter cover. To determine the effects of each treatment on soil temperature, I compared means of the absolute maximum temperature and absolute minimum temperature for each treatment during the seven-day period.

In February 2003, I collected soil samples from four different microhabitats and two different levels of time-since-fire and sent subsamples to Oregon State University's Central Analytical Laboratory to be measured for total % C and % N using a Leco CNS-2000 Macro Analyzer. I collected samples from two sites each in two different time-since-fire categories: long-unburned (>30 years since last fire) and recently burned (<2 years since last fire). At long-unburned sites, I sampled three replicates each of four different microhabitat types. I defined four microhabitat types: 1) >90 % bare sand, >2 m from any *Ceratiola* >50 cm, and > 1 m from any *Quercus* >50 cm, 2) >90 % lichen and litter cover, >2 m from any *Ceratiola* >50 cm, and > 1 m from any *Quercus* >50 cm, 3) under the dripline of a *Ceratiola* >50 cm tall, and 4) under the dripline of a *Quercus* >50 cm tall. At the recently burned sites, I only was able to locate and sample microhabitat types 1 and 4. At each site, I randomly sampled three replicates for each microhabitat type. For each microhabitat sampling location, I removed two soil samples 7 cm in diameter by 5 cm deep which were then combined and homogenized. One 5 g subsample was removed from each sample, and subsamples were packaged in Ziploc bags and sent to OSU for analysis within 24 hours of collection.

In May 2003, I measured soil moisture gravimetrically with soil samples collected from four different microhabitats and two different levels of time-since-fire. I collected samples from the same sites, in the same time-since-fire categories, and using the same microhabitat type definitions described above. At each site, I randomly sampled five replicates for each microhabitat type. For each microhabitat sampling location, I removed and combined two soil samples 7 cm in diameter by 5 cm deep. I weighed the samples immediately after collection, then dried them for 24 hours at 37 °C and weighed them again. I calculated soil moisture as percentage of dry weight.

Data Analysis

All data were analyzed using The SAS System for Windows, Version 8.02 (Copyright 1999-2001 by SAS Institute Inc., Cary, North Carolina, USA). Microhabitat data were not normally distributed and could not be transformed to normality. I summarized the frequencies of plants and random points for each level of each microhabitat variable and generated cumulative percent frequency distributions. I conducted Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1995) of pairs of distributions of each microhabitat variable. For each congeneric pair, I compared the distributions of each species and compared each species with random points. For the random point data only, I conducted Kruskal-Wallis tests (PROC NPAR1WAY) for mean differences between each pair of the three time-since-fire categories. In both the Kolmogorov-Smirnov and the Kruskal-Wallis tests, I adjusted α for the three comparisons made by using the Bonferroni correction, resulting in $\alpha = 0.017$. Seedling survival data were analyzed by species using logistic regression (PROC LOGISTIC) with microhabitat treatment and initial height as explanatory variables. Seedling size data were normally distributed, and I compared treatment means of final seedling size by species with ANOVA using general linear models (PROC GLM).

Soil temperature, soil carbon, and soil moisture data were also normally distributed; therefore I compared means with ANOVA using general linear models (PROC GLM), and tested for differences among multiple means using the Tukey-Kramer adjustment.

RESULTS

Microhabitat Effects on Plant Distribution

Rosemary scrub specialists, *L. cernua*, and *P. basiramia* occurred in microhabitats with significantly more bare sand than their habitat generalist congeners and more than twice the cover of bare sand as random points (mean = 82% for *L. cernua*, 85 % for *P. basiramia*, 54% for *L. deckertii*, 47% for *P. robusta*, 38% for random points). For both rosemary scrub specialists, over 70% of all individuals sampled occurred in microhabitats with ≥ 80 % bare sand (73% for *L. cernua* and 80 % for *P. basiramia*), whereas only 36% of *L. deckertii* individuals and 29% of *P. robusta* individuals occurred with ≥ 80 % bare sand (Figs. 2.1A and 2.1B). The distributions of the generalist congeners are not as skewed towards the highest levels of bare sand as are those of the rosemary scrub specialists (Figs. 2.1A and 2.1B, Table 2.1). The striking restriction of the rosemary scrub specialists predominantly to microhabitats with ≥ 80 % bare sand can also be illustrated by their relatively small coefficients of variation for percent bare sand (CV= 27.9 for *L. cernua*; CV= 24.7 for *P. basiramia*). The coefficients of variation for percent bare sand of the habitat generalist congeners are much higher (CV= 59.8 for *L. deckertii*; CV= 72.6 for *P. robusta*).

Plants of all four species were farther from *Ceratiola* than random points, but rosemary scrub specialists, *L. cernua* and *P. basiramia*, were not consistently farther from *Ceratiola* than their generalist congeners. *L. deckertii* was less likely than random points to occur within 320 cm of *Ceratiola*, followed by *L. cernua*, (less likely within 210 cm), *P. basiramia* (less likely

within 180 cm), and *P. robusta* (less likely within 110 cm) (Figs. 2.1C and 2.1D). Fewer plants of *P. basiramia* occurred near *Ceratiola* than plants of *P. robusta* (Fig. 2.1D), but distance from *Ceratiola* did not differentially affect the distributions of *L. cernua* and its generalist congener (Fig. 2.1C).

Three of four species (*L. cernua*, *P. basiramia*, and *P. robusta*) occurred less frequently near *Quercus* than random points, but the rosemary scrub specialists were not consistently farther from *Quercus* than the habitat generalists. *L. cernua* was less likely than random points to occur within 180 cm of *Quercus*, followed by *P. robusta* (less likely within 170 cm), and *P. basiramia* (less likely within 130 cm) (Figs. 2.1E and 2.1F). Fewer plants of *L. cernua* occurred near *Quercus* than plants of *L. deckertii* (Fig. 2.1E), but distance from *Quercus* did not differentially affect the distributions of *P. basiramia* and its generalist congener (Fig. 2.1F).

Nearest shrub height was not correlated with the distributions of any of the four species. The nearest neighboring shrubs of the rosemary scrub specialist, *Lechea cernua*, were slightly shorter than those of its generalist congener (mean = 82 cm for *L. cernua*, 86 cm for *L. deckertii*), but neighboring shrub height did not differentially affect the distributions of *P. basiramia* and its generalist congener (Table 2.1). *L. cernua*, *L. deckertii*, and *P. basiramia*, did not occur near shorter shrubs than those near random points; however, nearest neighboring shrubs of the habitat generalist, *P. robusta*, were somewhat shorter than those near random points (mean = 84 cm for *P. basiramia*, 76 cm for *P. robusta*, 87 cm for random points) (Table 2.1).

Microhabitat Effects on Seedlings

Although bare sand was an important determinant of the distributions of the rosemary scrub specialists, and the habitat generalists to a lesser degree, seedlings were not consistently affected by soil surface microhabitat treatments. Seedling survival was not affected by the soil

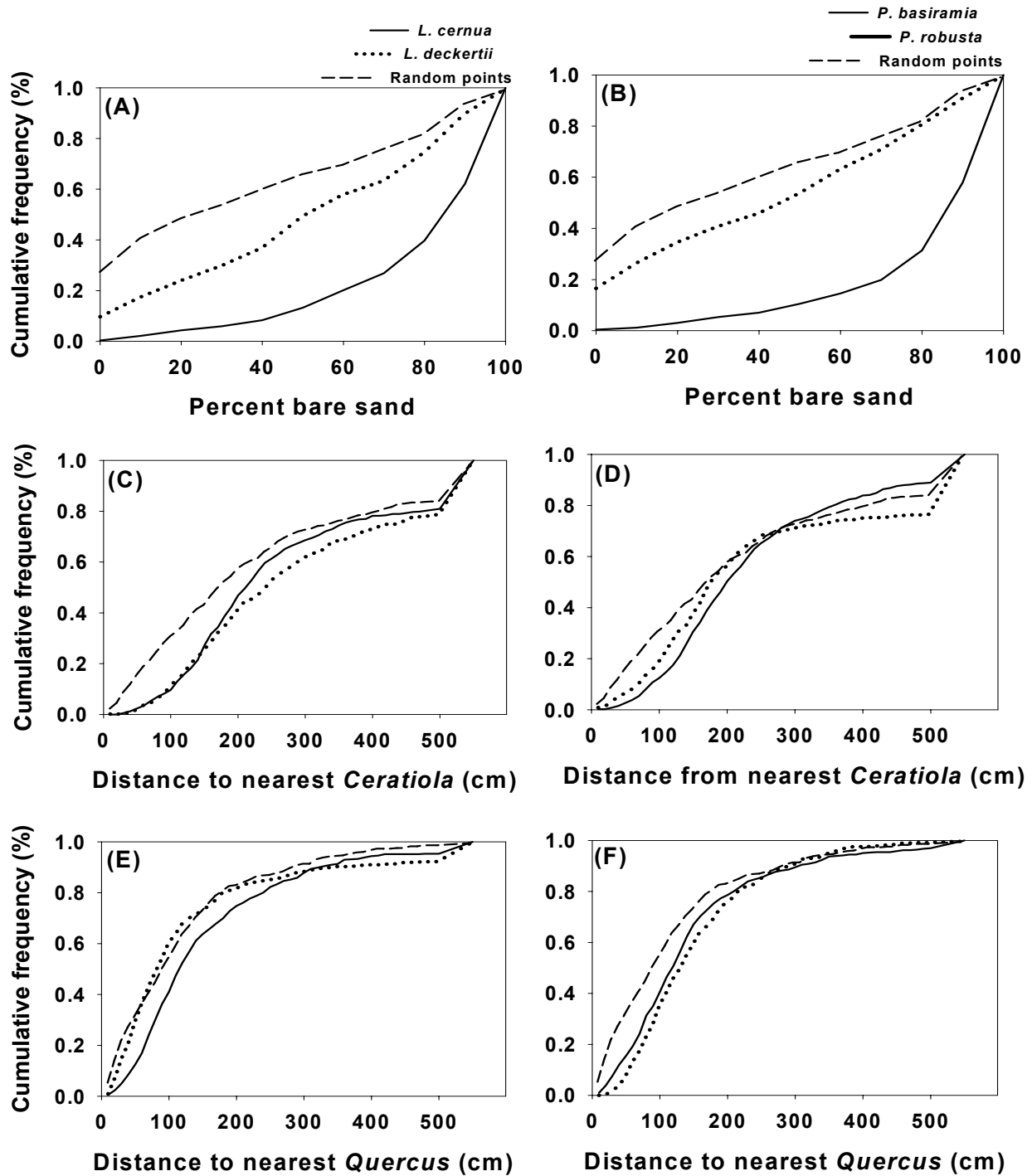


Figure 2.1. Cumulative frequency distributions of (A, C, and E) both *Lechea* species and (B, D, and F) both *Polygonella* species compared to random points in rosemary scrub habitat for three microhabitat variables: (A and B) percent bare sand, (C and D) distance to nearest *Ceratiola*, and (E and F) distance to nearest *Quercus* spp. Data for habitat specialists, *L. cernua*, and *P. basiramia*, are depicted with solid lines, generalists, *L. deckertii* and *P. robusta*, with dotted lines, and random points with dashed lines. Kolmogorov-Smirnov tests are shown in Table 2.1.

Table 2.1. Results of Kolmogorov-Smirnov tests between pairs of cumulative frequency distributions of four microhabitat variables. Distributions that are significantly different at $p=0.017$ are designated with asterisks. Cumulative frequency distributions are shown in Fig. 2.1 for all variables except height of nearest shrub.

Microhabitat variable	Comparison	D_{\max}	$D_{\max} > D_{\alpha}$
Percent bare sand	<i>L. cernua</i> x random points	0.533	*
	<i>L. deckertii</i> x random points	0.250	*
	<i>L. cernua</i> x <i>L. deckertii</i>	0.381	*
	<i>P. basiramia</i> x random points	0.567	*
	<i>P. robusta</i> x random points	0.148	*
	<i>P. basiramia</i> x <i>P. robusta</i>	0.511	*
Distance from nearest <i>Ceratiola</i>	<i>L. cernua</i> x random points	0.216	*
	<i>L. deckertii</i> x random points	0.203	*
	<i>L. cernua</i> x <i>L. deckertii</i>	0.101	*
	<i>P. basiramia</i> x random points	0.188	*
	<i>P. robusta</i> x random points	0.128	*
	<i>P. basiramia</i> x <i>P. robusta</i>	0.120	*
Distance from nearest <i>Quercus</i>	<i>L. cernua</i> x random points	0.196	*
	<i>L. deckertii</i> x random points	0.072	
	<i>L. cernua</i> x <i>L. deckertii</i>	0.197	*
	<i>P. basiramia</i> x random points	0.172	*
	<i>P. robusta</i> x random points	0.240	*
	<i>P. basiramia</i> x <i>P. robusta</i>	0.083	
Height of nearest shrub	<i>L. cernua</i> x random points	0.064	
	<i>L. deckertii</i> x random points	0.056	
	<i>L. cernua</i> x <i>L. deckertii</i>	0.113	*
	<i>P. basiramia</i> x random points	0.052	
	<i>P. robusta</i> x random points	0.138	*
	<i>P. basiramia</i> x <i>P. robusta</i>	0.097	

surface microhabitat treatment for three out of four species (Fig. 2.2, Table 2.2); however, for *P. basiramia*, seedling survival was higher in lichen and litter covered microhabitats than bare sand microhabitats (Fig. 2.2C, Table 2.2). Final seedling size was not affected by the soil surface microhabitat treatment for *L. deckertii* and *P. robusta*; however, final seedling size was greater in bare sand microhabitats than in lichen and litter covered microhabitats for the two specialists, *L. cernua* and *P. basiramia* (Fig. 2.3, Table 2.3). This difference was significant ($p < 0.05$) for *L. cernua* (Fig. 2.3A, Table 2.3), and marginally significant ($p < 0.1$) for *P. basiramia* (Fig. 2.3C, Table 2.3).

Microhabitat and Time-since-fire

Microhabitat characteristics for random points in rosemary scrub habitat change with time-since-fire. As time-since-fire increases, percent cover of bare sand decreases (Fig. 2.4A), density of *Ceratiola* increases, (as measured by shorter distance to nearest *Ceratiola*), (Fig. 2.4B), density of *Quercus* does not change (Fig. 2.4C), and neighboring shrub heights increase (Fig. 2.4D).

Soil temperatures were affected by microhabitat. Bare sand microhabitats had significantly lower minimum temperatures than lichen and litter covered microhabitats, but maximum temperatures were similar with respect to sand surface treatment (Fig. 2.5A, Table 2.4).

Microhabitats greater than 2 m from the nearest *Ceratiola* had higher maximum temperatures than microhabitats under the dripline of *Ceratiola*, but similar minimum temperatures (Fig. 2.5B, Table 2.4). I found no significant interactions between sand surface treatment and distance from *Ceratiola*; therefore, I present models with main effects only (Table 2.4).

Physical Characteristics of Microhabitats

Percent soil carbon was lowest in bare sand microhabitats, but similar among other types of microhabitats (Fig. 2.5C). There was no difference in soil carbon with respect to time-since-fire

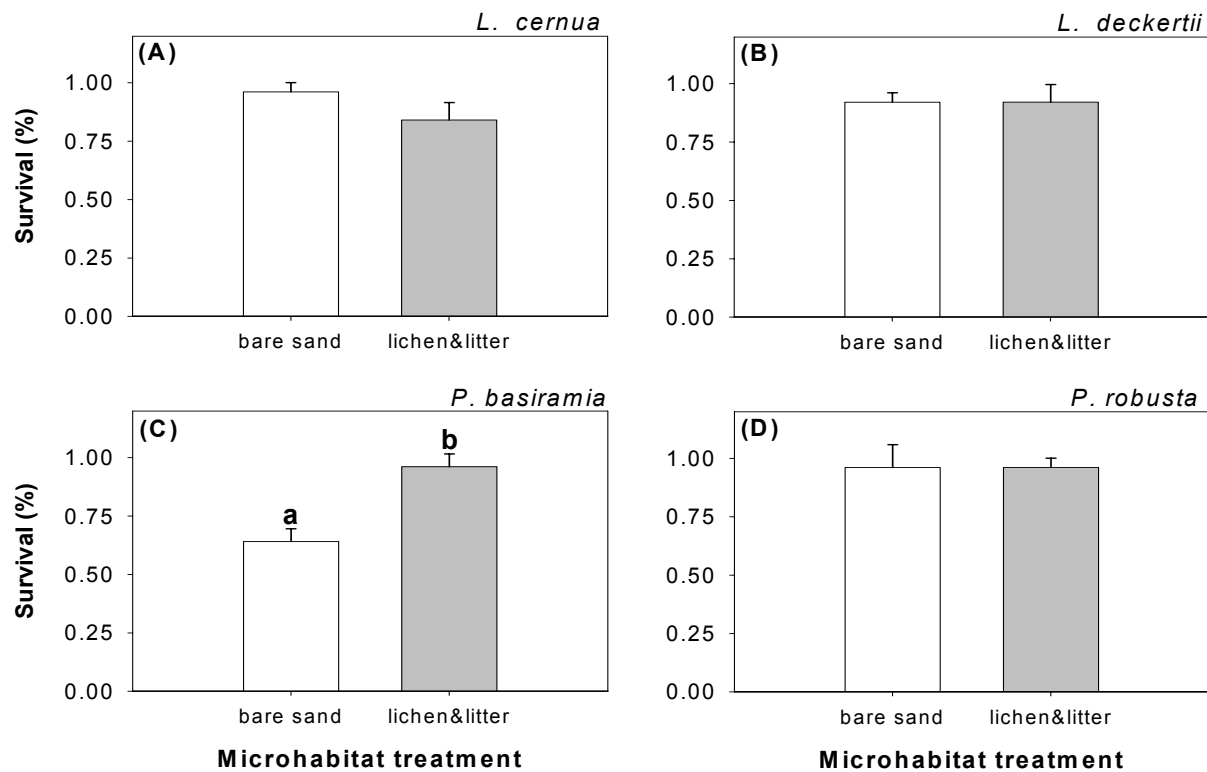


Figure 2.2. Means and standard errors of percent survival of (A) *L. cernua*, (B) *L. deckertii*, (C) *P. basiramia*, and (D) *P. robusta* in manipulated soil surface treatments (bare sand vs. lichens and litter added to 100% coverage). Significant differences at $p < 0.05$ are designated with different letters. Results of logistic regression analyses are shown in Table 2.2.

Table 2.2. Results of logistic regressions conducted to examine the effects of soil surface microhabitat treatment (bare sand vs. lichen and litter covered) on survival of seedlings. Initial seedling height is included as a covariate to control for its effect. Means of survival for each species by microhabitat treatment are shown in Fig. 2.2.

Species	Source	n	Wald χ^2	Df	p
<i>L. cernua</i>	Microhabitat	50	1.8141	1	0.1780
	Initial height		0.3945	1	0.5299
<i>L. deckertii</i>	Microhabitat	50	0.0002	1	0.9891
	Initial height		0.2827	1	0.5950
<i>P. basiramia</i>	Microhabitat	50	5.5717	1	0.0183
	Initial height		0.0360	1	0.8494
<i>P. robusta</i>	Microhabitat	50	0.0006	1	0.9799
	Initial height		1.3984	1	0.2370

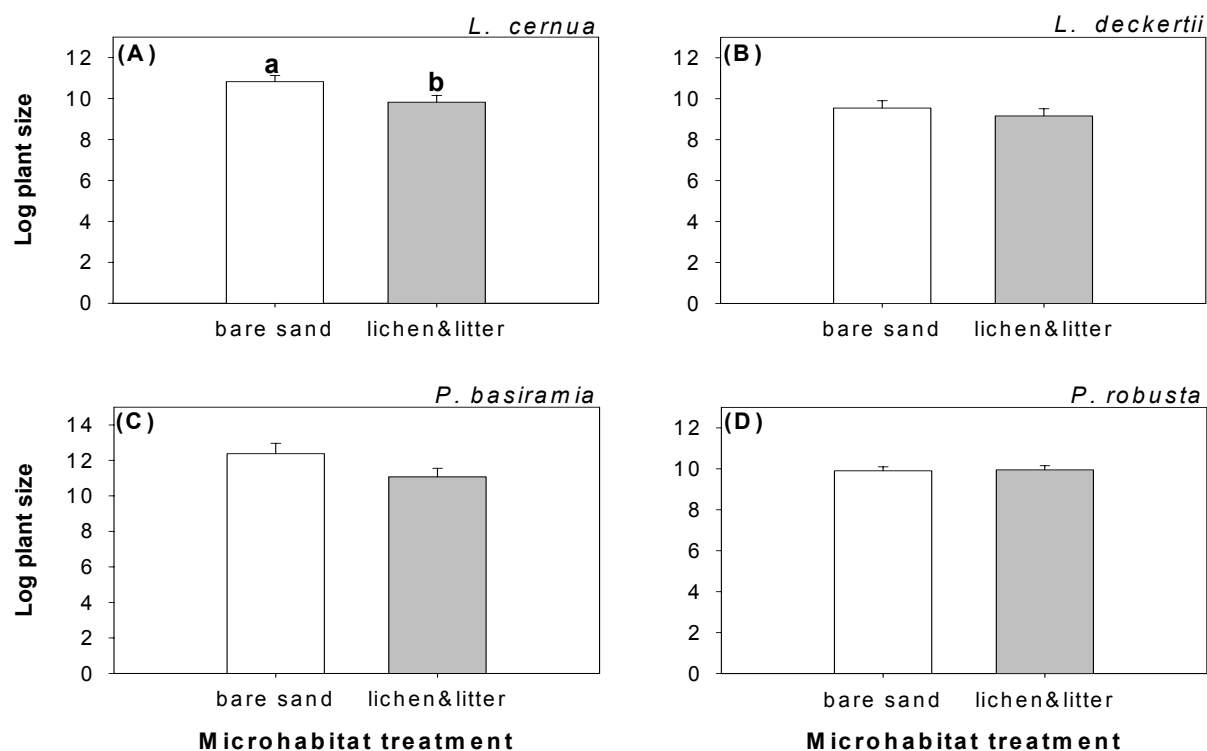


Figure 2.3. Final size of (A) *L. cernua*, (B) *L. deckertii*, (C) *P. basiramia*, and (D) *P. robusta* seedlings in manipulated soil surface treatments (bare sand vs. lichens and litter added to 100% coverage). Least squares means of final size (measured as natural log-transformed volume of an inverted cone) that were adjusted for effects of initial height are shown with standard errors. Means that are significantly different at $p < 0.05$ are designated with different letters. Results of ANOVAs are shown in Table 2.3.

Table 2.3. Results of ANOVAs conducted to examine the effects of soil surface microhabitat treatment (bare sand vs. lichen and litter covered) on final size (measured as volume of an inverted cone). Initial seedling height is included as a covariate to control for its effect. Least squares means of final size adjusted for effects of initial height are shown in Fig. 2.3.

Species	Source	F	df	p
<i>L. cernua</i>	Microhabitat	4.87	1, 42	0.0328
	Initial height	10.30	1, 42	0.0026
<i>L. deckertii</i>	Microhabitat	0.61	1, 43	0.4395
	Initial height	3.08	1, 43	0.0862
<i>P. basiramia</i>	Microhabitat	2.93	1, 37	0.0951
	Initial height	4.41	1, 37	0.0426
<i>P. robusta</i>	Microhabitat	0.03	1, 45	0.8667
	Initial height	35.81	1, 45	<.0001

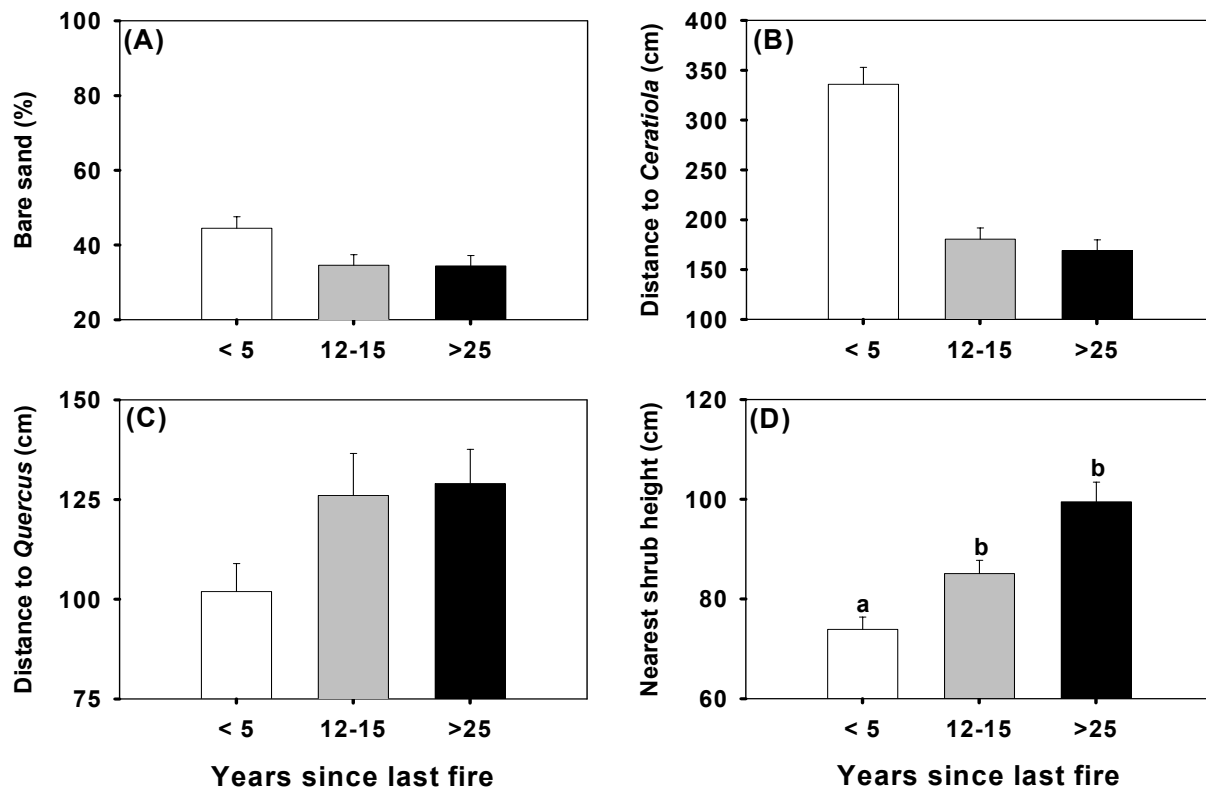


Figure 2.4. Means and standard errors of four microhabitat variables, (A) percent cover of bare sand, (B) distance to nearest *Ceratiola*, (C) distance to nearest *Quercus* spp., and (D) height of nearest shrub, for random points in rosemary scrub habitat patches of three different postfire age classes. Bars with the same letter within a panel are not significantly different at $p < 0.017$ (Kruskal-Wallis).

(Fig. 2.5D). I found no significant interactions between microhabitat and time-since-fire; therefore, I present models with main effects only (Table 2.4). Total soil nitrogen was highly correlated with soil carbon ($r = 0.892$, $p = < 0.0001$), and the effects of microhabitat and

time-since-fire on soil nitrogen were similar to their effects on soil carbon and are not shown. Total soil nitrogen in all samples was low (overall mean = 0.02%).

Soil moisture levels were lower near *Ceratiola* than the other microhabitats, which were similar (Fig 2.5E, Table 2.4). Time-since-fire did not affect soil moisture levels (Fig. 2.5F, Table 2.4). I found no significant interactions between microhabitat and time-since-fire; therefore, I present models with main effects only (Table 2.4).

DISCUSSION

Percent cover of bare sand most consistently differed between the rosemary scrub specialists and the habitat generalists, for both congeneric pairs. Although percent bare sand was correlated with the distribution of all species, the rosemary scrub specialists were significantly more likely to occur in sites with high percentage bare sand, whereas microhabitats of generalists were more variable with respect to percent bare sand. These results are consistent with the results of Hawkes and Menges (1996), who found that the densities of *L. cernua* and *P. basiramia* were higher in patches with greater percent bare sand. Two additional rosemary scrub specialist species, *Hypericum cumulicola* and *Eryngium cuneifolium* had higher survival in microhabitats with less ground lichen and litter cover (Menges and Kimmich 1996, Quintana-Ascencio and Morales-Hernandez 1997). Other studies have also found that characteristics of microhabitat, such as bare ground and soil texture, are critical requirements for the occurrence of particular locally rare species. In a study of microhabitat requirements for seedling establishment in old fields, Gross and Werner (1982) found that two old field species could establish only in 1-year-old fields where bare ground was abundant, and were not present in 15-year-old fields where bare ground patches were rare. In a microhabitat manipulation study, Bruno (2002) found that

Figure 2.5. Means and standard errors of, (A) and (B) soil temperature, (C) and (D) percent soil carbon, and (E) and (F) percent soil moisture, with respect to microhabitat and/or time-since-fire. For the soil temperature study, there were two levels of the soil surface cover treatment (lichens and litter added vs. bare sand) and two levels of distance from nearest *Ceratiola* (near *Ceratiola* vs. > 2 m from nearest *Ceratiola*). For the total carbon and soil moisture study, there were four levels of microhabitat, (1) bare sand, 2 m from *Ceratiola*, and 1 m from *Quercus*, (2) lichens and litter at >90% cover, 2 m from *Ceratiola*, and 1 m from *Quercus*, (3) under the dripline of *Quercus*, and (4) under the dripline of *Ceratiola*, and two levels of time-since-fire (<2 years since last fire vs. >30 years since last fire). Means within the same panel that are significantly different at $p < 0.05$ are designated with different letters. ANOVA results are shown in Table 2.4.

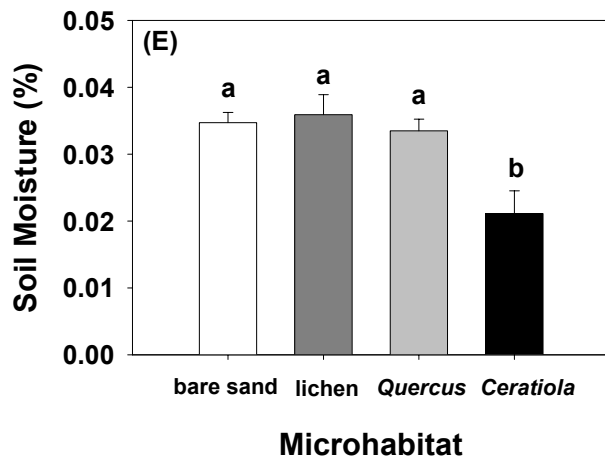
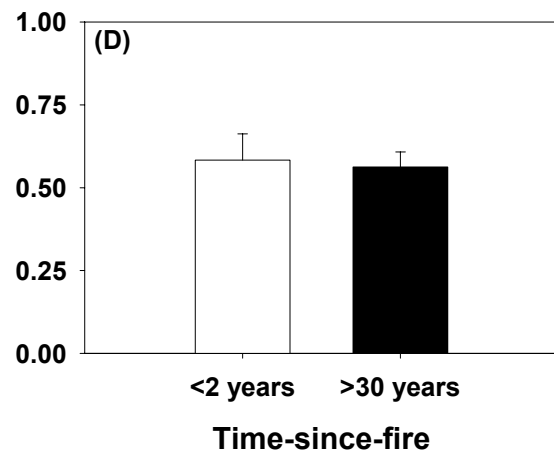
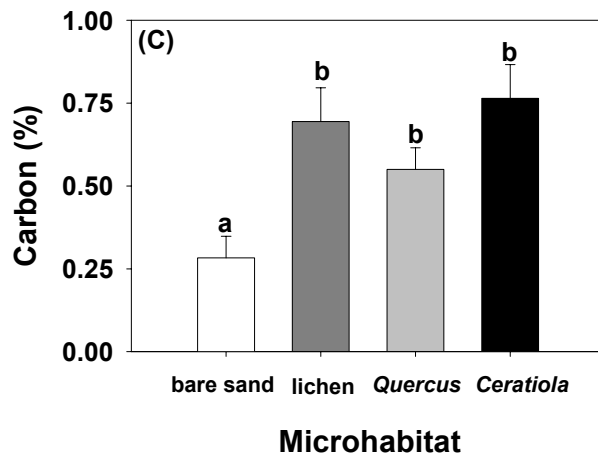
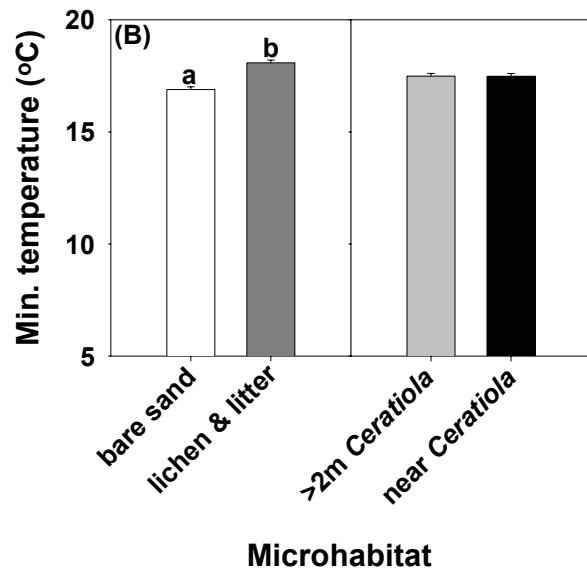
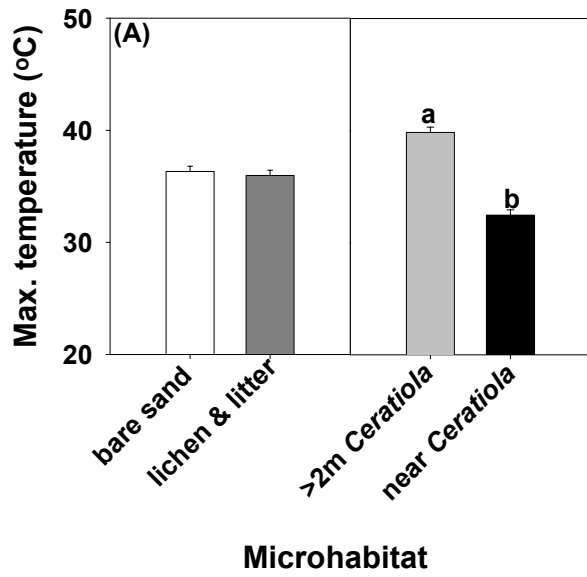


Table 2.4. Summary of ANOVAs conducted to examine the effects of microhabitat variables and time-since-fire on soil properties. In the soil temperature study, there were two levels of the soil surface cover treatment (lichens and litter added or bare sand) and two levels of distance from nearest *Ceratiola* (near *Ceratiola* and > 2 m from nearest *Ceratiola*). In the total carbon and soil moisture study, there were four levels of microhabitat (bare sand, lichens and litter at >90% cover, under the dripline of *Quercus*, and under the dripline of *Ceratiola*) and two levels of time-since-fire (<2 years since last fire and >30 years since last fire). Means are shown in Fig. 2.5.

Soil variable	Treatment	F	df	P
Maximum Temperature	Soil surface cover	0.29	1,17	0.5962
Maximum Temperature	Distance from <i>Ceratiola</i>	122.54	1,17	<.0001
Minimum Temperature	Soil surface cover	47.31	1,17	<.0001
Minimum Temperature	Distance from <i>Ceratiola</i>	0.00	1,17	0.9546
Percent Total Carbon	Microhabitat	6.86	3,31	0.0011
Percent Total Carbon	Time-since-fire	0.05	1,31	0.8210
Percent Soil Moisture	Microhabitat	8.137	3,55	<.0001
Percent Soil Moisture	Time-since-fire	1.806	1,55	0.1850

the abundances of three locally rare annual cobble beach plant species were limited by scarcity of their required microhabitat, fine-grained sands with low tidal flow velocity.

Plants of both rosemary scrub specialists and habitat generalists occurred less frequently near neighboring shrubs, *Ceratiola* and *Quercus* spp. than random points. Our results, and those of Menges and Kimmich (1996) and Quintana-Ascencio and Morales-Hernandez (1997), suggest that *Ceratiola ericoides* has an inhibitory effect on both rosemary scrub specialist species and habitat generalists. *Ceratiola ericoides* has been shown to have allelopathic effects on pines and grasses of sandhills (Richardson and Williamson 1988) as well as on several perennial herb species that occur in rosemary scrub, including rosemary scrub specialists and habitat generalists (Hunter and Menges 2002). Our results suggest that the same may be true for all four species included in our study. I also found that soil moisture was significantly lower in microhabitats

near *Ceratiola* shrubs, in comparison to other microhabitats. The combined effects of allelopathy and reduced soil moisture may make microhabitats near *Ceratiola* difficult to colonize for many perennial herbs that occur in rosemary scrub. With the exception of the habitat generalist, *L. deckertii*, plants occurred less frequently near *Quercus* shrubs than random points. Competition from *Quercus* spp. did not substantially affect survival and growth of transplanted seedlings of three rosemary scrub specialists in a field experiment (Quintana-Ascencio and Menges 2000); however the favorable growing conditions during that study due to high rainfall associated with El Niño may have reduced differences between microsites near to and far from *Quercus* spp. Our study occurred during a drought year; competitive effects of *Quercus* on perennial herbs are likely to be most noticeable during low rainfall years.

Bare sand microhabitats may be critical to seed and seedling life history stages of rosemary scrub specialist species, which would support the narrower regeneration niche hypothesized mechanism of specialization. In contrast to Quintana-Ascencio and Menges (2000), I found that seedling survival was higher in the presence of ground lichens and litter for *P. basiramia*. They monitored both germination and seedling establishment of *P. basiramia* in microsites with and without the presence of ground lichens; I measured the effects of ground lichens and litter on seedling survival after seedlings had already established. Ground lichens and litter may have negative effects on seedling germination and establishment (Hawkes and Menges 2003), but not survival after seedlings reach a critical size. I also found that seedlings of the two rosemary scrub specialist species grew larger in the absence of lichens and litter, although these differences in growth were not dramatic. Seedling growth is one of the most important life history parameters for population growth of another rosemary scrub specialist species, *Eryngium cuneifolium* (Menges and Quintana-Ascencio 2004), and is expected to be a

critical life history parameter for *L. cernua* and *P. basiramia*, in part because these species are short-lived (Maliakal-Witt, unpublished data). Thus, greater germination rates, seedling establishment, and seedling growth of these rosemary scrub specialists in bare sand may be significant in determining their strong tendency to occur in these types of microhabitats.

As time-since-fire increases, microhabitat characteristics in rosemary scrub habitat become less suitable for rosemary scrub specialist species. *Ceratiola* shrubs become denser and all shrubs become taller as time-since-fire increases (Abrahamson 1984a, Quintana-Ascencio and Morales-Hernandez 1997, Schmalzer 2003, this study). Fires eliminate adult *Ceratiola* shrubs, and new individuals establish slowly from seed (Menges and Kohfeldt 1995). However, *Quercus* species resprout quickly following fire (Abrahamson 1984b, Menges and Kohfeldt 1995) and recruitment events are not associated with fires, but rather annual precipitation and masting years (Abrahamson and Layne 2002, Abrahamson and Layne 2003). Therefore, it is not surprising that *Quercus* density did not change with time since fire. Percent cover of bare sand decreases with time since fire, as ground lichens and leaf litter increase in cover (Menges and Kohfeldt 1995, Hawkes and Menges 1996, this study). Thus fires can help maintain suitable microhabitats for rosemary scrub specialist herbs by reducing competition from *Ceratiola ericoides* and exposing bare sand microsites for seedling establishment. Frequent fires increase the population viability of *Hypericum cumulicola* and *Eryngium cuneifolium*, two rosemary scrub specialist herbs (Quintana-Ascencio *et al.* 2003, Menges and Quintana-Ascencio 2004). Management agencies can assess the benefits of prescribed fires for rosemary scrub specialist species by conducting post-fire monitoring of the availability of bare sand microhabitats that are free from competition from neighboring *Ceratiola*.

Differences in physical characteristics of microhabitats I measured do not fully account for the tendency of rosemary scrub specialists to occur in bare sand microhabitats. Although soils near *Ceratiola* exhibited lower soil moisture levels than other types of microhabitats, soils near *Quercus* do not have lower soil moisture levels than microhabitats greater than 2 m from any neighboring shrub, which suggests that *Quercus* may have less of a competitive effect than *Ceratiola*. Gagnon *et al.* (in prep) also found that *Ceratiola* has a much greater effect on soil moisture availability than *Quercus* species. Among the variables I measured, bare sand microhabitats can be distinguished from the other types of microhabitats only by lower minimum temperatures and total soil carbon. The magnitude of the temperature difference is small, about 1°C, which is unlikely to produce ecologically meaningful differences in metabolic rate (Criddle *et al.* 1994). Soil carbon content generally is positively correlated with nutrient supply (Madsen and Larsen 1997). Greater seedling growth in bare sand microhabitats occurs despite lower levels of soil carbon and nitrogen. Other biotic characteristics also may affect seedling establishment and growth, such as cryptogamic soil crusts (Hawkes and Flechtner 2002).

In conclusion, our results support the hypothesis that habitat-specialists occur in a narrower range of microhabitat conditions than species that occur in a broader range of habitats. Previous studies have demonstrated the importance of microhabitat for the persistence of individual geographically restricted, rare species (Griffith 1996, Hilton and Boyd 1996, Menges and Kimmich 1996, Kephart and Paladino 1997, Dinsdale *et al.* 2000, Wolf 2001, Colling *et al.* 2002). Other studies have shown that the local distributions of geographically widespread, but locally rare species are determined by availability of suitable microhabitat (Platt 1975, Gross and Werner 1982, Bruno 2002). Our comparison of two sympatric pairs of habitat-specialist and habitat-generalist congeners suggests that microhabitat specialization may underlie habitat

specificity. In this case, the limited amount of rosemary scrub habitat that also contains sufficiently high levels of bare sand appears to directly restrict the distributions of *L. cernua* and *P. basiramia*. Rosemary scrub habitat is characterized by large gaps lacking shrubs, and a high percentage of bare sand (Menges 1999). In neighboring scrubby flatwoods and sandhill habitats, gaps are less common, smaller, less persistent, and contain less percentage bare sand than gaps in rosemary scrub (Abrahamson *et al.* 1984, Menges and Hawkes 1998). These differences in microhabitat availability among habitat types may preclude the occurrence of rosemary scrub specialists in other habitats, because they can only persist in a narrow range of microhabitat conditions with high levels of bare sand. Conversely, the generalist species can tolerate a wider range of variation in lichen and litter cover, including and exceeding the range of microhabitats preferred by rosemary scrub specialists. As a result, the generalist species can occur in multiple habitat types, and thus over a larger geographic area. Consideration of habitat specificity, microhabitat requirements, and microhabitat distribution is needed for appropriate management of rare species. If habitat-specialist species are also specialized on particular microhabitat features within their preferred habitat, they may be more vulnerable to extinction than can be predicted by their degree of habitat specificity alone.

CHAPTER 3. TEMPORAL VARIATION IN VITAL RATES AND POPULATION GROWTH RATES OF TWO HABITAT-SPECIALIST PLANT SPECIES AND THEIR GENERALIST CONGENERS

INTRODUCTION

Understanding the causes of commonness and rarity and the processes that influence the relative abundance of organisms is fundamental to ecology (May 1999). The study of rare species, particularly those that are specialized on a narrow range of environmental conditions, is increasingly urgent due to current high rates of species extinctions (Pimm *et al.* 1995, Pitman *et al.* 2002, Thomas *et al.* 2004b). Determining the causes of commonness can help control of invasive species, which endanger native ecosystems (Williamson 1996, Parker *et al.* 1999, Mooney and Hobbs 2000) and have negative economic impacts (Pimentel *et al.* 2000). Rare species are less abundant than other species; however, abundance can be measured on a variety of different scales (Harper 1981).

Rarity can be defined by geographic regional abundance, local abundance, and habitat specificity, and it is important to specify which type of rarity is being examined (Rabinowitz 1981). Regionally rare species have limited geographic distributions. Locally rare species have small population sizes and are never dominant members of any community. Habitat specialist species can only persist in a small subset of habitat types. Different processes may regulate different forms of rarity. For example, biogeographic and evolutionary history may be most relevant to explaining patterns of global abundance; whereas ecological processes may be most important in determining patterns of local abundance and habitat specialization. Habitat specialization is the most frequent type of rarity (Rabinowitz *et al.* 1986). Habitat specialization is a relative concept, and should be measured relative to other, related species (Futuyma and Moreno, 1988).

Studies of individual habitat specialist species have used both genetic and demographic approaches. Genetic studies have suggested many habitat specialist species have low levels of genetic variation (Lesica *et al.* 1988, Hamrick and Godt 1989, Soltis *et al.* 1992, Godt and Hamrick 1998). However, persistence of endangered species more likely depends on demographic processes in variable environments than on their genetic structure (Lande 1988). Matrix projection modeling has been useful in identifying the limiting demographic parameters for particular rare, habitat specialist species (e. g. Menges 1990, Menges and Dolan 1998, Kaye *et al.* 2001, Morris *et al.* 2002, Schultz and Hammond 2003, Quintana-Ascencio *et al.* 2003, Menges and Quintana-Ascencio 2004). Using this detailed demographic approach in a comparative framework is a promising method to accelerate progress in the understanding of rarity and habitat specialization (Bevill and Louda, 1999).

Comparative demographic studies to date have suggested that specialist and generalist species differ consistently with respect to demographic parameters such as fecundity and recruitment. In studies comparing rare species with narrower ranges and habitat distributions to their widespread, habitat generalist congeners, Fiedler (1987) found higher mortality of reproductive stages in rarer *Calochortus* spp., and Byers and Meagher (1997) found lower seed production in a rare species of *Eupatorium* relative to its generalist congener. In a study of six congeneric pairs of tropical tree species that differed in their patterns of local abundance and gap specialization, Kelly *et al.* (2001) found greater recruitment fluctuation in the rarer species.

Here I use a comparative demographic approach to examine the hypothesis that demographic vital rates and population growth rates of habitat specialists are more variable in space and time than those of habitat generalists. General differences in variability of demographic parameters between rare, habitat specialist and generalist species may be related to

differences in degree of habitat specialization. For example, the regeneration niche hypothesis holds that habitat restricted species require narrower environmental conditions for successful recruitment (Hubbell and Foster 1986). In habitats where specialists and generalist species co-occur, they are subject to similar degrees of variation in environmental conditions. Under these circumstances, specialist species with a narrower regeneration niche would be expected to undergo more severe temporal fluctuations in recruitment.

This issue is best approached by comparing environmental variation in demographic parameters within pairs of closely related, co-occurring species, which differ in their degree of habitat specialization. Our objective was to compare vital rates and population growth rates of two habitat specialist plant species (both Florida scrub endemics) with their sympatric, habitat-generalist congeners over five years. Annually during 1999-2003, I measured survival, growth, seed production, and recruitment in six populations of all four study species, including two populations in each of three time-since-fire categories. I conducted matrix population analyses to estimate population growth rates for each population in each year and the mean and variance of stochastic population growth rates for each species. I also conducted population viability analyses under varying probabilistic weather and fire scenarios, to determine whether the habitat-specialist species are consistently more vulnerable to extinction than the generalist species. I addressed the following questions: 1) do habitat-specialist species have more variable vital rates and population growth rates over time, and 2) do demographic parameters and extinction probabilities of habitat-specialists and generalists differ with respect to variation in rainfall, time-since-fire, or both?

METHODS

Study Species, Location, and Habitat

I studied the demography of two congeneric pairs of species with differing degrees of habitat specialization. One member of each pair is a Florida scrub endemic. *Lechea cernua* Small is patchily distributed throughout the Lake Wales Ridge and other scrubland in central peninsular Florida (Christman and Judd 1990). *Polygonella basiramia* (Small) Nesom and Bates is restricted to the Lake Wales and Avon Park Bombing Range Ridges in Highlands and Polk Counties, central Florida (Christman and Judd 1990), and is currently listed as endangered by the U. S. Fish and Wildlife Service (1999). Both of these species are restricted predominantly to white-sand gaps in Florida rosemary scrub (Christman and Judd 1990, Hawkes and Menges 1995, USFWS 1999), and individuals occur preferentially in bare sand microhabitats (Maliakal Witt, this dissertation, chapter two). The other member of each pair has a wider distribution. *Lechea deckertii* Small occurs throughout Florida and southern Georgia, and *Polygonella robusta* (Small) Nesom and Bates occurs throughout Florida. Both of these species occur in a variety of sandy habitats, such as sandhills and scrubby flatwoods, in addition to co-occurring in Florida rosemary scrub (Wunderlin 1982, Menges and Salzman 1992). They are not as restricted to bare sand microhabitats as their congeners are (Maliakal-Witt *et al.* in review). All four species are short-lived, perennial, suffrutescent herbs (Wunderlin 1982).

The preferred habitat of the habitat-specialist species, Florida rosemary scrub, occurs on nutrient-poor, excessively drained, xeric white sands (Entisols of the St. Lucie or Archbold series) on ridges in central and coastal Florida (Abrahamson *et al.*, 1984; Carter, 1999). Florida rosemary scrub is dominated by the shrub Florida rosemary, *Ceratiola ericoides*, which occurs in pure stands or intermixed with scrub oaks (*Quercus inopina*, *Q. chapmannii*, and *Q. geminata*)

and sand pines (*Pinus clausa*) (Abrahamson *et al.*, 1984). Fire-return intervals in rosemary scrub average between 15-60 years (Menges, 1999). Periodic fires maintain open-structured habitat with large bare-sand gaps, which are distinguished from the surrounding shrub matrix by the lack of large *Ceratiola* shrubs and lower levels of ground lichens (*Cladonia* and *Cladina* spp.) and leaf litter (Menges, 1999).

This study was conducted primarily at Archbold Biological Station (ABS), a 2000-ha private biological station located in Highlands County, Florida. A variety of habitats are found at ABS, including approximately 36 ha of Florida rosemary scrub (Abrahamson *et al.*, 1984). Annual rainfall exceeds 1200 mm, with the majority falling during June through September in convective thunderstorms and tropical storm systems (Abrahamson *et al.*, 1984; Menges, 1999). Historical records dating to 1967 document the occurrence of multiple natural, accidental, and prescribed fires throughout the station property (Main and Menges 1997).

Demographic Data Collection

I collected demographic data in five annual censuses (1999-2003) and from seed dormancy and seedling recruitment experiments to construct population projection matrices for each of the four study species. I studied six populations of each species in rosemary scrub patches representing a gradient of time-since-fire. Two populations of each species were selected from rosemary scrub patches of each of three time-since-fire categories: recently-burned (≤ 6 years since fire), intermediate-aged (14-17 years since fire), and long-unburned (> 25 years since fire). For *L. cernua*, *L. deckertii*, and *P. basiramia*, all populations were located at ABS. For *P. robusta*, five populations were located at ABS, and one recently-burned population was located in burn unit LC01 of the 5467 ha Arbuckle Tract of Lake Wales Ridge State Forest, Polk County, Florida, approximately 40 km N of ABS. This study population was located on Archbold sand

(Anonymous 1990), in rosemary scrub habitat. The burn unit LC01 was burned under prescription in 1998 (Weekley and Menges 2003). Data from this population were included beginning in 2000. One rosemary scrub patch in the recently-burned category containing study populations of *L. cernua*, *L. deckertii*, and *P. basiramia*, was burned in an accidental fire at Archbold in February 2001. Populations of *L. cernua* and *L. deckertii* recovered from the fire via resprouting; however, *P. basiramia* was eliminated almost completely from the rosemary scrub patch. At this site, I continued to census populations of *L. cernua* and *L. deckertii*, and I monitored the site for potential recovery of the *P. basiramia* population. In 2001, I added another population of *P. basiramia* in the recently-burned category to compensate for this loss. In most cases, individual sites included all or most of the study species. Eleven sites in total were included in this study.

I estimated the survival, growth, and fecundity of individuals from annual (mid-October-mid-November) censuses of marked individuals (*L. cernua*: n= 1088, *L. deckertii*: n=1002, *P. basiramia*: n=1814, and *P. robusta*: n=875) conducted for five years (1999-2003). At each site, I sampled individuals of each study species present at the site in multiple bare sand gaps of varying sizes using a stratified random sampling method. I marked individual plants with wire stake flags and aluminum tags. Additional individuals were added to the study each year using the same stratified random sampling method to compensate for losses due to mortality. When the total population size of a given species fell below 100 plants, all individuals found at a site were sampled. I measured height, crown diameter (the longest axis of the crown), crown width (the horizontal distance perpendicular to crown diameter), and number of fruiting branches greater than 5 cm in length for every individual of each species in each year.

I estimated seed production for each species from linear regressions relating number of fruiting branches to seed number. In 1999, I sampled fifty plants, randomly selected from all study populations of *L. cernua*, *L. deckertii*, and *P. robusta*. Since *P. basiramia* is gynodioecious, I sampled 50 female plants and 50 hermaphroditic plants, randomly selected from all study populations. For each selected plant, I counted the total number of fruits. In all four study species, fruits are one-seeded, so fruit number approximates seed number. I conducted forward stepwise linear regressions relating seed number to number of fruiting branches, height, crown diameter and crown width for each species, and for hermaphrodites and females in *P. basiramia*. I found that seed production in hermaphrodites of *P. basiramia* was negligible (mean <50 seeds per plant), and difficult to predict using size estimates and number of fruiting branches ($r^2 < 0.30$); therefore I used only females to estimate seed production in *P. basiramia*. For all four species, the only significant explanatory factor predicting seed number was number of fruiting branches. I used power functions, in which both number of fruiting branches and number of seeds were log-transformed, to predict number of seeds produced by each species, because these models produced the best fit (all $r^2 > 0.70$, $n=50$, per species).

I conducted a long-term seed bank study to evaluate the importance of the seed bank for each study species. In the winter of 1999-2000, I collected and mixed ripe fruits of each species from a variety of rosemary scrub patches outside our study populations. I extracted seeds from fruits and placed 20 seeds of each species into separate triangular nylon mesh bags (mesh size= 0.25 mm, 90 bags total per species). For each species, I buried 15 bags at 5 cm depth at each demography study site. Since in 1999 I only had 1 recently burned population of *P. robusta*, I placed the second batch of 15 bags at a recently burned site where *P. robusta* occurred nearby in an unburned area. I unearthed one third of the bags per site after each of three different intervals

(1 year, 2 years, and 3 years). I examined and counted the remaining seeds in each recovered bag under a microscope, placed them in petri plates on moist filter paper in outdoor conditions (4 hours of direct morning sunlight) for 3 months, and recorded germination at weekly intervals. I dissected ungerminated seeds to determine viability. After dissection, seeds that had not rotted and contained firm white tissue were placed back onto fresh moist filter paper; these seeds were determined to be viable if they germinated. All seeds (100%) that contained firm white tissue were viable.

I estimated aboveground density and seedling recruitment of each species using 0.5 x 0.5 m permanent quadrats. Forty quadrats were located randomly across all study gaps. I monitored permanent quadrats at each annual census, and all new recruits in these quadrats were tagged and added to the study.

Matrix Construction and Verification

For each population and year combination, I built Lefkovitch population projection matrices (Caswell 2001) with the form $n_{(t+1)} = An_{(t)}$, where $n_{(t)}$ and $n_{(t+1)}$ are vectors whose elements, n_i , are the numbers of individuals in the i -th category at times t and $t+1$ respectively. The non-negative square matrix, A , contains elements, a_{ij} , that represent the transitions or contributions from individuals in the j -th category to the i -th category after one time step. To construct projection matrices, I defined six life-history stages for each species by combining morphologically defined stages (*e.g.*, vegetative or reproductive) with stages based on size for the reproductive classes (Fig. 3.1). Size classes were based on crown area (see below). Crown area was calculated as the product of crown diameter and crown width (the horizontal distance perpendicular to crown diameter).

Our seed bank experiments documented the presence of at least some long-term seed dormancy in all of the study species (Table 3.1); therefore I included a stage for dormant seeds in the seed bank for each species. The probability of dormant seed remaining in the seed pool was calculated as the geometric mean of three estimates of annual seed viability in the seed bank by site for each species. The three estimates of annual seed viability were the estimate of seed viability after one year of burial, the square root of the estimate of seed viability after two years of burial, and the cubic root of the estimate of seed viability after three years of burial.

I was able to identify yearlings (seedlings that survived until census time) of each species as they recruited in permanent quadrats. I used those known yearlings as a guide to assign new extra-quadrat plants to the seedling stage class. Based on our size data for known yearlings and known non-yearlings in quadrats, I determined size criteria for first-year yearlings of each species. Correct classification rates were greater than 70% for each species. Our yearling size cutoffs based on crown area were 13 cm² for *L. cernua*, 15 cm² for *L. deckertii*, 7 cm² for vegetative yearlings of *P. basiramia*, 500 cm² for reproductive yearlings of *P. basiramia*, and 15cm² for *P. robusta*. All newly recruited plants in quadrats and all newly tagged plants less than or equal to these yearling size cutoffs were assigned to the yearling stage category. Vegetative plants were non-fruiting plants older than yearlings. Because of small sample sizes, I defined only a single vegetative category for each species.

In all four species, crown area was a better predictor of growth, survival and fecundity than crown diameter, crown width, height, or total volume. I used the Moloney algorithm based on variation in crown area to determine the optimal division of our reproductive stage classes for each species (Moloney 1986). This algorithm minimizes distribution and sample errors

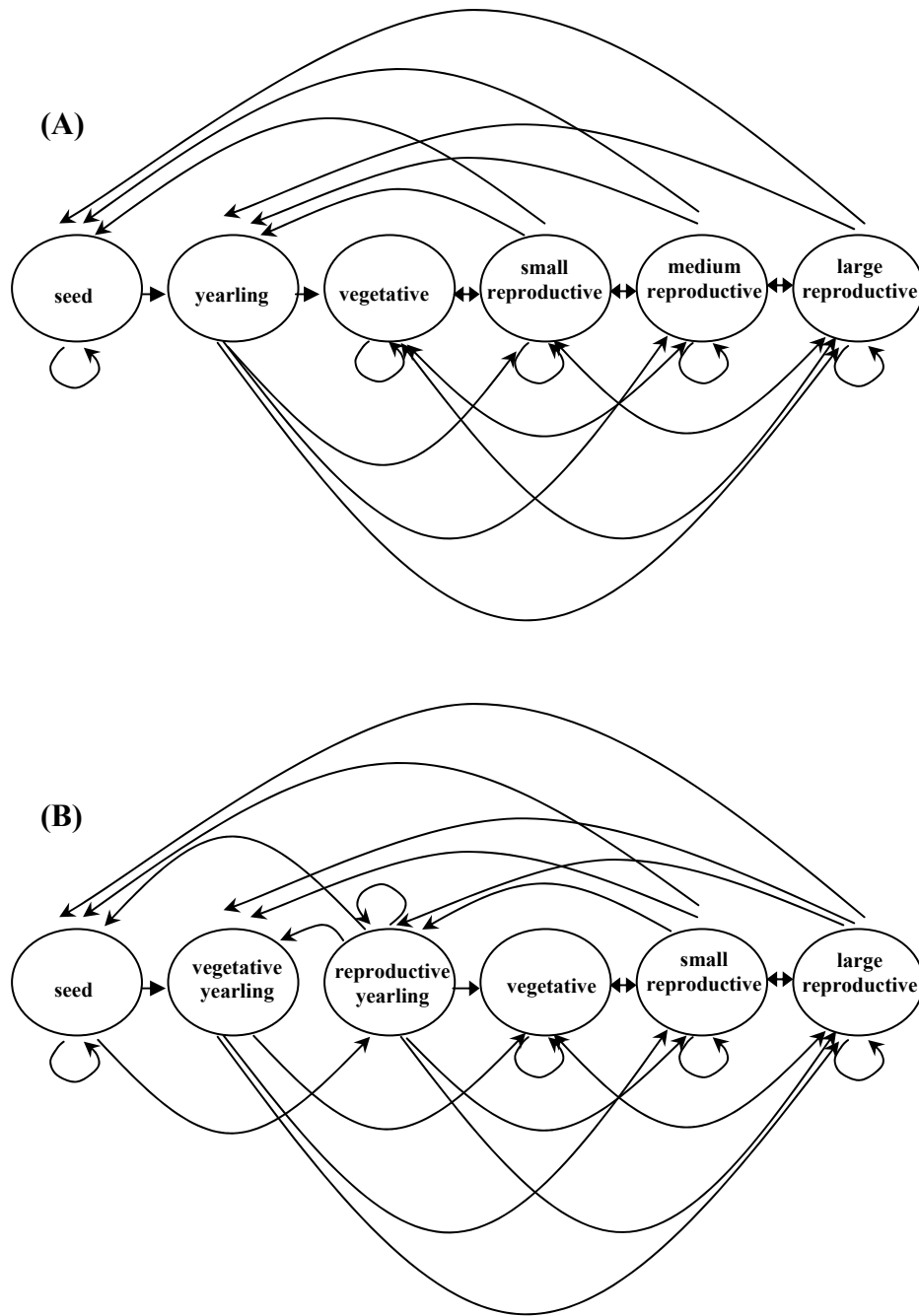


Figure 3.1. Life cycle graphs for four species of rosemary scrub herbaceous plants. The life cycles of *L. cernua*, *L. deckertii*, and *P. robusta* can all be represented using the same life cycle graph (A), and the life cycle of *P. basiramia* is depicted in (B).

Table 3.1. Natural history parameters for *L.cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*. Lifespan was calculated for each species by averaging the number of annual censuses through which the first cohort of known yearlings survived. Many yearlings did not survive until the next census; these were included as zeroes.

	<i>L. cernua</i>	<i>L. deckertii</i>	<i>P. basiramia</i>	<i>P. robusta</i>
Geographic Distribution	Lake Wales Ridge, central peninsular Florida	Throughout Florida and southern Georgia	Lake Wales Ridge, Avon Park Ridge	Throughout Florida
Habitat Specificity	rosemary scrub	sandhill, scrubby flatwoods, rosemary scrub	rosemary scrub	sandhill, scrubby flatwoods, rosemary scrub
Life history	iteroparous herb	iteroparous herb	iteroparous herb	iteroparous herb
Post-fire Recovery mode	resprouter and seeder	resprouter and seeder	obligate seeder	obligate seeder
Average Lifespan (yr)	1.55	1.49	0.31	1.67
Observed Maximum age (yr)	≥4	≥4	2	≥4
Seed Bank Viability (1 yr)	0.771	0.839	0.144	0.329
Seed Bank Viability (2 yr)	0.705	0.760	0.069	0.351
Seed Bank Viability (3 yr)	0.664	0.708	0.033	0.344

associated with stage classification. Distribution errors result if categories are so broad that their members no longer have similar transition probabilities, whereas sampling errors result from insufficient sample sizes, which cause imprecise estimates of transition probabilities (Moloney 1986). I set the smallest size as the initial minimum boundary value for each category, and chose the upper boundary of each sequential category to yield the minimum sum of the sampling and distribution errors, using 100 subsamples and 1 cm² increments. Stages were defined from samples of at least 50 plants. I was able to define three adult reproductive classes for *L. cernua* (small, ≤ 145 cm², medium >145 - 574 cm², and large >574 cm²), *L. deckertii* (small, ≤ 213 cm², medium >213 - 615 cm², and large >615 cm²), and *P. robusta* (small, ≤ 640 cm², medium >640 - 1810 cm², and large >1810 cm²), and only two adult reproductive classes for *P. basiramia* (small, ≤ 724 cm² and large >724 cm²). I found that these reproductive size classes were representative of size-specific variation in growth, survival, and fecundity. I found no evidence of plant dormancy (plants originally recorded as dead later found to be alive) for any of the four species.

Transitions other than fertility were calculated as the probability that a plant classified in stage *i* changed to stage *j* in the following census (a_{ij}). Most annual growth and survival transitions were estimated with population-specific demographic data. I pooled data across population groups defined by time-since-fire to estimate transitions when the sample size for a given stage in a given population fell below six (following Bullock *et al.* 1994). Overall $>75\%$ of the matrix entries for all four species had non-pooled, population-year-specific data (81.7%, *L. cernua*, 85.8%, *L. deckertii*, 79.2%, *P. basiramia*, 84.4%, *P. robusta*).

Fertility terms in the matrices represent newly recruited individuals that survived until their first annual census, or individual contributions to the seed bank. I estimated stage specific

contributions to the seed bank by multiplying the number of seeds produced per stage class by the probability of those seeds remaining in the seed bank. Since *P. basiramia* has a 50-50 sex ratio (Menges, unpublished data, Maliakal-Witt, unpublished data), I estimated seed production in females for each reproductive stage, and multiplied those estimates by 0.5 probability of being a reproductive female plant. The yearlings produced by adult plants comprise multiple vital rates, including seed germination and seedling survival until the next census. Although I was unable to directly estimate proportions of newly recruited seedlings coming from the seed bank versus coming from adult plants, I assumed that yearlings were coming from both places, because our seed bank experiments showed that all four species developed seed banks. Our model verifications validated this assumption (see below). I estimated yearling recruitment from permanent quadrats and assigned half of the newly recruited yearlings to the seed bank, and half to reproductive plants. I partitioned yearling numbers among reproductive stages in proportion to stage-specific abundance and seed production. I assigned the remaining yearlings to the seed bank, and estimated the seed-bank-to-yearling transition rate by calculating the proportion of yearlings recruited from the total number of seeds in the seed bank. Estimates of numbers of seeds in the seed bank were based on the abundances of reproductive adults. I always assumed that some recruitment occurred, even if no recruitment was detected in permanent quadrats. If no recruitment occurred in our permanent quadrats, I estimated recruitment transitions using results from site-specific field germination experiments, repeated annually since 1999.

Using data from permanent quadrats, I verified that all our matrices predicted the next year's population size and stage-class distribution reasonably well. I entered the initial population stage vector for each population in each year, and compared the predicted time $t+1$ population vector resulting from each matrix projection to the observed population vector in the

following year using a chi-square test. None of our predicted time $t+1$ population vectors ($n = 95$) differed significantly ($p < 0.05$) from our observed time $t+1$ vectors.

Analyses of Vital Rates

I conducted log-linear analyses to assess the effects of time-since-fire and year on fates of individuals of each species. Initial state ($stage_t$), time-since-fire class (recently-burned, intermediate-aged, or long-unburned), year (1999-2000, 2000-2001, and 2001-2002, and 2002-2003), and fate ($stage_{t+1}$; including “dead” as a stage) were the categorical variables in these analyses and are referred to as S , T , Y , and F , respectively. The response variable was the observed frequency of individuals per category. To remedy the potential for estimation bias associated with empty cells, a constant of 0.5 was added to each cell (Agresti 1996). I constructed a null model, denoted as STY , FS , in which fate is dependent on initial state but not on time or location. Following Caswell (2001), interaction terms, such as STY , imply that all single-factor terms (S , T , Y) and lower-order interactions (ST , SY , TY) are also present in the model. I tested for the overall significance of the effects of T and Y by calculating differences in the goodness-of-fit statistic (ΔG^2) between the null model and models that include the effects of T or Y . I tested the significance of an interaction between time-since-fire and year on fate by comparing the model STY , FST , FSY to the saturated model $FSTY$. Finally, I tested for the conditional effects of time-since-fire, given year, and year, given time-since-fire by comparing the models containing one or the other factor to the model containing both factors and their interaction. G^2 statistics were calculated for each model using PROC GENMOD with a Poisson distribution and log link in SAS Version 8 (Anonymous 2000).

I calculated the correlations of demographic parameters with rainfall in four quarters: winter (December-February), spring (March-May), summer (June-August), and fall (September-

November). In all four species, survival, recruitment, and population growth rate (λ , see below for description of how λ s were calculated) correlated more significantly with winter rainfall than with rainfall in any other quarter. Growth rates (natural logarithm of annual crown area change) of individuals correlated most significantly with summer rainfall for *Lechea* spp., whereas growth rates correlated most significantly with fall rainfall for *Polygonella* spp. Seed production of individuals (natural-logarithm-transformed) correlated most significantly with winter rainfall for *Lechea* spp., whereas seed production correlated most strongly with fall rainfall for *Polygonella* spp. Each subsequent mixed model analysis included the rainfall quarter most strongly correlated with the demographic parameter of interest.

I conducted mixed-model logistic regression analyses to determine the effects of initial stage, time-since-fire, and winter rainfall on individual survival for each species. I constructed a generalized model using a logit link and binomial error distribution with initial stage, time-since-fire, and winter rainfall as fixed effects while variation among sites was considered to be random for each species. Stage, time-since-fire, and site were entered as class variables, while winter rainfall was entered as a continuous variable. Analyses were conducted by invoking PROC MIXED within the GLIMMIX macro (Littell et al. 1996) in SAS Version 8 (Anonymous 2000).

I conducted generalized linear mixed model analyses to examine the effects of explanatory variables on growth (natural logarithm of annual area change) and seed production (natural-logarithm-transformed) of individuals of each species, as well as on seedling recruitment and finite rates of growth (λ) of populations of each species. In analyses with growth of individuals as the dependent variable, initial stage, time-since-fire, and summer or fall rainfall were entered as explanatory variables. In analyses with seed production of individuals as the dependent variable, initial stage, time-since-fire, and winter or fall rainfall were entered as

explanatory variables. In the analyses with seedling recruitment and growth rate of populations (λ), time-since-fire and winter rainfall were entered as explanatory variables. Variation among sites within time-since-fire classes was considered to be random in all of these analyses. I used PROC MIXED in SAS Version 8 (Anonymous 2000) to conduct these analyses.

I calculated mean coefficients of variation of vital rate parameters for each study species as an estimate of temporal variability of vital rates. By population, I calculated the coefficients of variation ($CV=100 \times SD/\text{mean}$) of survival, growth, seed production, and recruitment of the four interval-years. Coefficients of variation were not calculated for populations for which I was missing data for a particular interval-year. For each vital rate parameter, I then calculated mean coefficients of variation of all the populations over the four study years for each species.

For each population-year-specific projection matrix, I calculated population growth rates (λ_s) and the elasticity of every matrix element to λ . Lambda is calculated as the dominant eigenvalue of each transition matrix (Caswell 2001). Elasticity analysis measures the relative effect on λ to proportional perturbations in individual transition matrix elements (Caswell 2001). Because elasticity values for the elements in a projection matrix sum to one, they can be used to compare the relative importance of different life history transitions for population growth rate both between populations and among species of varying life histories (Caswell 2001), and elasticity matrices can be divided into three regions, representing growth (G), survival (L), and fecundity (F) to facilitate comparisons among species (Silvertown et al. 1993, 1996). I calculated the total elasticity values for the G, L, and F regions by summing the appropriate matrix elements, and plotted them on demographic triangles as in Silvertown et al. (1993, 1996). I calculated λ_s and elasticity values using MATLAB Student Version 6.0 Release 12 (Anonymous 2001).

Stochastic Modeling Simulations

Because winter rainfall correlated most strongly with λ for all four species, I used frequencies of winter rainfall amounts to model population growth as a function of different climate scenarios.

Over a 71-year period at Archbold Biological Station, total annual precipitation was highly variable, with a mean of 1351 mm, a maximum of 1948 mm, and a minimum of 693 mm.

During the winter quarter (December-February), mean rainfall was 157 mm, with a maximum of 546 mm, and a minimum of 18 mm (Fig. 3.2A). I divided winter rainfall history into four categories of winter rainfall amounts that represented well-below average, below-average, average, and above-average winter precipitation, and matched each of the four study transitions to one of these rainfall categories. In 12.7% of years winter rainfall was below 64 mm (observed in 2000-01), in 31.0 % of years winter rainfall was between 64 and 128 mm (observed in 1999-2000), in 25.4% of years winter rainfall was between 128 and 192 mm (observed in 2001-02), and in 31.0% of years winter rainfall was >192 mm (observed in 2002-03, Figure 3.2B).

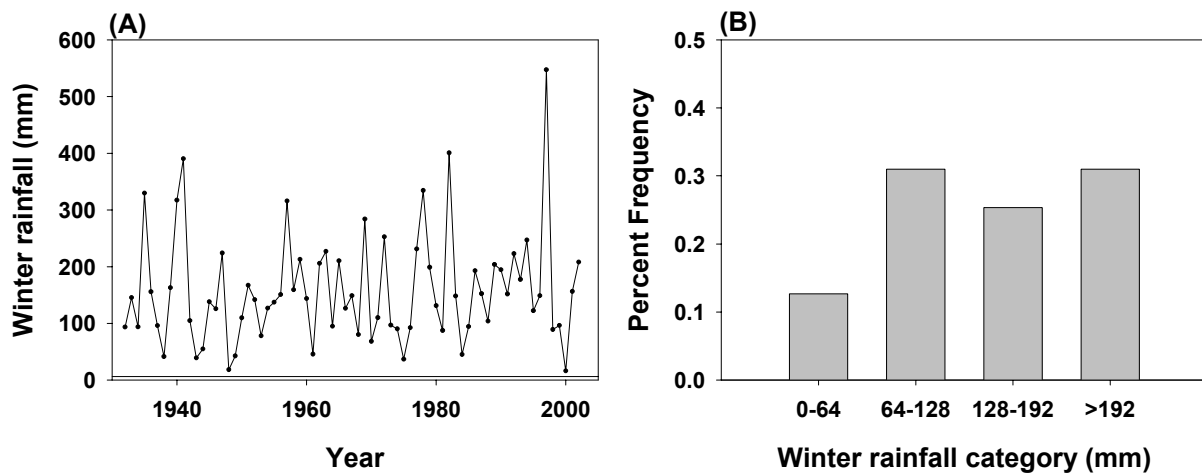


Figure 3.2. Winter rainfall (December to February) at Archbold Biological Station over the past 71 years (1931-2002) (A). The horizontal line depicts the mean winter rainfall amount over the 71-year period. Percent frequency of each winter rainfall category over a 71-year period (B). These frequencies were used to generate probabilities of winter rainfall amounts in subsequent stochastic modeling simulations.

I estimated extinction probabilities of all four species from simulations of population trajectories under various probabilistic winter rainfall scenarios. For each species, I ordered all population projection matrices by year, and calculated the probability of selecting each individual matrix by dividing the probability of a given winter rainfall year by the number of population projection matrices I had for that species in that year. For each species, I ran stochastic modeling simulations under four different scenarios: 1) using matrix selection probabilities calculated from historic (last 71 yr) winter rainfall patterns and observed population projection matrices, 2) using matrix selection probabilities calculated from historic winter rainfall patterns and current population projection matrices but with seed bank survival reduced by 50%, 3) using matrix selection probabilities calculated by doubling the probability of the well-below-average rainfall year and evenly adjusting downward all other probabilities, and 4) using matrix selection probabilities calculated by doubling the probability of the well-below-average rainfall, increasing the probability of above-average winter rainfall by 50%, and evenly adjusting downward all other probabilities. An initial vector consisting of 1000 seeds and 100 plants evenly distributed across all stages was used in each modeling simulation. I calculated mean cumulative frequency distribution (CDF) functions for time to reach a quasi-extinction threshold of 25 plants for each species from 5000 simulations of 50 years under contrasting scenarios. To conduct all the above-described modeling simulations, I modified existing programs presented in Morris and Doak (2002), and ran them in MATLAB Student Version 6.0 Release 12 (Anonymous 2001).

I also calculated mean stochastic population growth rates with 95% confidence intervals by simulation and estimated variance in log population growth rates for each species using matrix selection probabilities calculated with historic winter rainfall patterns and observed population projection matrices. I projected population growth over many successive time

intervals using a matrix drawn at random from each time interval from the total set of matrices with their associated selection probabilities. I then calculated $N(t)$ and $N(t+1)$, the total population densities in successive years, and calculated the arithmetic mean of $\log [N(t+1)/N(t)]$ over all pairs of adjacent years to estimate $\log \lambda$. I obtained approximate 95% confidence intervals by using the mean and variance of 50,000 simulated population growth increments for each species. I used MATLAB code presented in Morris and Doak (2002) to estimate the mean, variance, and 95% confidence intervals of stochastic λ from simulations for each species in MATLAB Student Version 6.0 Release 12 (Anonymous 2001).

I estimated extinction probabilities of all four species from simulations of population trajectories under various fire-return intervals. I used an algorithm that incorporates changes in probabilities of occurrence of specific matrices with time since last fire for each population-year matrix, while matrices within a time-since-fire category were chosen with equal probabilities. For each species, I sorted all population-year matrices in order of years since last fire. All simulations began with an initial post-fire population. Matrix selections during each simulation were governed by a sequence of seven phases of the post-fire cycle which represent different time periods after a fire. For all four species (with exceptions noted below), the phases were defined as: 1) fire year, 2) first year after fire, 3) 2-6 years after fire, 4) 7-13 years after fire, 5) 14-17 years after fire, 6) 18-27 years after fire, and 7) >27 years after fire. Using the exact number of years since fire for each population-year specific matrix, I defined phases 3 and 4 as 2-5 and 6-13 years after fire respectively for *P. robusta* fire modeling. Phases 6 and 7 were defined as 18-31 and >31 years after fire, respectively, for *L. cernua* fire modeling. As each simulation proceeded through phases 1, 2, 3, 5, and 7 following a fire event, I used a random sequence of matrices chosen from among those belonging to each appropriate phase. During

phases 4 and 6, for which I had no specific population-year matrices, I interpolated by choosing a random sequence of matrices with the probabilities of occurrence of the matrices in the adjacent-lower phase linearly decreasing with each successive time step and those in the adjacent-higher phase linearly increasing with each successive time step. I modeled extinction probabilities for each species using 2000 replicated simulations to estimate extinction probability for each fire regime. I used the following fire regimes: average fire-return intervals of 11, 20, and 29 years, and no fires. To generate fire regimes with fires, I used fire occurrence cumulative probability functions of the following form: $p = 1/(1+\beta_1*\exp(\beta_2*y))$, where p is the fire occurrence probability, y is the number of years since fire, and β_1 and β_2 are constants that differ depending on the average fire frequency (for average fire-return intervals of 11, 20, and 29 years, $\beta_1= 80, 40, \text{ and } 90$, and $\beta_2= -0.4, -0.19, \text{ and } -0.16$, respectively). I used modified versions of a program called DISTPROJW (Quintana-Ascencio et al. 2003) written for MATLAB, to run all fire modeling simulations in MATLAB Student Version 6.0 Release 12 (Anonymous 2001).

To model the response of both *Lechea* species to various fire regimes, I estimated times to quasi-extinction after 50 years under average fire-return intervals of 11, 20, and 29 years, and no fires. Because plants of both *Lechea* species resprout following fires, I used an initial post-fire population that consisted of a vector containing 1000 seeds and 100 plants distributed evenly across all stages for all fire modeling simulations involving *Lechea* species. One of our study sites that contained populations of *L. cernua* and *L. deckertii* was burned during our study; therefore, I was able to use the matrices from these populations for the fire year and year after fire phases of the fire modeling simulations. I compared quasi-extinction thresholds of only aboveground plants, and all individuals (including seeds), because populations of *Lechea* species

may disappear aboveground but still have a substantial belowground population. I ran simulations using quasi-extinction thresholds of 25 plants under all fire regimes.

To model the response of *Polygonella* species to various fire regimes, I added a seed dispersal component to our simulations to compensate for complete loss of plants and almost complete loss of seeds following fires, and estimated times to quasi-extinction after 50 years under average fire-return intervals of 11, 20, and 29 years, and no fires under various amounts of annual seed dispersal. Because all aboveground individuals of both *Polygonella* species are killed by fires, I used an initial post-fire population consisting of a vector of 1000 seeds. I modeled fires using a matrix with only the probability of seeds remaining in the seed bank for the fire year phase. For each *Polygonella* species, I averaged seed survival in the soil seed bank using all populations for this fire year matrix. I did not have empirical data for either *Polygonella* species in the first year after fire, because I did not locate any appropriate study populations of either of these species after a recent fire. Thus, I assumed that some seed germination from the soil seed bank occurred in the absence of another fire, and used a matrix containing only seeds remaining in the seed bank and seedling recruitment from the soil seed bank. For each *Polygonella* species, I used averages of seed survival in the soil seed bank and seedling recruitment from the soil seed bank of all populations for this year after fire matrix. Seeds dispersed were added to the current stage vector in each year of each modeling simulation. For each fire regime, I ran simulations for *P. basiramia* with annual seed dispersal of 775, 825, 875, and 925 seeds, and for *P. robusta* with annual seed dispersal of 250, 260, 270, and 280 seeds. Annual seed dispersal below 775 seeds for *P. basiramia* yielded extinction rates of 100% in all fire regimes, and seed dispersal below 250 seeds for *P. robusta* yielded extinction rates of 100% in fire regimes with frequent fires. Annual seed dispersal above 925 seeds for *P.*

basiramia and 280 seeds for *P. robusta* yielded 0 extinctions in all fire regimes. I used quasi-extinction thresholds of 250 individuals (including seeds) for every simulation.

RESULTS

Relationship of Time-since-fire and Rainfall to Demographic Parameters

Both time-since-fire and year had significant effects on individual fates (death, or stage in the following year) for all four species (Table 3.2). The strong effect of year can be attributed at least partially to variation in rainfall among years. Survival was significantly higher in years with high winter rainfall in all four species (Figs. 3.3 and 3.4, Table 3.3). The effect of winter rainfall on survival was dependent on stage in all four species (Figs. 3.3 and 3.4, Table 3.3). Survival was higher in long-unburned sites in high winter rainfall years relative to low winter rainfall years in *L. cernua* and *P. basiramia* producing a significant time-since-fire-by-winter rainfall interaction (Figs. 3.3 and 3.4, Table 3.3). Interactive effects of winter rainfall and time-since-fire in *L. deckertii* and *P. robusta* are dependent on initial stage (Figs. 3.3 and 3.4, Table 3.3). Survival percentages were more variable over four annual intervals in populations of the rosemary scrub specialist species than in generalist species (mean coefficient of variation (CV) of survival for populations of *L. cernua*=27.7, *L. deckertii*=22.5, *P. basiramia*=54.3, and *P. robusta*=31.5).

In all four species, growth was greatest in yearling plants, and decreased with increasing size for adult stages (Figs. 3.5 and 3.6), resulting in highly significant overall effects of stage (Table 3.4). Growth was significantly greater in high summer rainfall years for *Lechea* species (Fig. 3.5, Table 3.4) and in high fall rainfall years for *Polygonella* species (Fig. 3.6, Table 3.4). The effects of summer rainfall on growth differed among stages in both *Lechea* species;

Table 3.2. Loglinear analyses of effects of initial stage at time t (S), time-since-fire (T), and year (Y) on individual fate (stage $t+1$; including “dead” as a stage) for each species. ΔG^2 statistics indicate the difference in fit between the appropriate model and the model containing each explanatory factor. Interaction terms, such as *STY*, imply that all single-factor terms (*S*, *T*, *Y*) and lower-order interactions (*ST*, *SY*, *TY*) are also present in the model. Conditional effects evaluate the effect of one variable (time-since-fire or year) given the effect of the other variable.

<i>Lechea cernua</i>					
Model	Effect	df	G^2	ΔG^2	p
STY, FS		220	668.8	—	—
STY, FST		180	574.7	—	—
	T	40	—	94.1	<0.001
STY, FSY		160	286.1	—	—
	Y	60	—	382.7	<0.0001
STY, FST, FSY	T*Y	120	191.3	—	<0.001
	conditional T	40	—	94.8	<0.001
	conditional Y	60	—	383.4	<0.0001
<i>Lechea deckertii</i>					
Model	Effect	df	G^2	ΔG^2	p
STY, FS		220	503.5	—	—
STY, FST		180	433.2	—	—
	T	40	—	70.3	<0.005
STY, FSY		160	180.0	—	—
	Y	60	—	323.5	<0.0001
STY, FST, FSY	T*Y	120	120.9	—	NS
	conditional T	40	—	59.1	<0.05
	conditional Y	60	—	312.3	<0.0001
<i>Polygonella basiramia</i>					
Model	Effect	df	G^2	ΔG^2	p
STY, FS		165	375.1	—	—
STY, FST		135	311.7	—	—
	T	30	—	63.4	<0.001
STY, FSY		120	153.5	—	—
	Y	45	—	221.6	<0.0001
STY, FST, FSY	T*Y	90	95.4	—	NS
	conditional T	30	—	58.1	<0.005
	conditional Y	45	—	216.3	<0.0001
<i>Polygonella robusta</i>					
Model	Effect	df	G^2	ΔG^2	p
STY, FS		220	641.4	—	—
STY, FST		180	513.4	—	—
	T	40	—	128.0	<0.0001
STY, FSY		160	378.5	—	—
	Y	60	—	262.9	<0.0001
STY, FST, FSY	T*Y	120	257.1	—	<0.0001
	conditional T	40	—	121.4	<0.0001
	conditional Y	60	—	256.3	<0.0001

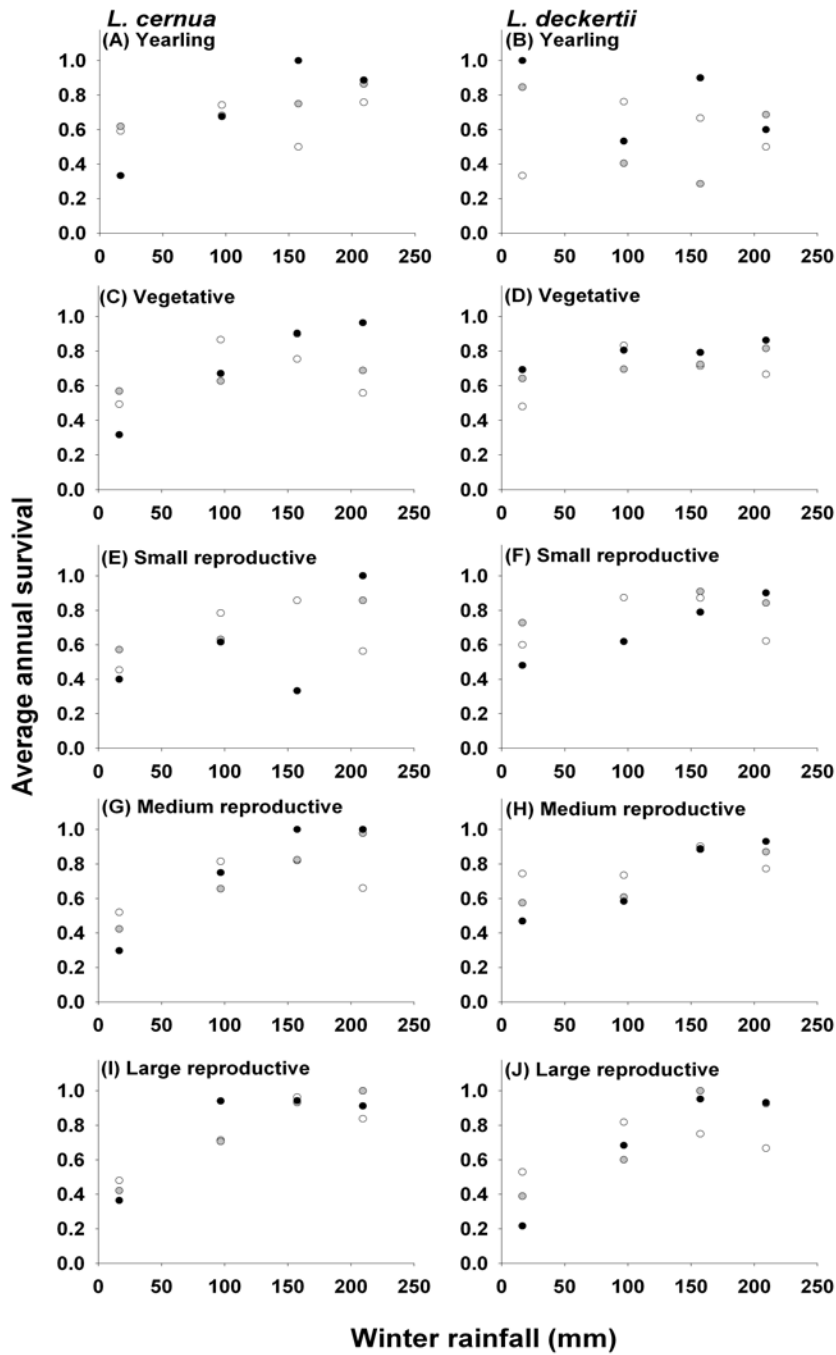


Figure 3.3. Annual survival of each stage class of *L. cernua* (A, C, E, G, I) and *L. deckertii* (B, D, F, H, J) plotted by winter rainfall (December-February) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

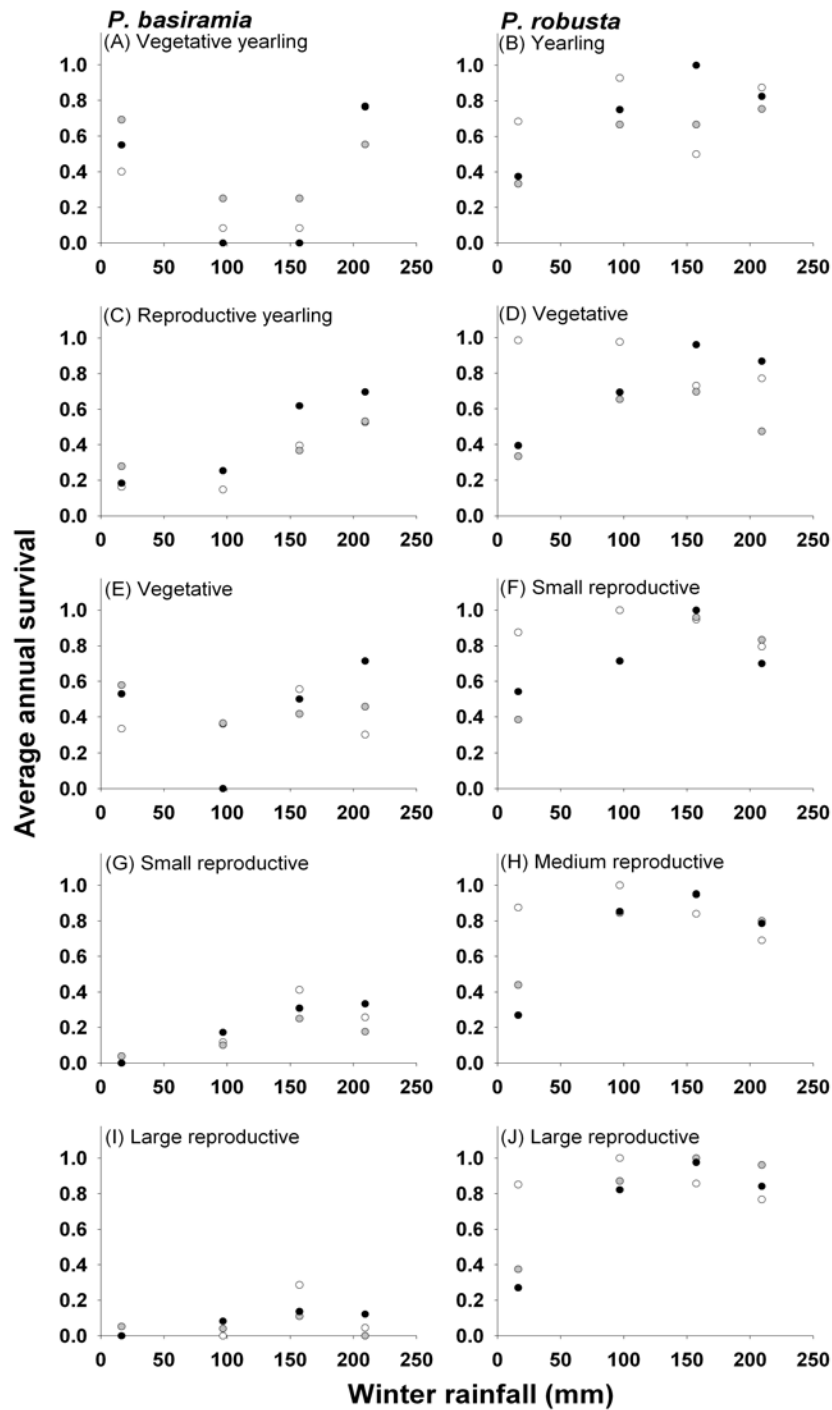


Figure 3.4. Annual survival of each stage class of *P. basiramia* (A, C, E, G, I) and *P. robusta* (B, D, F, H, J) plotted by winter rainfall (December-February) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

Table 3.3. Mixed model logistic regression analyses of the effects of initial stage, time-since-fire, and winter rainfall on survival of individuals of *L. cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*.

<i>L. cernua</i>			
Source	df	F value	p value
Stage	4, 2038	1.20	0.3098
Time-since-fire	2, 3	3.42	0.1682
S*T	8, 2038	0.88	0.5339
Winter rainfall	1, 2038	106.47	<0.0001
S*R	4, 2038	3.62	0.0060
T*R	2, 2038	13.00	<0.0001
S*T*R	8, 2038	1.74	0.0853
<i>L. deckertii</i>			
Source	df	F value	p value
Stage	4, 2026	2.64	0.0320
Time-since-fire	2, 3	0.87	0.5036
S*T	8, 2026	4.10	<0.0001
Winter rainfall	1, 2026	44.21	<0.0001
S*R	4, 2026	3.63	0.0059
T*R	2, 2026	2.91	0.0549
S*T*R	8, 2026	2.84	0.0039
<i>P. basiramia</i>			
Source	df	F value	p value
Stage	4, 2131	18.32	<0.0001
Time-since-fire	2, 4	3.34	0.1404
S*T	8, 2131	1.24	0.2692
Winter rainfall	1, 2131	50.25	<0.0001
S*R	4, 2131	4.63	0.0010
T*R	2, 2131	5.20	0.0056
S*T*R	8, 2131	1.27	0.2548
<i>P. robusta</i>			
Source	df	F value	p value
Stage	4, 1766	1.62	0.1662
Time-since-fire	2, 3	32.78	0.0092
S*T	8, 1766	1.80	0.0725
Winter rainfall	1, 1766	48.57	<0.0001
S*R	4, 1766	3.27	0.0110
T*R	2, 1766	31.13	<0.0001
S*T*R	8, 1766	2.59	0.0082

yearlings grew substantially faster in with increasing summer rainfall; whereas the growth rates of other stage classes were less dramatically affected by higher summer rainfall (Fig. 3.5, Table 3.4). Time-since-fire affected growth only in *P. robusta*, and the interactive effects of time-since-fire and fall rainfall on growth were also dependent on initial stage (as evidenced by a significant 3-way interaction for *P. robusta*, Fig. 3.6, Table 3.4). In *P. robusta*, growth was greater in long-unburned sites in high fall rainfall years, but this effect is pronounced only in yearling and vegetative stage classes. Growth rates were less variable over four annual intervals in populations of the rosemary scrub specialist species than in generalist species (mean coefficient of variation (CV) of growth rate for populations of *L. cernua*=51.3, *L. deckertii*=96.5, *P. basiramia*=85.2, and *P. robusta*=128.6).

Seed production was affected by variation in rainfall but not time-since-fire. Seed production was greatest in the largest reproductive class in all four species (Figs. 3.7 and 3.8, Table 3.5). Seed production was greater in high winter rainfall years in *Lechea* species and in high fall rainfall years in *Polygonella* species (Figs. 3.7 and 3.8, Table 3.5). Time-since-fire did not substantially affect seed production in any species (Figs. 3.7 and 3.8, Table 3.5). Variation in seed production did not consistently differ among rosemary scrub specialists and generalists over four annual intervals in populations (mean coefficient of variation (CV) of seed production for populations of *L. cernua*=33.5, *L. deckertii*=37.9, *P. basiramia*=33.5, and *P. robusta*=30.4).

Higher seedling recruitment occurred in high winter rainfall years for all four species (Fig. 3.9, Table 3.6). In *L. deckertii*, and *P. robusta*, seedling recruitment was higher in long-unburned populations than recently-burned or intermediate-aged sites, but only in high winter rainfall years (Fig. 3.9, Table 3.6). Recruitment rates were approximately two times more

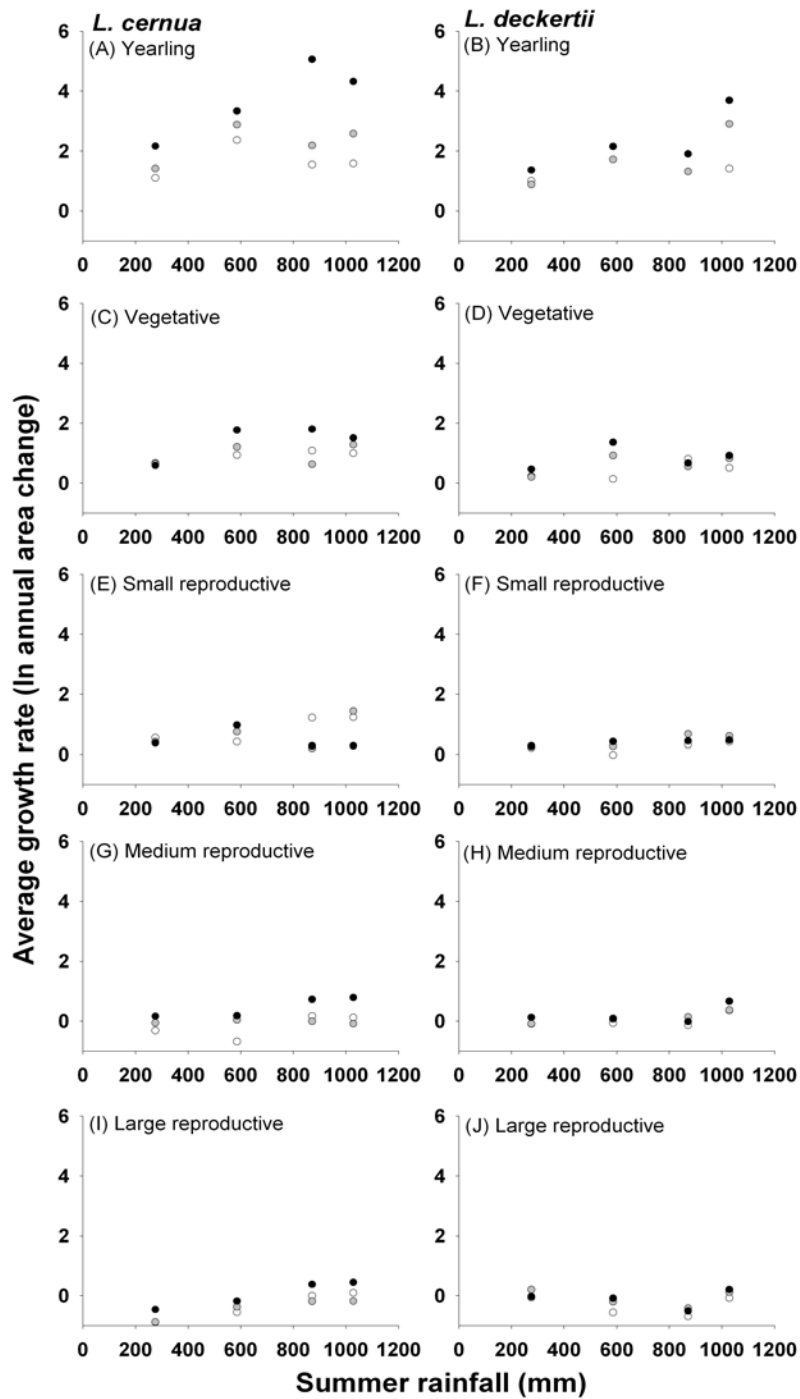


Figure 3.5. Average annual growth rates (ln of annual area change) of each stage class of *L. cernua* (A, C, E, G, I) and *L. deckertii* (B, D, F, H, J) plotted by summer rainfall (June-August) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

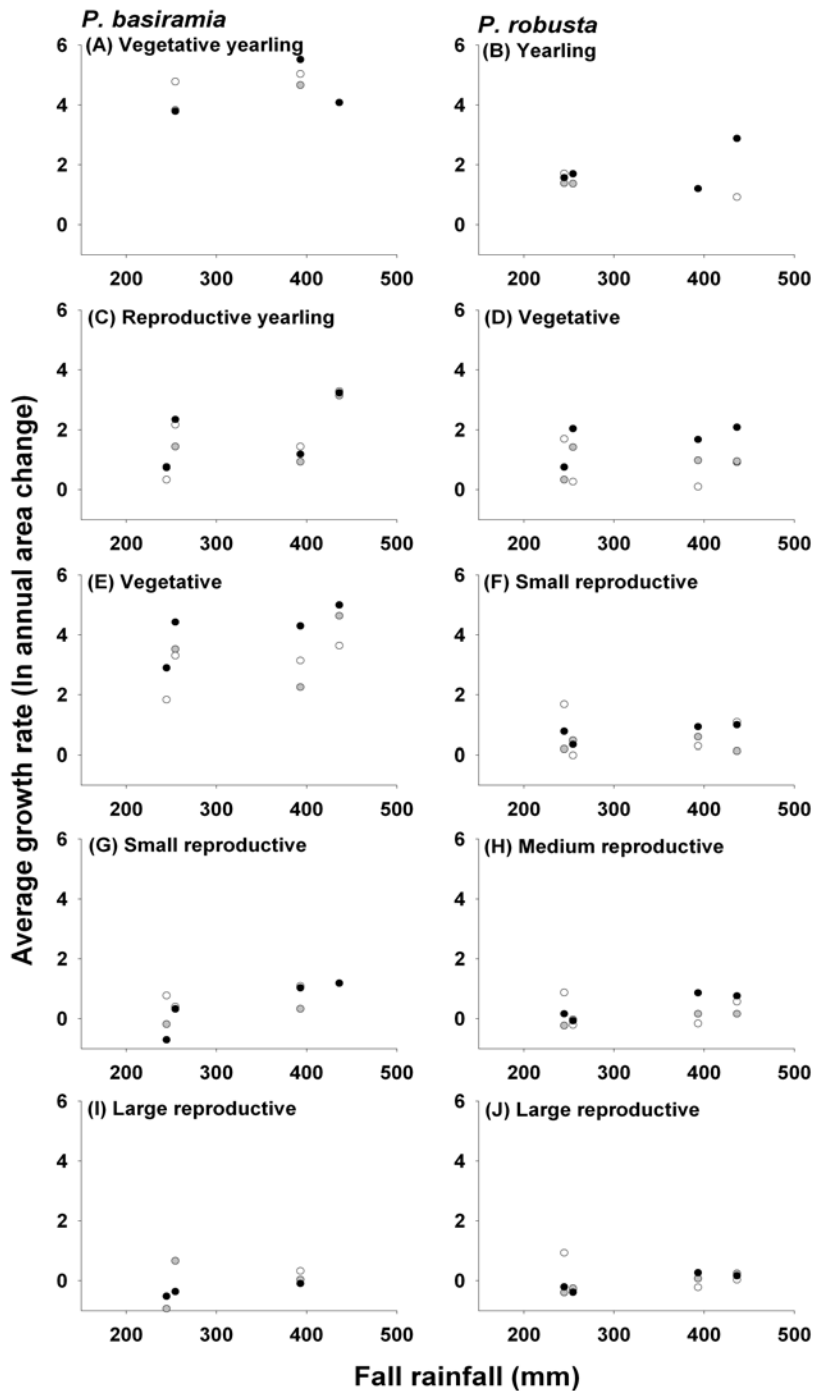


Figure 3.6. Average annual growth rates (ln of annual area change) of each stage class of *P. basiramia* (A, C, E, G, I) and *P. robusta* (B, D, F, H, J) plotted by fall rainfall (September-November) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

Table 3.4. Generalized linear mixed model analyses of the effects of initial stage, time-since-fire, and quarterly rainfall on growth (natural logarithm of annual area change) of individuals of *L. cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*. Summer rainfall was most highly correlated with growth of individuals for *Lechea* spp., and fall rainfall was most highly correlated with growth of individuals for *Polygonella* spp. Denominator degrees of freedom based on Satterthwaite approximation.

<i>L. cernua</i>			
Source	df	F value	p value
Stage	4, 1443	21.28	<0.0001
Time-since-fire	2, 16.9	0.98	0.3955
S*T	8, 1443	0.37	0.9372
Summer rainfall	1, 1442	33.01	<0.0001
S*R	4, 1443	3.57	0.0067
T*R	2, 1442	1.50	0.2224
S*T*R	8, 1442	1.39	0.1980
<i>L. deckertii</i>			
Source	df	F value	p value
Stage	4, 1437	6.24	<0.0001
Time-since-fire	2, 36.2	0.31	0.7347
S*T	8, 1437	0.73	0.6686
Summer rainfall	1, 1437	27.78	<0.0001
S*R	4, 1437	2.85	0.0228
T*R	2, 1437	3.03	0.0488
S*T*R	8, 1437	1.68	0.0982
<i>P. basiramia</i>			
Source	df	F value	p value
Stage	4, 589	4.92	0.0007
Time-since-fire	2, 468	0.54	0.5821
S*T	8, 588	1.18	0.3087
Fall rainfall	1, 597	11.08	0.0009
S*R	4, 594	0.12	0.9740
T*R	2, 597	0.58	0.5608
S*T*R	8, 594	0.75	0.6434
<i>P. robusta</i>			
Source	df	F value	p value
Stage	4, 1339	11.33	<0.0001
Time-since-fire	2, 78.6	6.20	0.0032
S*T	8, 1339	2.02	0.0412
Fall rainfall	1, 1340	22.59	<0.0001
R	4, 1339	0.71	0.5881
T*R	2, 1340	14.14	<0.0001
S*T*R	8, 1339	2.44	0.0127

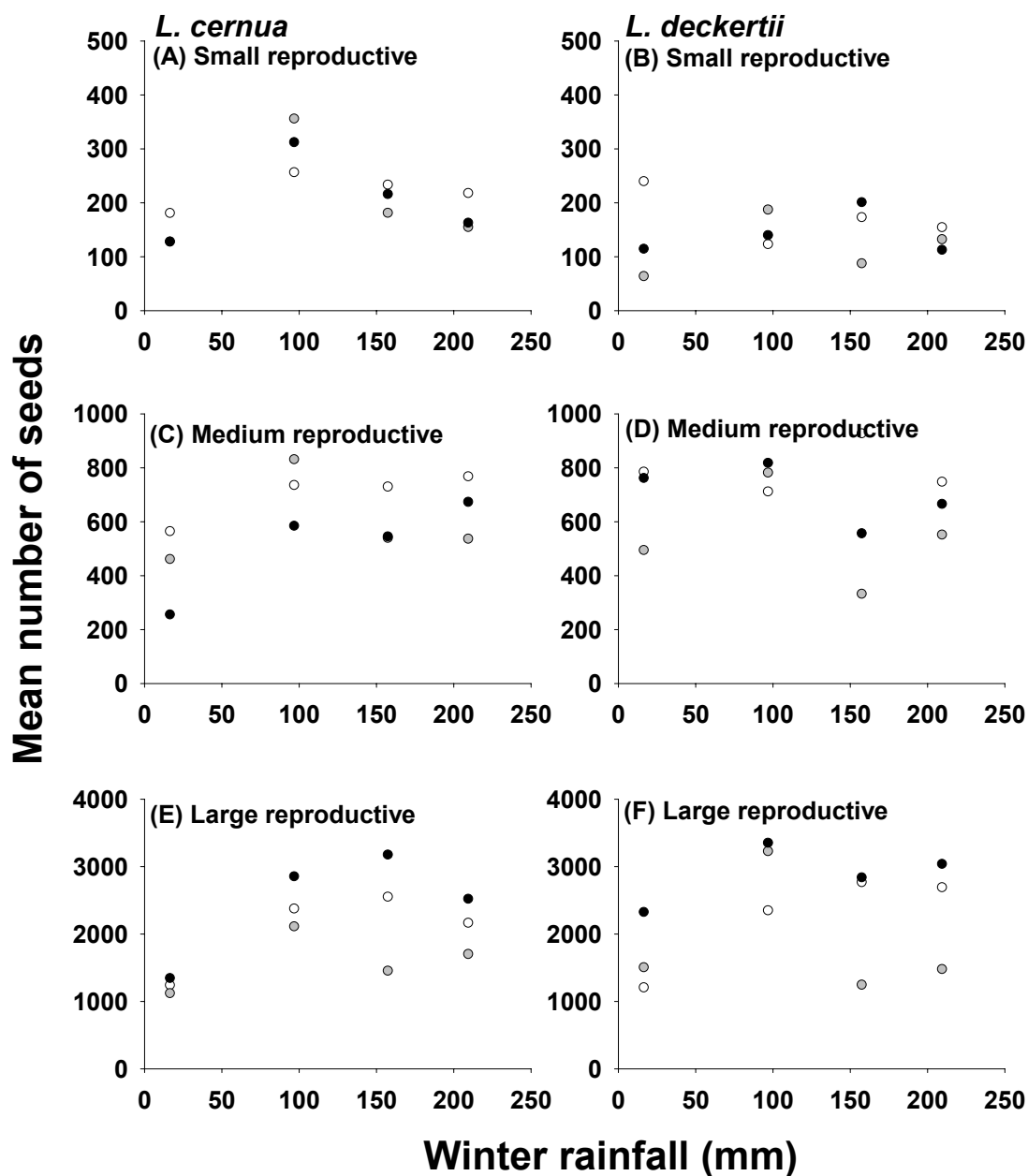


Figure 3.7. Mean seed number of each reproductive stage class of *L. cernua* (A, C, E) and *L. deckertii* (B, D, F) plotted by winter rainfall (December-February) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago. X-axes are not all the same scale.

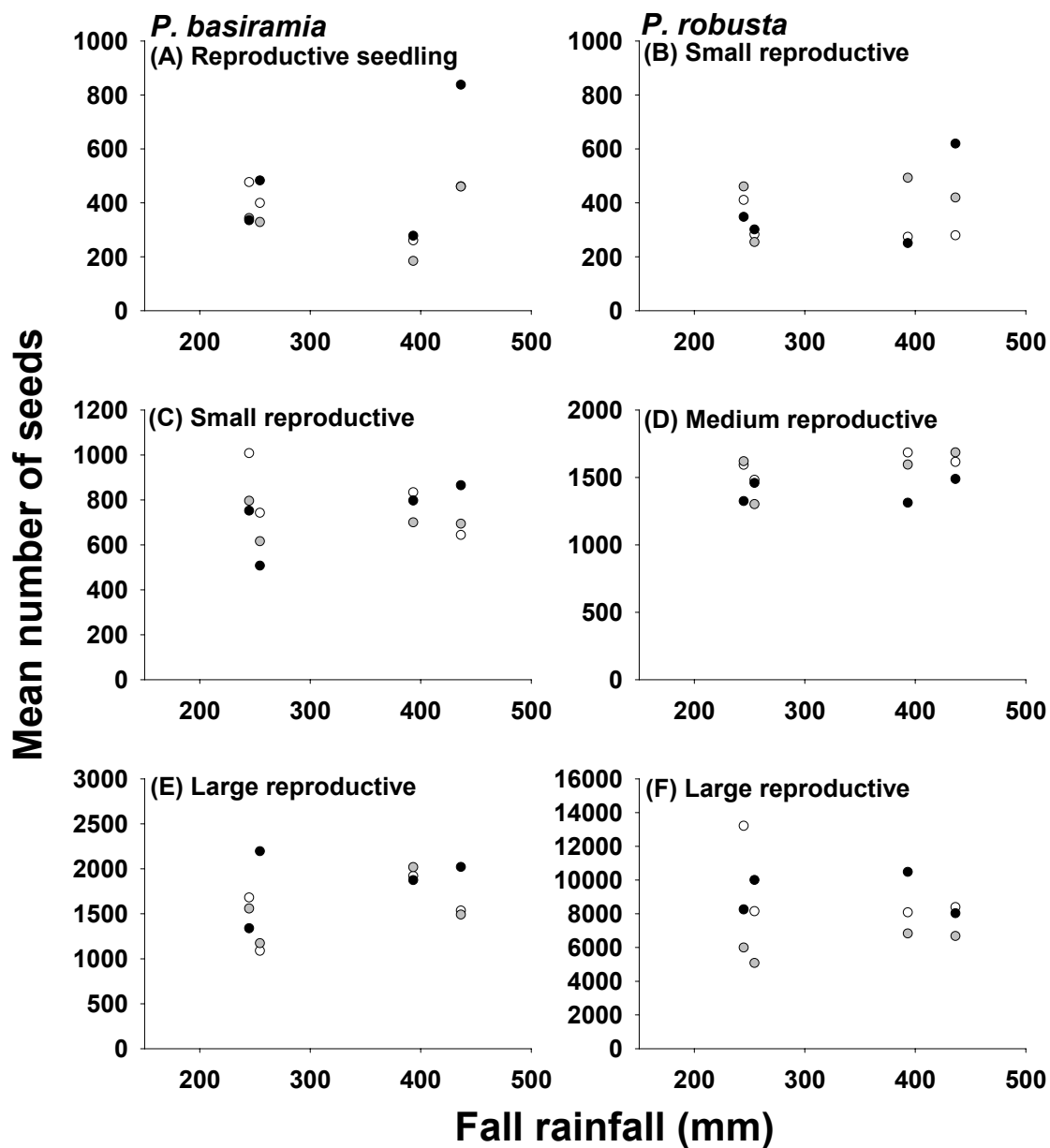


Figure 3.8. Mean seed number of each reproductive stage class of *P. basiramia* (A, C, E) and *P. robusta* (B, D, F) plotted by fall rainfall (September-November) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago. X-axes are not all the same scale.

Table 3.5. Generalized linear mixed model analyses of the effects of initial stage, time-since-fire, and quarterly rainfall on seed production (natural logarithm transformed) of individuals of *L. cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*. Winter rainfall was most highly correlated with seed production for *Lechea* spp., and fall rainfall was most highly correlated with seed production for *Polygonella* spp. Denominator degrees of freedom based on Satterthwaite approximation.

<i>L. cernua</i>			
Source	df	F value	p value
Stage	2, 1151	47.64	<0.0001
Time-since-fire	2, 7.13	0.19	0.8332
S*T	4, 1151	0.66	0.6232
Winter rainfall	1, 1152	8.80	0.0031
S*R	2, 1150	4.44	0.0121
T*R	2, 1152	3.33	0.0362
S*T*R	4, 1150	0.35	0.8473
<i>L. deckertii</i>			
Source	df	F value	p value
Stage	2, 1232	101.66	<0.0001
Time-since-fire	2, 8.77	1.94	0.2012
S*T	4, 1232	0.72	0.5763
Winter rainfall	1, 1233	8.71	0.0032
S*R	2, 1232	0.39	0.6773
T*R	2, 1232	0.43	0.6524
S*T*R	4, 1231	0.93	0.4442
<i>P. basiramia</i>			
Source	df	F value	p value
Stage	2, 651	13.26	<0.0001
Time-since-fire	2, 49.8	0.15	0.8592
S*T	4, 651	2.66	0.0319
Fall rainfall	1, 653	7.60	0.0060
S*R	2, 651	0.03	0.9723
T*R	2, 649	0.56	0.5736
S*T*R	4, 651	1.80	0.1266
<i>P. robusta</i>			
Source	df	F value	p value
Stage	2, 1207	70.08	<0.0001
Time-since-fire	2, 1207	3.48	0.0312
S*T	4, 1207	0.75	0.5593
Fall rainfall	1, 1207	6.19	0.0130
S*R	2, 1207	0.52	0.5957
T*R	2, 1207	3.49	0.0308
S*T*R	4, 1207	0.50	0.7382

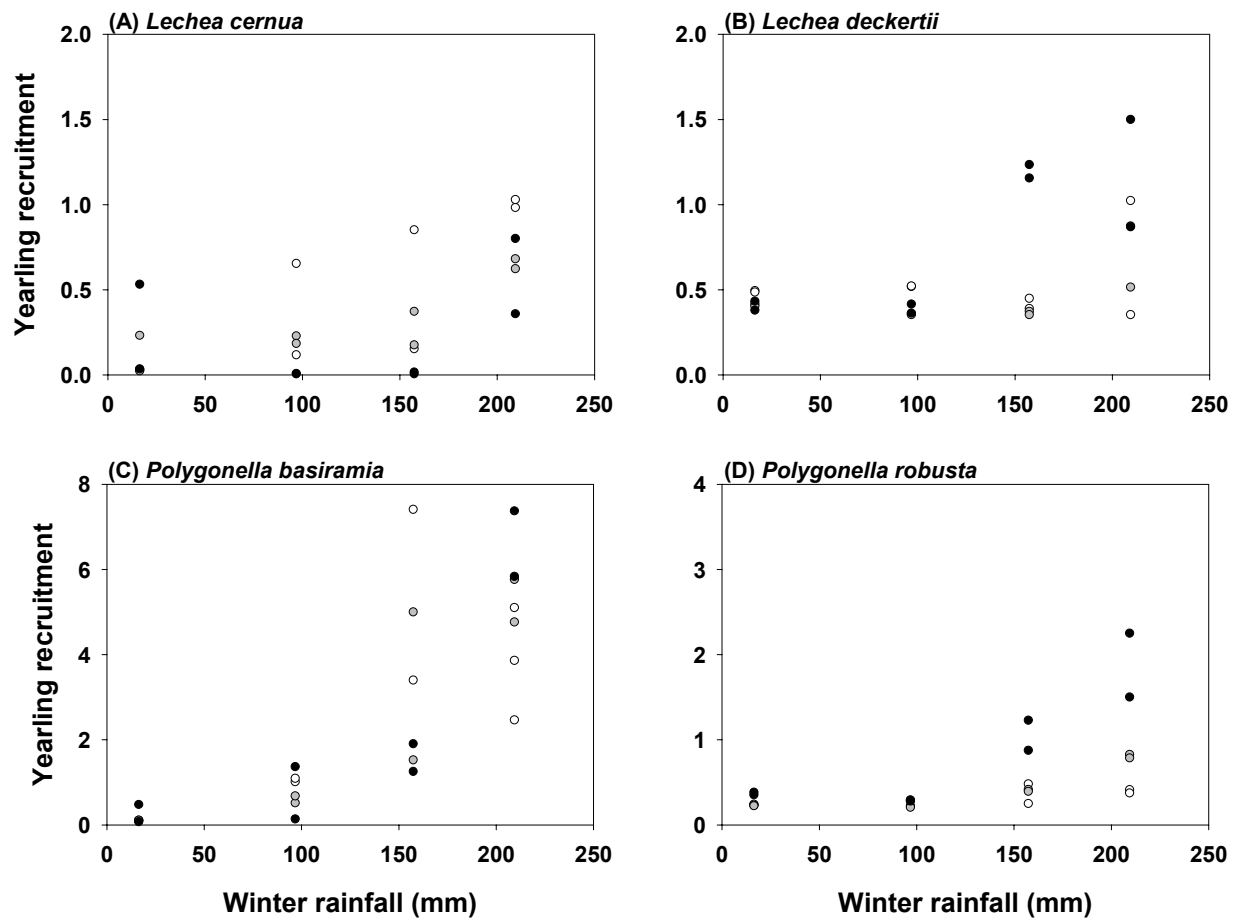


Figure 3.9. Yearling recruitment of *L. cernua* (A), *L. deckertii* (B), *P. basiramia* (C), and *P. robusta* (D) plotted by winter rainfall (December-February) of each year of study in rosemary scrub sites of different post-fire ages. White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago. X-axes are not all the same scale.

Table 3.6. Generalized linear mixed model analyses of the effects of time-since-fire, and winter rainfall on seedling recruitment of *L. cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*. Denominator degrees of freedom based on Satterthwaite approximation.

<i>L. cernua</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.23	0.7986
Winter rainfall	1, 18	13.98	0.0015
T*R	2, 18	2.03	0.1608
<i>L. deckertii</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.54	0.5921
Winter rainfall	1, 18	11.81	0.0029
T*R	2, 18	3.97	0.0372
<i>P. basiramia</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.14	0.8721
Winter rainfall	1, 18	28.43	<0.0001
T*R	2, 18	0.14	0.8746
<i>P. robusta</i>			
Source	df	F value	p value
Time-since-fire	2, 17	0.52	0.6034
Winter rainfall	1, 17	25.34	0.0001
T*R	2, 17	7.47	0.0047

variable over four annual intervals in populations of the rosemary scrub specialist species than in generalist species (mean coefficient of variation (CV) of recruitment for populations of *L. cernua*=106.2, *L. deckertii*=41.4, *P. basiramia*=120.5, and *P. robusta*=59.1).

Population growth rates of all four species were highly variable with respect to winter rainfall, but less variable with respect to time-since-fire. Population growth rates (λ s) were significantly higher in years of high winter rainfall for all four species (Fig. 3.10, Table 3.7). In *P. robusta*, the effects of winter rainfall on population growth rate differed with respect to time-since-fire (Table 3.7). Population growth rates of recently burned populations of *P. robusta* were relatively unaffected by winter rainfall, whereas growth rates of long-unburned populations were greater in high rainfall years (Fig. 3.10).

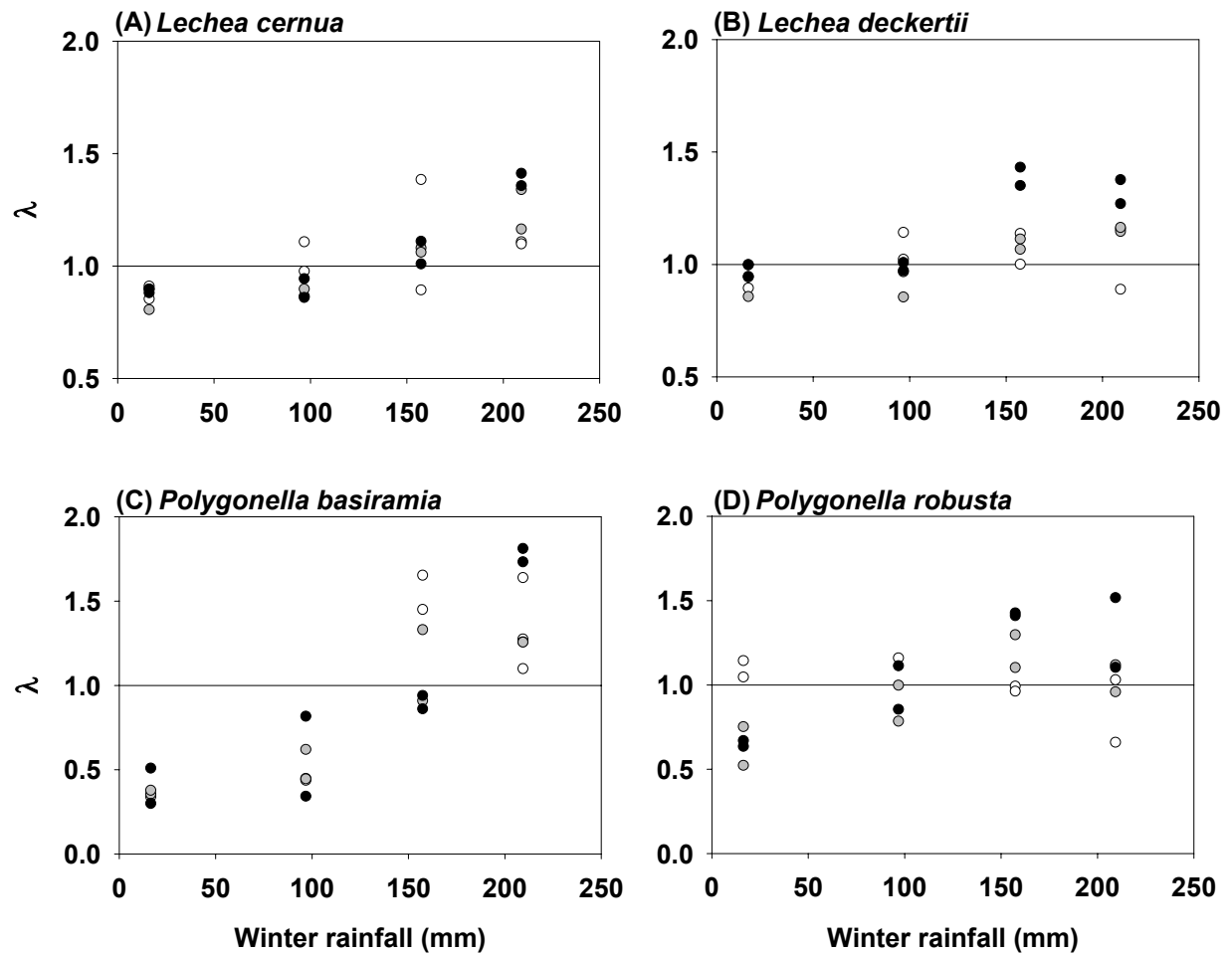


Figure 3.10. Relationship between population growth rate (λ) of *L. cernua* (A), *L. deckertii* (B), *P. basiramia* (C), and *P. robusta* (D) populations and winter rainfall (December through February). White fill-color depicts recently-burned (<6 years) populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

Table 3.7. Generalized linear mixed model analyses of the effects of time-since-fire, and winter rainfall on population growth rate (λ) of *L. cernua*, *L. deckertii*, *P. basiramia*, and *P. robusta*. Denominator degrees of freedom based on Satterthwaite approximation.

<i>L. cernua</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.76	0.4831
Winter rainfall	1, 18	30.13	<0.0001
T*R	2, 18	1.03	0.3784
<i>L. deckertii</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.43	0.6548
Winter rainfall	1, 18	20.97	0.0002
T*R	2, 18	2.80	0.0871
<i>P. basiramia</i>			
Source	df	F value	p value
Time-since-fire	2, 18	0.07	0.9307
Winter rainfall	1, 18	50.02	<0.0001
T*R	2, 18	0.36	0.7024
<i>P. robusta</i>			
Source	df	F value	p value
Time-since-fire	2, 11.6	5.95	0.0166
Winter rainfall	1, 14.1	14.33	0.0020
T*R	2, 14.1	12.21	0.0008

The summed elasticities representing growth (G), survivorship (L), and fecundity (F) were more similar in *L. cernua*, *L. deckertii*, and *P. robusta* than in *P. basiramia*; however the summed elasticities of all four species varied with respect to year. In *L. cernua*, *L. deckertii*, and *P. robusta*, summed elasticities were low for fecundity, intermediate for growth, and high for survivorship (Fig. 3.11). However, fecundity elasticities in *P. basiramia*, with its shorter average lifespan (Table 3.1), were high, and growth and survivorship elasticities were low (Fig. 3.11). In addition, survivorship elasticities of all four species were much higher in low winter rainfall years (1999-2000 and 2000-2001), whereas growth and fecundity elasticities of all four species were higher in high winter rainfall years (2001-2002 and 2002-2003, Fig. 3.11). Summed elasticities did not differ substantially with respect to time-since-fire (Fig. 3.11).

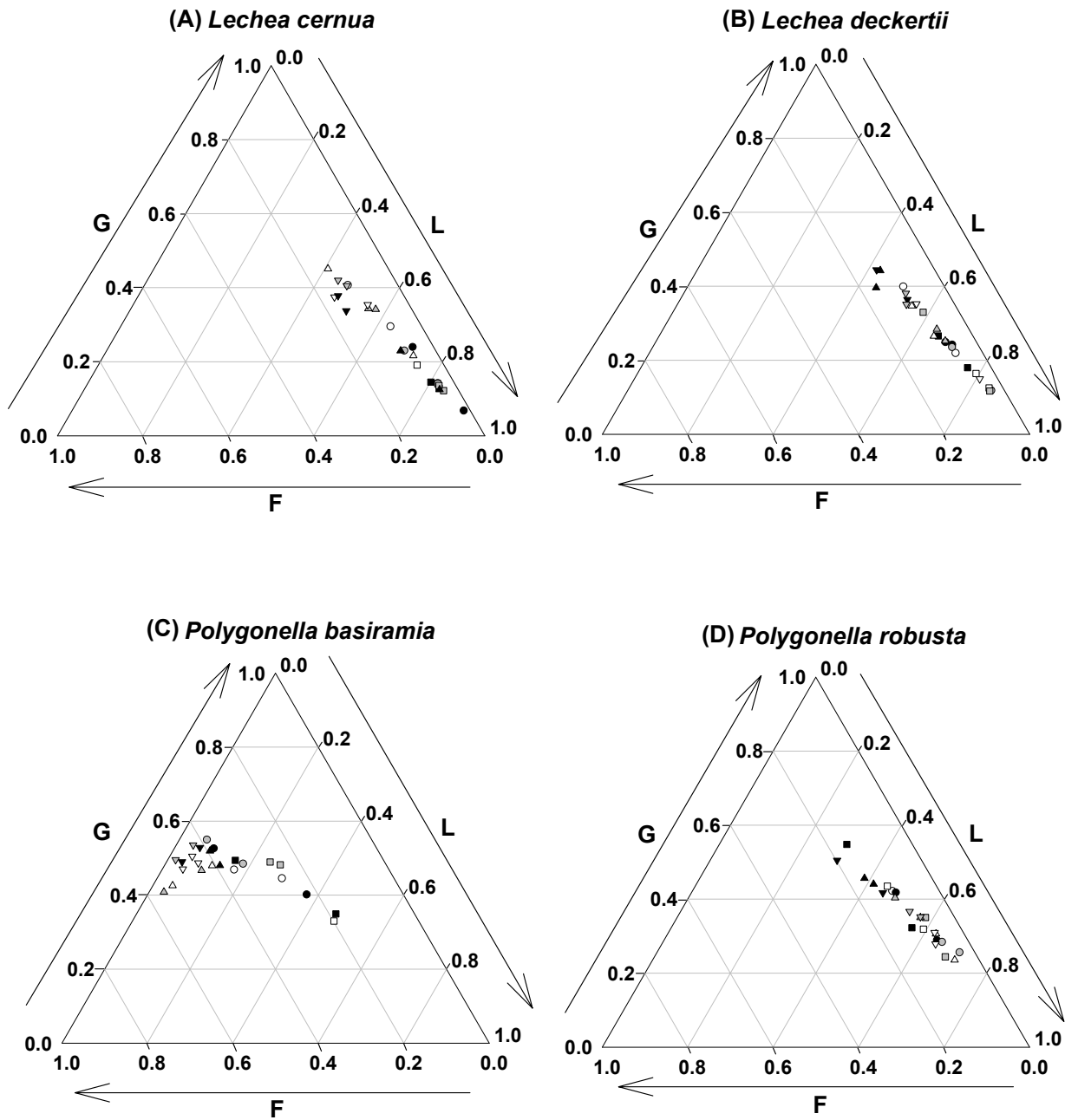


Figure 3.11. Triangular ordination of G/L/F elasticities for each study population of *Lechea cernua* (A), *Lechea deckertii* (B), *Polygonella basiramia* (C), and *Polygonella robusta* (D) in each year of study. Circles depict year 1999-2000, squares depict year 2000-2001, triangles depict year 2001-2002, and upside-down triangles depict year 2002-2003. White fill-color depicts recently-burned populations, gray fill-color depicts populations last burned 14-17 years ago, and black fill-color depicts populations last burned over 25 years ago.

Stochastic Modeling Simulations under Probabilistic Weather Patterns

The habitat-specialist species did not consistently differ from their generalist congeners with respect to mean stochastic growth rates, but they did consistently differ from their congeners with respect to the variance in log population growth rates. The stochastic growth rates of the two *Lechea* species did not significantly differ, but *P. basiramia* has a significantly lower stochastic growth rate than *P. robusta* (Fig. 3.12). However, stochastic population growth rates were more variable over four annual intervals in populations of the rosemary scrub specialist species than in generalist species (CV of stochastic λ of *L. cernua*=24.0, *L. deckertii*=17.1, *P. basiramia*=74.1, and *P. robusta*=53.6).

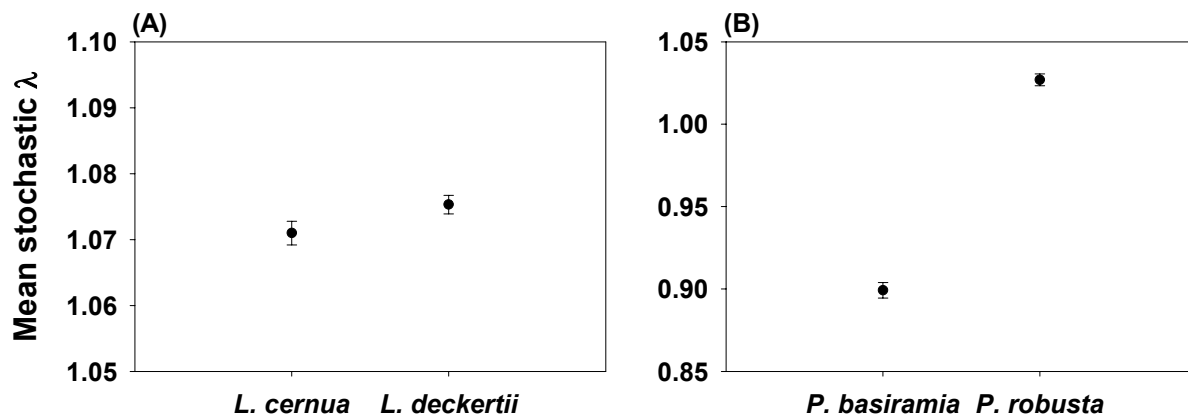


Figure 3.12. Mean stochastic population growth rates for *L. cernua* and *L. deckertii* (A) and *P. basiramia* and *P. robusta* (B). Means are shown with 95% confidence intervals. Axes in (A) and (B) are not the same scale.

Both habitat-specialist species had consistently higher quasi-extinction probabilities than their generalist congeners in modeling scenarios with historic weather patterns. After 20 years, simulations with historically probabilistic weather patterns suggested that 12.1% of *L. cernua*

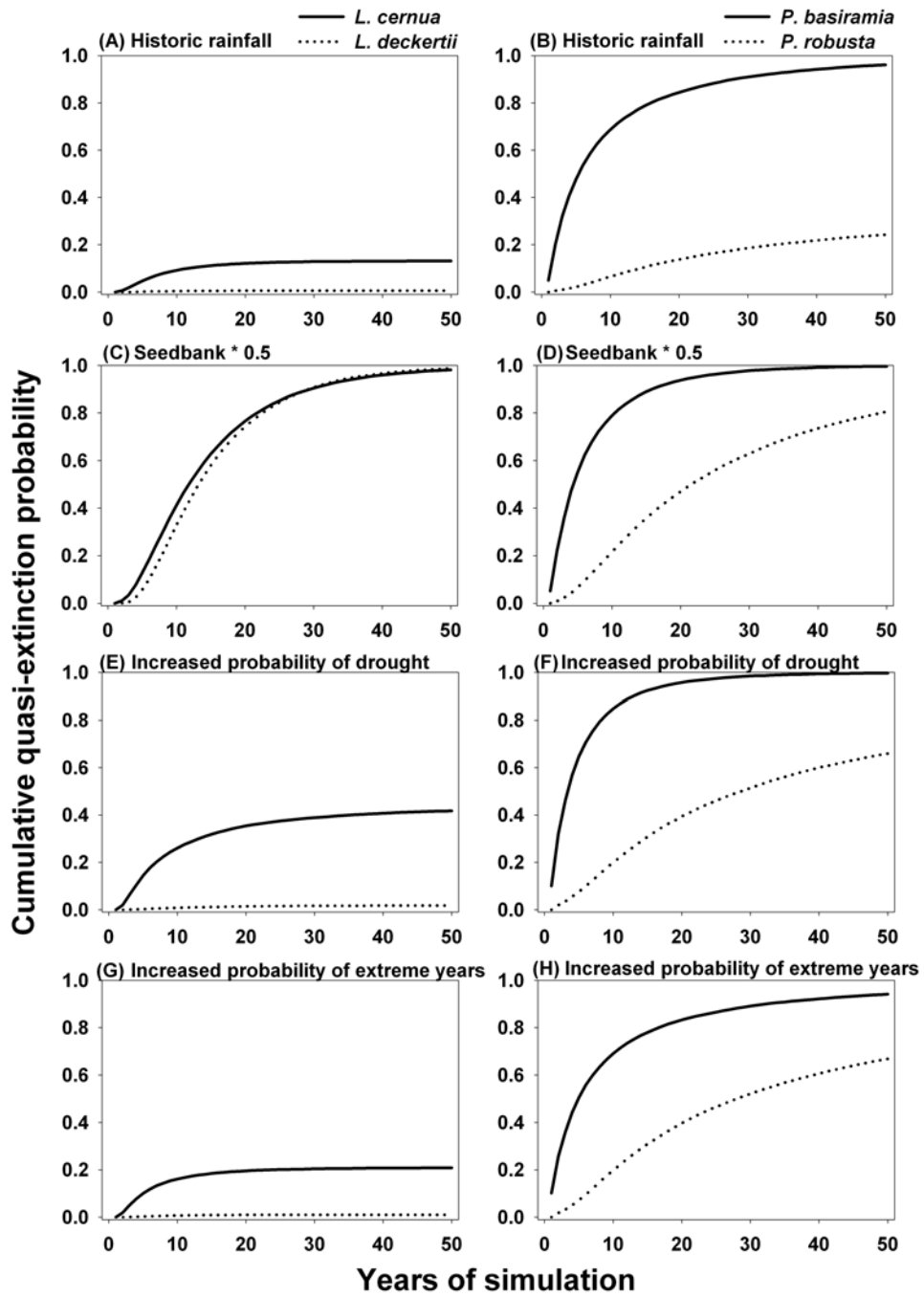
populations, 0.6% of *L. deckertii* populations, 84.5% of *P. basiramia* populations, and 13.7% of *P. robusta* populations would fall below the quasi-extinction threshold of 25 plants (Fig. 3.13, A and B). Reducing seed bank survival dramatically increased extinction probabilities of *Lechea* species, and increased extinction probabilities of *Polygonella* species to a lesser degree. When seed bank survival was reduced by half, 76.5% of *L. cernua* populations, 74.2% of *L. deckertii* populations, 93.8% of *P. basiramia* populations, and 47.0% of *P. robusta* populations fell below the quasi-extinction threshold within 20 years (Fig. 3.13, C and D).

Altered climate scenarios increased extinction risks for all four species, but almost imperceptibly in *L. deckertii*. In all four species, modeling scenarios with increased probability of drought yielded higher extinction probabilities than scenarios with increased frequencies of extremes in weather or with historic rainfall patterns. If the probability of drought (well-below average winter rainfall) was doubled, 35.4% of *L. cernua* populations, 1.4% of *L. deckertii* populations, 95.8% of *P. basiramia* populations, and 39.4% of *P. robusta* populations fell below the quasi-extinction threshold within 20 years (Fig. 3.13, E and F). In addition, if the probability of drought was doubled and the probability of above-average winter rainfall was increased by half, 19.6% of *L. cernua* populations, 1.0% of *L. deckertii* populations, 83.3% of *P. basiramia* populations, and 39.6% of *P. robusta* populations fell below the quasi-extinction threshold within 20 years (Fig. 3.13, G and H).

Stochastic Modeling Simulations under Contrasting Fire Regimes

Frequent fires increased quasi-extinction rates in three out of four study species. The *Lechea* species, which can resprout following fire, exhibited contrasting patterns of quasi-extinction risk

Figure 3.13. Mean cumulative frequency distribution (CDF) functions for time to reach a quasi-extinction threshold of 25 plants for populations of *L. cernua* and *L. deckertii* (A), (C), (E), and (G) and *P. basiramia* and *P. robusta* (B), (D), (F) and (H) modeled using contrasting scenarios. Plots (A) and (B) show the results of modeling simulations under probabilistic weather patterns (probabilities were calculated based on 71 years of rainfall data collected at Archbold Biological Station). Plots (C) and (D) show the results of simulations in which the observed rate of survival in the soil seed bank was reduced by 50% while holding rainfall patterns constant. Plots (E) and (F) show the results of simulations with twice the observed frequency of drought years (calculated by doubling the observed probabilities of drought based on 71 years of rainfall data collected at Archbold Biological Station). Plots (G) and (H) show the results of simulations with increased probabilities of both extremes in winter rainfall (driest and wettest).



under different fire regimes. Quasi-extinction risk of *L. cernua* increased slightly with longer fire return intervals, whereas quasi-extinction risk of *L. deckertii* decreased sharply with longer fire return intervals (Fig. 3.14A). In *Polygonella* species, which are killed by fire and can recover only by seedling recruitment, quasi-extinction risk is higher with increasing frequency of fires (Fig. 3.14B).

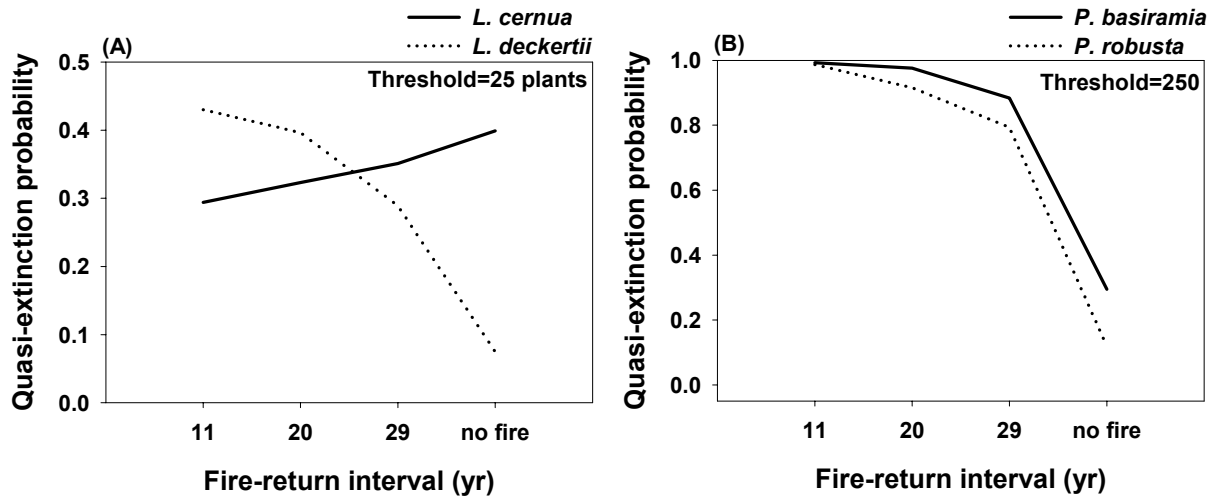


Figure 3.14. Modeled quasi-extinction probabilities of *L. cernua* and *L. deckertii* (A), and *P. basiramia* and *P. robusta* (B) after 50 years of simulation under various fire regimes (average fire-return intervals of 11, 20, and 29 years, and no fires). Modeling simulations for *Lechea* species were performed with quasi-extinction thresholds of 25 starting with initial vectors of 1000 seeds and 100 plants. *Polygonella* species were modeled with an initial vector of 1000 seeds, a quasi-extinction threshold of 250 individuals (including seeds), and under various amounts of annual seed dispersal (775 seeds annually dispersed for *P. basiramia* and 250 seeds annually dispersed for *P. robusta*). Seeds dispersed were added to the current stage vector in each year of each modeling simulation.

DISCUSSION

Rainfall and Demography

Survival, growth, seed production, recruitment, and population growth rates of all four study species were positively correlated with quarterly rainfall. Although for certain plant species,

above-average rainfall can be correlated with high mortality rates (Rose *et al.* 1998), rainfall more often is positively correlated with survival (Wagner and Spira 1994, Pfab *et al.* 2000, Mondragon *et al.* 2004), growth (Olmsted and Alvarez-Buylla 1995, Pfab *et al.* 2000, Riba *et al.* 2002), flowering (Olmsted and Alvarez-Buylla 1995, Pfab *et al.* 2000), fruit production (Olmsted and Alvarez-Buylla 1995, Riba *et al.* 2002), seed production (Wagner and Spira 1994), recruitment (Mondragon *et al.* 2004), population size (Figueroa and Davy 1991), and population growth rate (O'Connor 1993, Lennartson and Oostermeijer 2001, Mondragon *et al.* 2004, Nordbakken *et al.* 2004) in numerous plant species with a range of life history characteristics. In long-lived species, the effects of rainfall on recruitment and mortality may be delayed. The highest rates of recruitment of two long-lived arid-zone shrubs, *Eremophila maitlandii* and *E. forrestii* were observed in a wet year and two subsequent years, and the highest rates of mortality were found in the two years following a low rainfall year (Watson *et al.* 1997).

Rainfall in the winter months was correlated most strongly with population growth rate for all four of our species, presumably due to the positive correlations of winter precipitation with survival and recruitment. Winter rainfall has also been found to be correlated most strongly with population growth rates in *Hypericum cumulicola*, another Florida rosemary scrub specialist (Quintana-Ascencio *et al.* 2003). Because rosemary scrub is a highly water-limited habitat, and winter is on average the driest season of year in southern peninsular Florida (Fernald and Purdum 1992), perhaps it is not surprising that winter precipitation dramatically affects demographic parameters in rosemary scrub specialist species.

Fire and Demography

Time-since-fire did not have strong independent effects on demographic parameters of any study species. Our results contrast with those of Quintana-Ascencio *et al.* (2003) and Menges and

Quintana-Ascencio (2004), who found that seed production, survival, and population growth rates were all higher in recently burned than in long-unburned populations of two other Florida rosemary scrub specialist species, *Hypericum cumulicola* and *Eryngium cuneifolium*, respectively. Other studies of species in fire-prone habitats also have found positive effects of individual fires on demographic traits such as flowering (Brewer and Platt 1994, McConnell and Menges 2002), growth (Silva *et al.* 1991, Menges and Dolan 1998, Kaye *et al.* 2001), survival (Silva *et al.* 1991), fecundity (Silva *et al.* 1991, Menges and Dolan 1998, Kaye *et al.* 2001), seedling establishment (McConnell and Menges 2002), and population growth rates (Silva *et al.* 1991, Menges and Dolan 1998, Kaye *et al.* 2001, Satterwaithe *et al.* 2002).

The lack of a strong effect of time-since-fire on demographic parameters in our study species may be related to microhabitat availability. Hawkes and Menges (1995) found that time-since-fire was not related to density and seed production of *P. basiramia*, but that these parameters were positively correlated with percent bare sand. Their results taken together with ours suggest that as long as enough suitable bare sand microhabitat is present, species like *P. basiramia* can persist. Long-unburned (>25 years post-fire) rosemary scrub patches still contain some suitable bare sand microhabitat, although the proportion is lower than in recently burned patches (Maliakal-Witt *et al.*, in press). Despite less suitable bare sand microhabitat in long-unburned (>25 years post-fire) patches, there is no strong demographic difference between populations in recently burned and long-unburned patches. However, as time-since-fire increases to periods greater than 50 years post-fire, suitable bare sand microhabitat may disappear completely.

Annual variation in precipitation may also contribute to the lack of effect of time-since-fire on demographic parameters. Johnson and Abrahamson (1990) found that *L. cernua* and *L.*

deckertii both had slightly higher percent cover in rosemary scrub patches after a fire when compared to pre-burn levels. In the two years following the fire event, our post-burn populations of *L. cernua* and *L. deckertii* had high survival, recruitment, and population growth rates. However, the years following the fire event were both years of relatively high winter rainfall; thus, the long-unburned populations also had high population growth rates in these years. High rainfall may override effects of time-since-fire in some years.

Interaction of Fire and Rainfall

Observed effects of time-since-fire on survival were dependent on winter rainfall. In all species, I found that survival in long-unburned populations was lower than in recently-burned populations only in the year of lowest winter rainfall, although this pattern also was dependent on stage for *L. deckertii* and *P. robusta*. Quintana-Ascencio *et al.* (2003) also found that effects of time-since-fire on survival of *H. cumulicola*, another Florida rosemary scrub specialist, were only detected in certain years. I verified that the years in which they detected significant time-since-fire effects also had less than average winter precipitation. Competition for water from large Florida rosemary shrubs in long-unburned patches may be severe enough to affect survival of some rosemary scrub specialist herbs only in drought years. Locations under large Florida rosemary shrubs had significantly less soil moisture only than locations in the centers of bare sand gaps during drought periods (Gagnon *et al.* in prep).

I also observed interactive effects of time-since-fire and winter rainfall on seedling recruitment in the two habitat-generalist species, *L. deckertii* and *P. robusta*. In high winter rainfall years, seedling recruitment was higher in long-unburned populations than recently burned populations of these two species. This pattern of recruitment could be caused by amelioration of potential allelopathic effects of large Florida rosemary shrubs on *L. deckertii* and

P. robusta germination in high rainfall years, or a greater build-up of seeds of these species in the seed bank in long-unburned patches.

Fire and rainfall were found to have different interactive effects on seedling recruitment in *Banksia* spp., which are long-lived shrubs that have fire-stimulated pulses of seedling recruitment. Burgman and Lamont (1992) found that seedlings of *B. cuneata* established after fire are highly susceptible to drought. Thus fires in drought years can lead to recruitment failures and population extinctions in *B. cuneata*, which does not resprout (Burgman and Lamont 1992). Enright *et al.* (1998) found that fires that are followed by good summer rains produce strong recruitment events, which are important for population persistence in *B. attenuata*, a resprouting species.

Recruitment of all of our study species occurred in long-unburned sites; thus recruitment is not restricted to years immediately following fires. Recruitment also has been detected in long-unburned populations of other Florida rosemary scrub specialists, *H. cumulicola* (Quintana-Ascencio *et al.* 2003) and *E. cuneifolium* (Menges and Quintana-Ascencio 2004), although it was generally lower than in recently-burned populations. I did not find evidence of higher recruitment in recently burned populations in any of our study species, suggesting that strong recruitment events may be tied primarily to winter rainfall.

Temporal Variation in Demography

Recruitment and survival rates of both rosemary scrub specialist species were more variable than those of their habitat generalist congeners. High levels of temporal variation in recruitment rates have been found in several studies of individual rare species of varying life histories, for example in *Hypericum cumulicola* (Quintana-Ascencio *et al.* 2003), *Eryngium cuneifolium* (Menges and Quintana-Ascencio 2004), *Taxus floridana* (Kwit *et al.* 2004) and *Purshia subintegra*

(Maschinski *et al.* 2004). Our results suggest that greater temporal variability in recruitment and survival may be associated with habitat specialization. Habitat specialist species may be more specialized on particular environmental conditions, such as a suitable range of water availability during the winter months in the case of these rosemary scrub specialists; thus, some of their critical vital rates may be more sensitive to environmental variation than generalist species.

Kelly *et al.* (2001) also reported that the rare species had greater fluctuations in recruitment than the common species in their study of tropical trees. However, both Kelly *et al.*'s (2001) and Kelly and Bowler's (2002) studies inferred variable recruitment by comparing static size-class distributions; they did not measure recruitment rates directly nor population growth rates over time. Size-class distributions do not always correspond to age distributions (Lusk 2003), and are functions of recruitment, growth, and mortality (Baker and Wilson 2003), which were not differentiated by Kelly *et al.* (2001) or Kelly and Bowler (2002). Nonetheless, our findings based on direct measurements of recruitment rates and other vital rates over five years support Kelly *et al.*'s (2001) hypothesis of greater variation in recruitment in rarer species.

Not all vital rates of rosemary scrub specialists were more variable than those of their generalist congeners. Plant growth rates of rosemary scrub specialist species were less variable than those of their generalist congeners. This result could be explained potentially by differences in growth capacity between the rosemary scrub specialist species and their habitat generalist congeners. Growth of the specialist species appears to be less plastic than that of generalists. Thus specialists are less able to limit growth in low rainfall years or increase growth in high rainfall years, than their generalist congeners.

Rosemary scrub specialist species also exhibited greater temporal variation in population growth rates than their habitat generalist congeners. Previous studies have suggested that higher

temporal variability of population growth rates where species are rare may contribute to their distributional patterns by increasing extinction probabilities at their range limits. For example, both the vital rates and population growth rates of populations of *Helianthus divaricatus* and *Rhus aromatica* at the northern extent of their ranges were more temporally variable than populations in the centers of their ranges (Nantel and Gagnon 1999). Populations at range edges are often limited to a narrower set of environmental conditions than those at range centers; thus, populations at the edges of their ranges may resemble those of habitat specialists in that respect. Limitation to a narrower range of environmental conditions may be associated with an increased tendency for variable population growth rates when environmental conditions fluctuate over time. In this case, *P. basiramia* and *L. cernua* are more specialized on a particular set of physical microhabitat characteristics (Maliakal-Witt *et al.* in press), but they only achieve high population growth rates in these microhabitats in years when winter rainfall is high. At the same sites, population growth rates of the habitat generalist species, *P. robusta* and *L. deckertii*, are less susceptible to variation in rainfall. In general, inter-annual environmental variation may create conditions that exceed the narrower niche requirements of specialist species more frequently than the broader niche requirements of generalist species.

Temporal Variation in Elasticities

The patterns of summed elasticities of all four species tend to fall within the range of other iteroparous herbs. The high survivorship, intermediate growth, and low fecundity elasticities of populations of *L. cernua*, *L. deckertii*, and *P. robusta* are most similar to those of the iteroparous forest herbs in Silvertown *et al.*'s (1993) comparative study. This general pattern suggests that survival and growth may be relatively more important to population persistence in these species. The patterns of summed elasticities of *P. basiramia* populations fit best with iteroparous herbs of

open habitats (Silvertown *et al.* 1993); however, *P. basiramia* populations tend to have higher fecundity elasticities than most iteroparous herbs. Thus, *P. basiramia* population persistence is more dependent on fecundity than the other study species, most likely due to its short average lifespan.

I observed considerable temporal variation in elasticities in all four species corresponding to variation in population growth rates in relation to winter precipitation; variation in elasticities was not explained by time-since-fire. Previous studies have detected considerable variation in elasticities across populations of *Cirsium vulgare* and *Pedicularis furbishae* in relation to disturbance regime (Silvertown *et al.* 1996), across populations of *Primula vulgaris* in relation to forest canopy openness (Valaverde and Silvertown 1998), and across populations of *Eryngium cuneifolium* in relation to time-since-fire (Menges and Quintana-Ascenio 2004). Other studies have documented high levels of temporal variation in the relative contribution of growth, survivorship, and fecundity elasticity regions. For example, Nordbakken *et al.* (2004) detected temporal variation in growth, survivorship, and fecundity elasticities in populations of *Drosera anglica* and *D. rotundifolia*, but the rank order of importance of each to population growth rate did not change. Still other studies have detected both spatial and temporal variation in elasticities (Horvitz and Schemske 1995, Oostermeijer *et al.* 1996, Damman and Cain 1998); thus an understanding of the how elasticities vary across both of these scales is required to determine which life history stages may be more critical than others to population persistence. In our study species, it appears that temporal variation outweighs the effects of spatial variation on elasticities.

In addition, I found that survivorship elasticities were always higher than growth and fecundity elasticities in declining populations, but that the contribution of fecundity and growth

elasticities became larger in growing populations of all four species. Oostermeijer *et al.* (1996) and Menges and Quintana-Ascencio (2004) detected this same general pattern in *Gentiana pneumonanthe*, and *Eryngium cuneifolium*, respectively. In terms of long-term species persistence, environments with the highest population growth rates may be more important than other environments (Horvitz and Schemske 1995). Thus, life history stages with the highest elasticities in high winter rainfall years, such as those affecting fecundity and growth elasticities, may be most critical for long-term persistence of these species.

Demographic Variability and Extinction Risk

Both rosemary scrub specialist species had higher probabilities of quasi-extinction than their generalist congeners under every modeling scenario. Higher variance in stochastic population growth rates in rosemary scrub specialist species correlated with higher quasi-extinction probabilities relative to their generalist congeners. Although the link between population variability and extinction risk has been debated, Vucetich *et al.* (2000) presented strong evidence from simulations, experiments, and reanalysis of published data for a causal link between increased population variability and increased extinction risk. Higher temporal variability in the demography of habitat specialist species may make them more vulnerable to extinction than could be predicted solely from availability of suitable habitat patches.

Climate Change and the Fate of Habitat-specialist Species

Ample evidence exists that recent climatic changes (e.g. global warming) have already affected a broad range of organisms with diverse geographical distributions. Climate induced shifts have been observed in population dynamics, phenology of animals and plants, species distributions, community assemblages, and species interactions in both marine and terrestrial communities (see McCarty 2001, Walther *et al.* 2002, and Stenseth *et al.* 2002 for reviews). Projections on the

basis of mid-range climate-warming scenarios suggest that 15-37% of a sample of 1,103 animal and plant species will be extinct or in irreversible decline by 2050 (Thomas *et al.* 2004a).

Climate change is expected to exaggerate the earth's hydrological cycle in the next 100 years generally with increased precipitation, evapotranspiration, and occurrence of storms; however, changes are not expected to be uniform across the globe. For example, average annual precipitation is expected to decrease by 15 to 25 % over the next hundred years in Florida, and much of the southeastern United States (Jackson *et al.* 2001). Lower rainfall in Florida could lead to more frequent population declines and possibly extinctions in these rosemary scrub specialist species whose demographic parameters are so closely tied to precipitation.

High variability in vital rates and population growth rates in habitat specialist species may make them more vulnerable to extinction in the face of global climate change. Tsonis (1996) found that fluctuations around mean global precipitation have increased significantly on decadal to multi-decadal timescales over the past 150 years, such that extremes have become more probable. Easterling *et al.* (2000) also noted that climate change may lead to higher frequency of extreme weather events, and suggested that this increased frequency of extremes may be more significant ecologically than changes in mean climate. In all four study species, our modeling scenarios with increased frequencies of extremes in weather yielded higher extinction probabilities than scenarios with historic winter rainfall patterns, but lower extinction probabilities than scenarios with increased probability of drought. Thus, high winter rainfall years appear to exert a rescue effect that may allow populations to persist through drought periods. However, the periodicity of the extreme weather events can be critically important. Wichmann *et al.* (2003) found that fluctuating environments with short periods were found to decrease extinction risk, but long periods increased extinction risk because most populations can

not endure suboptimal conditions for long. If extreme weather events such as drought years tend to be clumped together, the vulnerability of habitat specialist species to extinctions may increase.

Implications for Fire Management

Our fire modeling results suggest that frequent fires can lead to population extinctions, especially in the rosemary scrub specialist, *P. basiramia*, in which individuals are killed by fires and seed bank viability is relatively low. In contrast, Quintana-Ascencio et al. (2003) and Menges and Quintana-Ascencio (2004), found that fire-return intervals of 15-30 years increased population viability of two other Florida rosemary scrub species, *H. cumulicola*, and *E. cuneifolium*. It is thus important to provide variability in fire regimes to accommodate the range of life histories of Florida rosemary scrub specialist species. Variation in fire return intervals and patchiness of burns are more likely to preserve populations of species such as *P. basiramia*, which could be eliminated from completely burned rosemary scrub patches.

CHAPTER 4. CONCLUSIONS, APPLICATIONS, AND FUTURE DIRECTIONS

In my dissertation, I addressed the following question, “do the ecological and demographic characteristics of two Florida rosemary scrub habitat specialist plant species distinguish them from their habitat generalist congeners in a way that may be linked to their rarity?” I evaluated hypotheses regarding the nature of habitat specialization by comparing the microhabitat distribution and demography of *L. cernua* and *P. basiramia*, two Florida rosemary scrub habitat specialist species, with their habitat generalist congeners, *L. deckertii* and *P. robusta*. Specifically, I addressed the following two hypotheses: 1) that habitat specialist species may occur in a narrower range of microhabitat conditions than habitat generalist species, and 2) that demographic parameters of habitat specialist species may be more variable than those of their habitat generalist congeners. For each pair of congeners, I compared the microhabitat distributions, variation in vital rates and population growth rates, and extinction probabilities under different climate and fire regimes to evaluate these hypotheses.

Both rosemary scrub specialist species occurred in a narrower range of bare sand microhabitat conditions than their habitat generalist congeners. Although percentage bare sand was correlated with the distribution of all species, the rosemary scrub specialists were significantly more likely to occur in sites with high percentage bare sand, whereas microhabitats of generalists were more variable with respect to percentage bare sand. For both rosemary scrub specialists, over 70% of all individuals sampled occurred in microhabitats with $\geq 80\%$ bare sand (73% for *L. cernua* and 80% for *P. basiramia*), whereas only 36% of *L. deckertii* individuals and 29% of *P. robusta* individuals occurred with $\geq 80\%$ bare sand. Plants of all four species occurred in microhabitats that were

farther from dominant shrubs, *Ceratiola* and *Quercus* spp., than random points. Seedlings of both habitat-specialists grew larger in bare sand microhabitats, whereas ground lichens and litter did not affect seedling growth of habitat-generalists. As time-since-fire increases, bare sand cover decreases, *Ceratiola* density increases, *Quercus* density remains constant, and shrubs become taller. Physical characteristics, such as soil temperature, soil carbon, and soil moisture, differ slightly with respect to microhabitat. Specialization of *P. basiramia* and *L. cernua* to microhabitats with high percentage bare sand may limit the distribution of these rare species.

Most demographic parameters of habitat specialist species were more variable with respect to variation in winter precipitation than those of their habitat generalist congeners. Survival, growth, seed production, recruitment, and population growth rates of all four study species were positively correlated with quarterly rainfall. Rainfall in the winter months was correlated most strongly with population growth rate for all four study species. Time-since-fire did not have strong independent effects on demographic parameters of any study species. Observed effects of time-since-fire on survival and seedling recruitment were dependent on winter rainfall. Recruitment and survival rates of both rosemary scrub specialist species were more variable than those of their habitat generalist congeners; however, plant growth rates of rosemary scrub specialist species were less variable than those of their generalist congeners. Rosemary scrub specialist species also exhibited greater temporal variation in population growth rates than their habitat generalist congeners. In all four species, variation in elasticities corresponded to variation in population growth rates in relation to winter precipitation; variation in elasticities was not explained by time-since-fire. Both rosemary scrub specialist species

had higher probabilities of quasi-extinction than their generalist congeners under every climate modeling scenario. High variability in vital rates and population growth rates in habitat specialist species may make them more vulnerable to extinction in the face of global climate change.

In answer to the overall question posed, it appears that the narrower microhabitat requirements and greater temporal variability of demographic parameters of *L. cernua* and *P. basiramia* distinguish them from their habitat generalist congeners. The restriction of *P. basiramia* and *L. cernua* to microhabitats with high percentage bare sand may limit their distribution to rosemary scrub habitat. Greater temporal variability in recruitment, survival, and population growth rates in *L. cernua* and *P. basiramia* may be associated with specialization on a narrower range of environmental conditions in these rosemary scrub specialist species. Greater temporal variability of demographic parameters in these rosemary scrub specialist species may make them more vulnerable to extinction than could be predicted solely from availability of suitable rosemary scrub habitat.

APPLICATIONS

These results can be applied to develop management plans for the conservation of viable populations of *L. cernua* and *P. basiramia*, as well as other rosemary scrub specialist species. Fires maintain suitable microhabitats for rosemary scrub specialist herbs by reducing competition from *Ceratiola ericoides* and exposing bare sand microsites for seedling establishment. Management agencies can assess the benefits of prescribed fires for rosemary scrub specialist species by conducting post-fire monitoring of the availability of bare sand microhabitats that are free from competition from neighboring

Ceratiola. Fires at return intervals of 15-30 years are critical to maintain viable populations of some Florida rosemary scrub specialist species, such as *H. cumulicola*, and *E. cuneifolium* (Quintana-Ascencio et al. 2003 and Menges and Quintana-Ascencio 2004). However, my fire modeling results suggest that frequent fires can lead to population extinctions, especially in the rosemary scrub specialist, *P. basiramia*, in which individuals are killed by fires and seed bank viability is relatively low. Thus, variability in fire regimes is required to accommodate the range of life histories of Florida rosemary scrub specialist species. Variation in fire return intervals and patchiness of burns are more likely to preserve populations of species such as *P. basiramia*, which could be eliminated from completely burned rosemary scrub patches.

FUTURE DIRECTIONS

A logical next step in this research program would be to identify the mechanisms behind these patterns of microhabitat specialization and variability in demographic parameters with experimental tests. Further characterization of contrasting microhabitats in terms of seasonal water availability and abundance of cryptogamic soil crusts could clarify the mechanisms behind the restriction of these rosemary scrub species to bare sand microhabitats. In addition, transplant experiments in which microhabitat conditions are manipulated could be used to further evaluate the effects of microhabitat on seedling establishment, survival, and growth. Over two growing seasons, I attempted to conduct these types of transplant experiments; unfortunately, spring droughts prevented their success. However, repeating experiments such as these in a more favorable rainfall year would aid in identifying exactly which life history stages are limited by microhabitat conditions in these rosemary scrub specialist species. Furthermore, manipulating both

microhabitat and soil moisture conditions in a field experiment could determine the relative importance of microhabitat and rainfall to generating the observed demographic variability of these rosemary scrub specialist species. Finally, a meta-analysis combining the results from this study with other similar demographic studies could determine whether these observed patterns are general features of habitat specialists.

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APPENDIX A. LETTER OF PERMISSION FROM THE AMERICAN JOURNAL OF BOTANY

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Dear Satya Maliakal-Witt,

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as a chapter in your dissertation, which will be submitted to the Graduate School at Louisiana State University.

Sincerely,

Caroline Spellman

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APPENDIX B. PROJECTION MATRICES OF *L. CERNUA*, *L. DECKERTII*, *P. BASIRAMIA*, AND *P. ROBUSTA* FOR EACH POPULATION IN EACH YEAR

<i>Lechea cernua</i> , site 19, 1999-2000, tsf=4					
0.831	0	0	80.74	346.32	681.70
0.0001	0	0	0.0085	0.0370	0.0725
0	0.545	0.421	0.261	0.171	0.000
0	0.273	0.105	0.261	0.057	0.000
0	0.000	0.263	0.304	0.371	0.294
0	0.000	0.105	0.043	0.200	0.353
<i>Lechea cernua</i> , site 29, 1999-2000, tsf=3					
0.806	0	0	81.68	183.79	633.48
0.0008	0	0	0.0595	0.1335	0.4605
0	0.667	0.385	0.214	0.350	0.000
0	0.042	0.077	0.071	0.150	0.000
0	0.000	0.231	0.357	0.200	0.350
0	0.000	0.154	0.000	0.150	0.350
<i>Lechea cernua</i> , site 59, 1999-2000, tsf=32					
0.835	0	0	83.37	180.91	510.11
0.0001	0	0	0.0010	0.0020	0.0050
0	0.700	0.400	0.231	0.130	0.182
0	0.000	0.067	0.000	0.000	0.000
0	0.100	0.267	0.308	0.304	0.091
0	0.100	0.067	0.077	0.348	0.636
<i>Lechea cernua</i> , site 62, 1999-2000, tsf=32					
0.843	0	0	92.61	161.98	401.11
0.0001	0	0	0.0010	0.0015	0.0035
0	0.542	0.476	0.200	0.333	0.000
0	0.000	0.024	0.000	0.095	0.000
0	0.000	0.095	0.200	0.190	0.400
0	0.000	0.024	0.100	0.095	0.600

<i>Lechea cernua</i> , site 90, 1999-2000, tsf=14					
0.772	0	0	95.94	210.83	486.34
0.0002	0	0	0.0275	0.0610	0.1405
0	0.591	0.235	0.200	0.065	0.000
0	0.000	0.059	0.133	0.065	0.111
0	0.045	0.294	0.200	0.435	0.222
0	0.045	0.000	0.000	0.065	0.333
<i>Lechea cernua</i> , site 92, 1999-2000, tsf=14					
0.852	0	0	119.44	194.12	366.10
0.0003	0	0	0.0325	0.0525	0.0990
0	0.684	0.545	0.263	0.190	0.375
0	0.000	0.030	0.105	0.095	0.000
0	0.000	0.060	0.211	0.238	0.000
0	0.000	0.030	0.053	0.190	0.375
<i>Lechea cernua</i> , site 19, 2000-2001, tsf=0					
0.831	0	0	223.04	603.23	2160.04
0.0001	0	0	0.0023	0.0061	0.0219
0	0.600	0.211	0.077	0.029	0.000
0	0.000	0.026	0.000	0.059	0.000
0	0.200	0.105	0.154	0.088	0.000
0	0.000	0.132	0.154	0.235	0.529
<i>Lechea cernua</i> , site 29, 2000-2001, tsf=4					
0.806	0	0	210.50	667.50	1684.95
0.0001	0	0	0.0025	0.0080	0.0203
0	0.471	0.297	0.000	0.000	0.000
0	0.059	0.027	0.222	0.111	0.000
0	0.000	0.162	0.333	0.556	0.125
0	0.000	0.027	0.000	0.056	0.250

<i>Lechea cernua</i> , site 59, 2000-2001, tsf=33					
0.835	0	0	282.65	611.26	2654.53
0.0001	0	0	0.0028	0.0060	0.0262
0	0.200	0.042	0.200	0.045	0.000
0	0.200	0.000	0.000	0.000	0.000
0	0.000	0.083	0.000	0.045	0.000
0	0.000	0.208	0.200	0.364	0.440
<i>Lechea cernua</i> , site 62, 2000-2001, tsf=33					
0.843	0	0	285.25	401.74	1694.04
0.0002	0	0	0.0637	0.0897	0.3784
0	0.200	0.204	0.200	0.000	0.000
0	0.200	0.000	0.000	0.000	0.000
0	0.000	0.020	0.000	0.083	0.000
0	0.000	0.082	0.200	0.000	0.143
<i>Lechea cernua</i> , site 90, 2000-2001, tsf=15					
0.772	0	0	261.41	759.79	1611.89
0.0001	0	0	0.0230	0.0670	0.1421
0	0.364	0.405	0.000	0.053	0.000
0	0.000	0.081	0.100	0.000	0.000
0	0.000	0.135	0.400	0.158	0.111
0	0.000	0.054	0.100	0.105	0.222
<i>Lechea cernua</i> , site 92, 2000-2001, tsf=15					
0.852	0	0	312.27	441.99	1883.25
0.0001	0	0	0.0027	0.0038	0.0164
0	0.900	0.367	0.143	0.071	0.000
0	0.000	0.000	0.071	0.000	0.000
0	0.000	0.061	0.286	0.357	0.100
0	0.000	0.061	0.071	0.286	0.400

<i>Lechea cernua</i> , site 19, 2001-2002, tsf=1					
0.831	0	0	109.19	470.70	1060.51
0.0004	0	0	0.0567	0.2445	0.5510
0	0.571	0.231	0.000	0.000	0.021
0	0.143	0.154	0.000	0.000	0.000
0	0.143	0.346	0.800	0.238	0.146
0	0.000	0.154	0.200	0.619	0.833
<i>Lechea cernua</i> , site 29, 2001-2002, tsf=5					
0.806	0	0	175.37	479.99	996.10
0.0001	0	0	0.0160	0.0445	0.0925
0	0.250	0.194	0.111	0.138	0.000
0	0.083	0.194	0.111	0.069	0.000
0	0.083	0.194	0.444	0.345	0.000
0	0.000	0.032	0.111	0.241	0.714
<i>Lechea cernua</i> , site 59, 2001-2002, tsf=34					
0.835	0	0	108.17	244.26	1312.91
0.0001	0	0	0.0011	0.0024	0.0130
0	0.600	0.176	0.000	0.000	0.000
0	0.100	0.059	0.000	0.000	0.000
0	0.100	0.059	0.333	0.429	0.000
0	0.200	0.647	0.000	0.571	0.933
<i>Lechea cernua</i> , site 62, 2001-2002, tsf=34					
0.843	0	0	109.16	246.50	245.35
0.0001	0	0	0.0010	0.0025	0.0025
0	0.600	0.071	0.000	0.000	0.000
0	0.100	0.071	0.000	0.000	0.000
0	0.100	0.071	0.333	0.419	0.000
0	0.200	0.714	0.000	0.561	0.943

<i>Lechea cernua</i> , site 90, 2001-2002, tsf=16					
0.772	0	0	100.04	364.00	994.70
0.0002	0	0	0.0255	0.0930	0.2545
0	0.500	0.241	0.000	0.074	0.000
0	0.083	0.276	0.000	0.111	0.000
0	0.083	0.276	0.333	0.370	0.176
0	0.000	0.172	0.000	0.222	0.765
<i>Lechea cernua</i> , site 92, 2001-2002, tsf=16					
0.852	0	0	110.53	407.92	798.07
0.0001	0	0	0.0150	0.0545	0.1065
0	0.625	0.390	0.000	0.231	0.167
0	0.000	0.024	0.000	0.077	0.000
0	0.250	0.293	0.333	0.231	0.250
0	0.000	0.146	0.000	0.385	0.500
<i>Lechea cernua</i> , site 19, 2002-2003, tsf=2					
0.831	0	0	250.04	744.29	2454.15
0.0002	0	0	0.0772	0.1477	0.7577
0	0.800	0.200	0.000	0.040	0.000
0	0.000	0.100	0.400	0.080	0.017
0	0.000	0.200	0.200	0.480	0.259
0	0.000	0.000	0.200	0.080	0.586
<i>Lechea cernua</i> , site 29, 2002-2003, tsf=6					
0.806	0	0	168.89	487.64	1097.30
0.0005	0	0	0.0991	0.2862	0.6440
0	0.286	0.208	0.091	0.143	0.063
0	0.214	0.083	0.091	0.107	0.125
0	0.071	0.250	0.273	0.321	0.313
0	0.143	0.042	0.000	0.071	0.250

<i>Lechea cernua</i> , site 59, 2002-2003, tsf=35					
0.835	0	0	174.46	484.44	3323.78
0.0001	0	0	0.0157	0.0436	0.2990
0	0.000	0.000	0.143	0.000	0.000
0	0.000	0.063	0.286	0.125	0.000
0	0.545	0.313	0.429	0.500	0.057
0	0.364	0.625	0.071	0.375	0.857
<i>Lechea cernua</i> , site 62, 2002-2003, tsf=35					
0.843	0	0	176.06	635.72	1601.25
0.0003	0	0	0.0584	0.2109	0.5313
0	0.476	0.132	0.143	0.000	0.056
0	0.095	0.105	0.286	0.000	0.000
0	0.167	0.474	0.429	0.800	0.000
0	0.143	0.237	0.071	0.200	0.889
<i>Lechea cernua</i> , site 90, 2002-2003, tsf=17					
0.772	0	0	159.51	517.82	1263.75
0.0003	0	0	0.0560	0.1817	0.4435
0	0.500	0.176	0.083	0.167	0.042
0	0.115	0.118	0.333	0.125	0.042
0	0.231	0.176	0.500	0.417	0.375
0	0.000	0.059	0.000	0.250	0.542
<i>Lechea cernua</i> , site 92, 2002-2003, tsf=17					
0.852	0	0	162.75	363.89	1081.57
0.0003	0	0	0.0631	0.1410	0.4190
0	0.636	0.214	0.071	0.045	0.000
0	0.000	0.071	0.286	0.091	0.118
0	0.273	0.321	0.429	0.182	0.059
0	0.000	0.179	0.071	0.682	0.824

<i>Lechea deckertii</i> , site 19, 1999-2000, tsf=4					
0.906	0	0	30.16	186.17	1091.34
0.0004	0	0	0.0120	0.0739	0.4331
0	0.750	0.655	0.400	0.316	0.000
0	0.063	0.138	0.367	0.053	0.000
0	0.000	0.034	0.100	0.263	0.167
0	0.000	0.034	0.000	0.000	0.500
<i>Lechea deckertii</i> , site 29, 1999-2000, tsf=3					
0.844	0	0	81.84	381.28	1224.50
0.0003	0	0	0.0253	0.1177	0.3780
0	0.600	0.231	0.098	0.067	0.200
0	0.000	0.077	0.341	0.000	0.000
0	0.000	0.385	0.390	0.400	0.200
0	0.000	0.077	0.049	0.400	0.600
<i>Lechea deckertii</i> , site 59, 1999-2000, tsf=32					
0.887	0	0	73.51	324.39	1562.38
0.0002	0	0	0.0156	0.0688	0.3313
0	0.500	0.526	0.333	0.059	0.000
0	0.000	0.053	0.133	0.029	0.036
0	0.000	0.158	0.133	0.265	0.036
0	0.000	0.053	0.000	0.206	0.607
<i>Lechea deckertii</i> , site 72, 1999-2000, tsf=28					
0.881	0	0	125.39	463.39	962.84
0.0002	0	0	0.0293	0.1083	0.2249
0	0.600	0.529	0.000	0.079	0.000
0	0.000	0.235	0.316	0.026	0.077
0	0.000	0.059	0.316	0.342	0.231
0	0.000	0.000	0.000	0.158	0.385

<i>Lechea deckertii</i> , site 90, 1999-2000, tsf=14					
0.822	0	0	101.98	315.30	647.50
0.0003	0	0	0.0344	0.1064	0.2185
0	0.263	0.516	0.286	0.156	0.000
0	0.000	0.097	0.071	0.000	0.000
0	0.000	0.065	0.286	0.250	0.000
0	0.000	0.000	0.000	0.094	0.500
<i>Lechea deckertii</i> , site 92, 1999-2000, tsf=14					
0.860	0	0	54.48	258.69	445.03
0.0004	0	0	0.0255	0.1208	0.2077
0	0.522	0.563	0.000	0.211	0.000
0	0.000	0.000	0.143	0.000	0.000
0	0.000	0.125	0.429	0.316	0.143
0	0.000	0.021	0.000	0.263	0.571
<i>Lechea deckertii</i> , site 19, 2000-2001, tsf=0					
0.906	0	0	34.03	239.77	1484.04
0.0003	0	0	0.0096	0.0675	0.4181
0	0.333	0.180	0.095	0.000	0.000
0	0.000	0.131	0.143	0.077	0.200
0	0.000	0.164	0.333	0.615	0.000
0	0.000	0.000	0.000	0.077	0.200
<i>Lechea deckertii</i> , site 29, 2000-2001, tsf=4					
0.844	0	0	168.56	708.52	2098.31
0.0001	0	0	0.0275	0.1158	0.3429
0	0.333	0.313	0.053	0.067	0.083
0	0.000	0.125	0.316	0.133	0.000
0	0.000	0.000	0.263	0.433	0.333
0	0.000	0.063	0.000	0.100	0.167

<i>Lechea deckertii</i> , site 59, 2000-2001, tsf=33					
0.887	0	0	28.99	557.65	3178.47
0.0001	0	0	0.0033	0.0641	0.3652
0	0.692	0.308	0.000	0.000	0.040
0	0.154	0.154	0.143	0.000	0.000
0	0.000	0.192	0.143	0.400	0.000
0	0.000	0.077	0.143	0.133	0.200
<i>Lechea deckertii</i> , site 72, 2000-2001, tsf=29					
0.881	0	0	147.30	719.21	1857.94
0.0001	0	0	0.0205	0.1001	0.2587
0	0.692	0.391	0.056	0.031	0.000
0	0.154	0.043	0.222	0.031	0.000
0	0.000	0.217	0.222	0.250	0.000
0	0.000	0.000	0.000	0.125	0.167
<i>Lechea deckertii</i> , site 90, 2000-2001, tsf=15					
0.822	0	0	144.54	803.01	3763.72
0.0001	0	0	0.0128	0.0710	0.3326
0	0.800	0.380	0.000	0.000	0.000
0	0.000	0.060	0.250	0.063	0.000
0	0.000	0.120	0.500	0.375	0.143
0	0.000	0.000	0.000	0.000	0.143
<i>Lechea deckertii</i> , site 92, 2000-2001, tsf=15					
0.860	0	0	145.53	411.65	1780.39
0.0001	0	0	0.0251	0.0711	0.3075
0	0.769	0.407	0.091	0.000	0.000
0	0.077	0.136	0.182	0.042	0.000
0	0.000	0.153	0.455	0.292	0.364
0	0.000	0.017	0.000	0.333	0.091

<i>Lechea deckertii</i> , site 19, 2001-2002, tsf=1					
0.906	0	0	287.66	864.96	1053.33
0.0002	0	0	0.0508	0.1527	0.1860
0	0.143	0.321	0.000	0.000	0.000
0	0.143	0.321	0.238	0.030	0.000
0	0.143	0.321	0.714	0.455	0.250
0	0.000	0.000	0.048	0.485	0.500
<i>Lechea deckertii</i> , site 29, 2001-2002, tsf=5					
0.844	0	0	122.32	421.56	786.43
0.0003	0	0	0.0413	0.1424	0.2655
0	0.142	0.143	0.115	0.034	0.000
0	0.142	0.071	0.385	0.069	0.000
0	0.142	0.000	0.269	0.517	0.333
0	0.000	0.000	0.000	0.207	0.333
<i>Lechea deckertii</i> , site 59, 2001-2002, tsf=34					
0.887	0	0	55.58	339.47	931.42
0.0008	0	0	0.0485	0.2958	0.8115
0	0.600	0.455	0.200	0.000	0.000
0	0.000	0.000	0.200	0.000	0.000
0	0.200	0.182	0.600	0.143	0.000
0	0.100	0.000	0.000	0.857	0.917
<i>Lechea deckertii</i> , site 72, 2001-2002, tsf=30					
0.881	0	0	102.83	774.07	3202.50
0.0003	0	0	0.0311	0.2343	0.9692
0	0.833	0.333	0.071	0.000	0.000
0	0.000	0.167	0.357	0.000	0.000
0	0.000	0.278	0.214	0.409	0.333
0	0.000	0.111	0.071	0.409	0.667

<i>Lechea deckertii</i> , site 90, 2001-2002, tsf=16					
0.822	0	0	77.68	445.98	1008.04
0.0002	0	0	0.0189	0.1085	0.2452
0	0.143	0.343	0.125	0.000	0.000
0	0.000	0.114	0.250	0.053	0.000
0	0.143	0.171	0.500	0.526	0.188
0	0.000	0.057	0.000	0.263	0.812
<i>Lechea deckertii</i> , site 92, 2001-2002, tsf=16					
0.860	0	0	36.96	334.08	524.72
0.0004	0	0	0.0146	0.1318	0.2071
0	0.143	0.366	0.071	0.042	0.000
0	0.000	0.098	0.214	0.042	0.000
0	0.143	0.244	0.643	0.333	0.200
0	0.000	0.049	0.000	0.500	0.800
<i>Lechea deckertii</i> , site 19, 2002-2003, tsf=2					
0.906	0	0	149.14	1104.10	3055.39
0.0002	0	0	0.0354	0.2623	0.7259
0	0.533	0.545	0.176	0.024	0.000
0	0.133	0.273	0.471	0.071	0.100
0	0.000	0.091	0.176	0.571	0.200
0	0.000	0.000	0.000	0.262	0.500
<i>Lechea deckertii</i> , site 29, 2002-2003, tsf=6					
0.844	0	0	129.49	424.93	1099.40
0.0002	0	0	0.0277	0.0909	0.2351
0	0.533	0.000	0.000	0.000	0.000
0	0.133	0.286	0.200	0.216	0.100
0	0.000	0.000	0.250	0.297	0.100
0	0.000	0.000	0.000	0.081	0.200

<i>Lechea deckertii</i> , site 59, 2002-2003, tsf=35					
0.887	0	0	154.04	324.67	2696.52
0.0002	0	0	0.0422	0.0889	0.7380
0	0.143	0.185	0.100	0.000	0.000
0	0.286	0.111	0.400	0.000	0.000
0	0.000	0.370	0.300	0.556	0.125
0	0.000	0.148	0.100	0.444	0.833
<i>Lechea deckertii</i> , site 72, 2002-2003, tsf=31					
0.881	0	0	179.46	528.01	1935.79
0.0005	0	0	0.1018	0.2996	1.0985
0	0.500	0.118	0.125	0.000	0.000
0	0.250	0.294	0.500	0.050	0.000
0	0.000	0.412	0.375	0.600	0.250
0	0.000	0.118	0.000	0.250	0.650
<i>Lechea deckertii</i> , site 90, 2002-2003, tsf=17					
0.822	0	0	80.49	263.87	820.66
0.0006	0	0	0.0604	0.1979	0.6153
0	0.538	0.211	0.000	0.000	0.000
0	0.154	0.263	0.778	0.217	0.000
0	0.000	0.184	0.000	0.435	0.455
0	0.000	0.105	0.111	0.130	0.455
<i>Lechea deckertii</i> , site 92, 2002-2003, tsf=17					
0.860	0	0	57.81	248.33	1067.27
0.0003	0	0	0.0217	0.0930	0.3998
0	0.500	0.091	0.100	0.032	0.000
0	0.188	0.409	0.200	0.161	0.034
0	0.000	0.227	0.500	0.548	0.207
0	0.000	0.182	0.000	0.194	0.690

<i>Polygonella basiramia</i> , site 19, 1999-2000, tsf=4					
0.196	0	44.55	0	111.88	128.55
0.0004	0	0.0606	0	0.1489	0.1702
0.0006	0	0.1010	0	0.2482	0.2836
0	0.083	0.032	0.091	0.000	0.000
0	0.000	0.063	0.182	0.000	0.000
0	0.000	0.048	0.182	0.000	0.000
<i>Polygonella basiramia</i> , site 29, 1999-2000, tsf=3					
0.248	0	59.57	0	123.66	251.68
0.0003	0	0.0575	0	0.1175	0.5100
0.0003	0	0.0575	0	0.1175	0.2318
0	0.091	0.038	0.143	0.000	0.000
0	0.000	0.096	0.071	0.125	0.000
0	0.000	0.019	0.071	0.125	0.000
<i>Polygonella basiramia</i> , site 59, 1999-2000, tsf=32					
0.222	0	53.31	0	79.52	156.18
0.0001	0	0.0093	0	0.0139	0.0273
0.0001	0	0.0164	0	0.0243	0.0465
0	0.062	0.022	0.000	0.000	0.000
0	0.062	0.065	0.053	0.154	0.000
0	0.188	0.130	0.421	0.000	0.024
<i>Polygonella basiramia</i> , site 72, 1999-2000, tsf=28					
0.231	0	43.29	0	110.46	221.67
0.0007	0	0.1010	0	0.2521	0.4913
0.0004	0	0.0621	0	0.1552	0.3023
0	0.037	0.059	0.000	0.063	0.000
0	0.185	0.235	0.053	0.000	0.089
0	0.408	0.059	0.421	0.125	0.036

<i>Polygonella basiramia</i> , site 90, 1999-2000, tsf=14					
0.197	0	51.09	0	71.72	191.63
0.0003	0	0.0576	0	0.0804	0.2067
0.0002	0	0.0288	0	0.0402	0.1033
0	0.154	0.022	0.077	0.000	0.000
0	0.154	0.065	0.154	0.077	0.069
0	0.231	0.022	0.000	0.000	0.000
<i>Polygonella basiramia</i> , site 92, 1999-2000, tsf=14					
0.192	0	58.12	0	80.45	148.26
0.0004	0	0.1000	0	0.1373	0.2471
0.0002	0	0.0400	0	0.0549	0.0988
0	0.059	0.000	0.000	0.000	0.000
0	0.353	0.267	0.222	0.000	0.000
0	0.412	0.133	0.333	0.143	0.000
<i>Polygonella basiramia</i> , site 29, 2000-2001, tsf=4					
0.248	0	59.10	0	89.52	187.54
0.0001	0	0.0090	0	0.0136	0.0285
0.0001	0	0.0090	0	0.0136	0.0285
0	0.000	0.000	0.000	0.000	0.000
0	0.333	0.000	0.111	0.000	0.000
0	0.067	0.162	0.222	0.000	0.000
<i>Polygonella basiramia</i> , site 59, 2000-2001, tsf=33					
0.222	0	41.21	0	70.56	100.66
0.0001	0	0.0072	0	0.0123	0.0176
0.0001	0	0.0072	0	0.0123	0.0176
0	0.077	0.000	0.000	0.000	0.000
0	0.077	0.000	0.058	0.000	0.000
0	0.231	0.067	0.471	0.000	0.000

<i>Polygonella basiramia</i> , site 72, 2000-2001, tsf=29					
0.231	0	34.62	0	100.31	254.05
0.0001	0	0.0058	0	0.0167	0.0423
0.0003	0	0.0390	0	0.1093	0.2661
0	0.037	0.000	0.000	0.000	0.000
0	0.185	0.033	0.063	0.000	0.000
0	0.407	0.267	0.500	0.000	0.000
<i>Polygonella basiramia</i> , site 90, 2000-2001, tsf=15					
0.197	0	33.62	0	80.34	153.53
0.0001	0	0.0068	0	0.0164	0.0313
0.0001	0	0.0068	0	0.0164	0.0313
0	0.182	0.029	0.000	0.000	0.000
0	0.136	0.029	0.083	0.000	0.000
0	0.273	0.200	0.333	0.000	0.053
<i>Polygonella basiramia</i> , site 92, 2000-2001, tsf=15					
0.192	0	33.20	0	75.47	145.67
0.0001	0	0.0070	0	0.0159	0.0307
0.0001	0	0.0070	0	0.0159	0.0307
0	0.059	0.000	0.000	0.000	0.000
0	0.353	0.077	0.429	0.000	0.000
0	0.412	0.231	0.429	0.059	0.067
<i>Polygonella basiramia</i> , site 29, 2001-2002, tsf=5					
0.248	0	64.46	0	74.84	225.73
0.0037	0	0.7316	0	0.8476	2.4576
0.0030	0	0.5986	0	0.7628	2.0108
0	0.000	0.000	0.000	0.000	0.000
0	0.333	0.111	0.556	0.000	0.000
0	0.067	0.222	0.000	0.200	0.207

<i>Polygonella basiramia</i> , site 35, 2001-2002, tsf=5					
0.248	0	53.71	0	83.76	121.14
0.0022	0	0.3476	0	0.5420	0.7839
0.0025	0	0.3972	0	0.4336	0.8958
0	0.000	0.000	0.000	0.000	0.000
0	0.556	0.246	0.625	0.143	0.154
0	0.000	0.174	0.000	0.571	0.308
<i>Polygonella basiramia</i> , site 59, 2001-2002, tsf=34					
0.222	0	72.57	0	96.19	202.91
0.0009	0	0.2173	0	0.2859	0.5850
0.0006	0	0.1630	0	0.2144	0.4388
0	0.077	0.000	0.000	0.000	0.000
0	0.077	0.400	0.095	0.077	0.000
0	0.231	0.100	0.429	0.231	0.257
<i>Polygonella basiramia</i> , site 72, 2001-2002, tsf=30					
0.231	0	116.20	0	108.64	246.17
0.0007	0	0.2490	0	0.2333	0.4900
0.0002	0	0.0711	0	0.0666	0.1458
0	0.037	0.000	0.000	0.000	0.000
0	0.185	0.091	0.095	0.111	0.000
0	0.407	0.636	0.429	0.222	0.067
<i>Polygonella basiramia</i> , site 90, 2001-2002, tsf=16					
0.197	0	36.26	0	64.33	165.58
0.0009	0	0.1406	0	0.2465	0.6130
0.0037	0	0.5624	0	0.9856	2.4520
0	0.174	0.125	0.182	0.000	0.033
0	0.174	0.083	0.273	0.000	0.033
0	0.261	0.125	0.000	0.143	0.067

<i>Polygonella basiramia</i> , site 92, 2001-2002, tsf=16					
0.192	0	52.64	0	68.13	130.36
0.0006	0	0.0925	0	0.1190	0.2230
0.0011	0	0.1851	0	0.2384	0.6690
0	0.059	0.040	0.000	0.000	0.000
0	0.353	0.160	0.375	0.235	0.023
0	0.412	0.200	0.375	0.059	0.070
<i>Polygonella basiramia</i> , site 19, 2002-2003, tsf=2					
0.196	0	29.04	0	84.82	277.59
0.0006	0	0.0676	0	0.1908	0.5921
0.0028	0	0.3381	0	0.9537	2.9608
0	0.130	0.000	0.167	0.000	0.000
0	0.348	0.385	0.000	0.143	0.000
0	0.348	0.269	0.167	0.143	0.143
<i>Polygonella basiramia</i> , site 29, 2002-2003, tsf=6					
0.248	0	34.61	0	99.40	201.51
0.0007	0	0.0762	0	0.2112	0.4165
0.0018	0	0.1906	0	0.5278	1.0412
0	0.130	0.059	0.200	0.000	0.000
0	0.348	0.147	0.000	0.188	0.000
0	0.348	0.235	0.200	0.094	0.059
<i>Polygonella basiramia</i> , site 35, 2002-2003, tsf=6					
0.248	0	21.45	0	102.46	229.61
0.0013	0	0.0852	0	0.4068	0.9117
0.0023	0	0.1491	0	0.7120	1.5955
0	0.100	0.000	0.000	0.000	0.000
0	0.450	0.222	0.214	0.179	0.000
0	0.150	0.278	0.071	0.071	0.000

<i>Polygonella basiramia</i> , site 59, 2002-2003, tsf=35					
0.222	0	28.01	0	87.62	175.79
0.0061	0	0.6280	0	1.8813	3.6754
0.0012	0	0.1208	0	0.3618	0.7068
0	0.286	0.077	0.000	0.000	0.000
0	0.143	0.154	0.125	0.333	0.000
0	0.286	0.564	0.625	0.167	0.167
<i>Polygonella basiramia</i> , site 72, 2002-2003, tsf=31					
0.231	0	36.36	0	95.63	257.37
0.0026	0	0.3220	0	0.8224	2.1229
0.0020	0	0.2530	0	0.6461	1.6680
0	0.000	0.000	0.000	0.000	0.000
0	0.542	0.037	0.231	0.222	0.067
0	0.250	0.519	0.462	0.111	0.000
<i>Polygonella basiramia</i> , site 90, 2002-2003, tsf=17					
0.197	0	18.85	0	86.34	211.32
0.0016	0	0.1289	0	0.5528	1.3028
0.0022	0	0.1804	0	0.7740	1.8238
0	0.156	0.083	0.042	0.000	0.000
0	0.313	0.250	0.167	0.125	0.000
0	0.094	0.125	0.250	0.250	0.000
<i>Polygonella basiramia</i> , site 92, 2002-2003, tsf=17					
0.192	0	17.31	0	52.23	180.20
0.0026	0	0.2028	0	0.5772	1.9087
0.0030	0	0.2318	0	0.6597	2.1814
0	0.143	0.050	0.091	0.000	0.000
0	0.314	0.375	0.182	0.000	0.000
0	0.086	0.150	0.182	0.000	0.000

<i>Polygonella robusta</i> , site 59, 1999-2000, tsf=32					
0.521	0	0	148.97	368.98	2349.46
0.0001	0	0	0.0145	0.0359	0.2284
0	0.625	0.429	0.000	0.231	0.000
0	0.000	0.143	0.125	0.077	0.000
0	0.125	0.214	0.500	0.385	0.059
0	0.000	0.000	0.125	0.308	0.941
<i>Polygonella robusta</i> , site 65, 1999-2000, tsf=2					
0.463	0	0	110.80	269.13	768.84
0.0002	0	0	0.0282	0.0683	0.1953
0	0.714	0.317	0.000	0.000	0.000
0	0.214	0.341	0.000	0.000	0.036
0	0.000	0.220	0.667	0.286	0.071
0	0.000	0.098	0.333	0.714	0.821
<i>Polygonella robusta</i> , site 72, 1999-2000, tsf=28					
0.437	0	0	161.28	330.55	1767.98
0.0001	0	0	0.0204	0.0419	0.2240
0	0.714	0.286	0.000	0.000	0.000
0	0.000	0.229	0.000	0.095	0.091
0	0.143	0.086	0.667	0.524	0.182
0	0.000	0.057	0.000	0.143	0.273
<i>Polygonella robusta</i> , site 85, 1999-2000, tsf=14					
0.672	0	0	168.18	643.94	3948.19
0.0001	0	0	0.0079	0.0303	0.1855
0	0.727	0.692	0.077	0.107	0.000
0	0.000	0.115	0.308	0.036	0.043
0	0.000	0.077	0.308	0.571	0.087
0	0.000	0.000	0.000	0.107	0.783

<i>Polygonella robusta</i> , site 90, 1999-2000, tsf=14					
0.449	0	0	138.00	410.02	1121.28
0.0001	0	0	0.0172	0.0510	0.1394
0	0.667	0.192	0.125	0.059	0.000
0	0.000	0.192	0.500	0.235	0.125
0	0.000	0.038	0.125	0.529	0.375
0	0.000	0.000	0.000	0.059	0.250
<i>Polygonella robusta</i> , site 1, 2000-2001, tsf=3					
0.495	0	0	189.88	648.01	3687.42
0.0001	0	0	0.0099	0.0337	0.1916
0	0.389	0.325	0.000	0.000	0.000
0	0.167	0.450	0.067	0.000	0.000
0	0.056	0.125	0.533	0.591	0.125
0	0.056	0.075	0.333	0.364	0.875
<i>Polygonella robusta</i> , site 59, 2000-2001, tsf=33					
0.521	0	0	101.92	674.05	4323.00
0.0001	0	0	0.0077	0.0507	0.3250
0	0.167	0.000	0.000	0.000	0.034
0	0.000	0.083	0.200	0.000	0.000
0	0.167	0.000	0.000	0.050	0.000
0	0.000	0.000	0.200	0.100	0.276
<i>Polygonella robusta</i> , site 65, 2000-2001, tsf=3					
0.463	0	0	172.85	840.45	6755.66
0.0000	0	0	0.0054	0.0262	0.2104
0	0.368	0.542	0.000	0.000	0.053
0	0.159	0.375	0.235	0.111	0.000
0	0.105	0.083	0.353	0.222	0.105
0	0.053	0.000	0.235	0.444	0.632

<i>Polygonella robusta</i> , site 72, 2000-2001, tsf=29					
0.437	0	0	159.72	542.93	2661.29
0.0001	0	0	0.0167	0.0569	0.2790
0	0.400	0.048	0.053	0.000	0.000
0	0.000	0.190	0.053	0.000	0.000
0	0.000	0.238	0.316	0.095	0.000
0	0.000	0.095	0.158	0.286	0.125
<i>Polygonella robusta</i> , site 85, 2000-2001, tsf=15					
0.672	0	0	223.62	863.77	3957.89
0.0001	0	0	0.0102	0.0394	0.1807
0	0.385	0.162	0.083	0.000	0.000
0	0.000	0.108	0.167	0.038	0.000
0	0.000	0.000	0.083	0.192	0.048
0	0.000	0.081	0.083	0.115	0.238
<i>Polygonella robusta</i> , site 90, 2000-2001, tsf=15					
0.449	0	0	239.78	922.00	2631.52
0.0000	0	0	0.0141	0.0542	0.1546
0	0.385	0.125	0.143	0.200	0.000
0	0.000	0.125	0.071	0.000	0.000
0	0.000	0.000	0.143	0.133	0.083
0	0.000	0.000	0.000	0.267	0.292
<i>Polygonella robusta</i> , site 1, 2001-2002, tsf=4					
0.495	0	0	82.80	748.27	3335.91
0.0001	0	0	0.0096	0.0864	0.3850
0	0.571	0.429	0.091	0.000	0.000
0	0.286	0.238	0.818	0.094	0.000
0	0.000	0.048	0.091	0.594	0.080
0	0.000	0.000	0.000	0.094	0.720

<i>Polygonella robusta</i> , site 59, 2001-2002, tsf=34					
0.521	0	0	218.85	396.52	3697.95
0.0002	0	0	0.0444	0.0805	0.7503
0	0.571	0.360	0.000	0.000	0.000
0	0.286	0.200	0.200	0.000	0.000
0	0.000	0.160	0.000	0.190	0.083
0	0.000	0.240	0.800	0.762	0.875
<i>Polygonella robusta</i> , site 65, 2001-2002, tsf=4					
0.463	0	0	180.29	786.15	4397.69
0.0001	0	0	0.0084	0.0366	0.2050
0	0.571	0.688	0.313	0.000	0.042
0	0.286	0.063	0.313	0.278	0.000
0	0.000	0.000	0.188	0.500	0.167
0	0.000	0.000	0.063	0.167	0.708
<i>Polygonella robusta</i> , site 72, 2001-2002, tsf=30					
0.437	0	0	318.55	758.28	3756.94
0.0002	0	0	0.0808	0.1924	0.9534
0	0.571	0.381	0.000	0.000	0.000
0	0.286	0.190	0.500	0.000	0.000
0	0.000	0.095	0.500	0.267	0.059
0	0.000	0.286	0.000	0.667	0.941
<i>Polygonella robusta</i> , site 85, 2001-2002, tsf=16					
0.672	0	0	174.99	994.63	4541.00
0.0001	0	0	0.0127	0.0723	0.3300
0	0.571	0.167	0.083	0.062	0.000
0	0.286	0.583	0.417	0.188	0.000
0	0.000	0.083	0.167	0.500	0.105
0	0.000	0.083	0.250	0.250	0.895

<i>Polygonella robusta</i> , site 90, 2001-2002, tsf=16					
0.449	0	0	241.88	778.47	2777.76
0.0001	0	0	0.0251	0.0808	0.2882
0	0.571	0.182	0.076	0.045	0.000
0	0.286	0.182	0.462	0.045	0.000
0	0.000	0.091	0.462	0.455	0.190
0	0.000	0.000	0.000	0.364	0.810
<i>Polygonella robusta</i> , site 1, 2002-2003, tsf=5					
0.495	0	0	117.50	982.75	3763.95
0.0001	0	0	0.0100	0.0834	0.3193
0	0.813	0.625	0.219	0.000	0.000
0	0.063	0.188	0.500	0.192	0.000
0	0.000	0.063	0.188	0.500	0.091
0	0.000	0.000	0.000	0.154	0.818
<i>Polygonella robusta</i> , site 59, 2002-2003, tsf=35					
0.521	0	0	123.57	659.08	6070.16
0.0004	0	0	0.0406	0.2164	1.9930
0	0.789	0.143	0.200	0.143	0.000
0	0.026	0.143	0.400	0.000	0.000
0	0.000	0.286	0.100	0.571	0.129
0	0.026	0.357	0.000	0.071	0.742
<i>Polygonella robusta</i> , site 65, 2002-2003, tsf=5					
0.463	0	0	154.04	471.45	3650.68
0.0001	0	0	0.0135	0.0413	0.3201
0	0.750	0.421	0.083	0.188	0.048
0	0.083	0.211	0.417	0.063	0.048
0	0.000	0.053	0.000	0.188	0.143
0	0.000	0.000	0.000	0.000	0.381

<i>Polygonella robusta</i> , site 72, 2002-2003, tsf=31					
0.437	0	0	115.68	542.46	3543.76
0.0003	0	0	0.0413	0.1936	1.2651
0	0.684	0.375	0.250	0.000	0.063
0	0.053	0.250	0.375	0.000	0.000
0	0.053	0.125	0.125	0.700	0.219
0	0.000	0.063	0.000	0.100	0.531
<i>Polygonella robusta</i> , site 85, 2002-2003, tsf=17					
0.672	0	0	288.39	1139.79	5307.15
0.0003	0	0	0.0353	0.1396	0.6501
0	0.658	0.231	0.111	0.077	0.000
0	0.000	0.154	0.278	0.154	0.000
0	0.000	0.077	0.389	0.538	0.111
0	0.000	0.000	0.056	0.154	0.889
<i>Polygonella robusta</i> , site 90, 2002-2003, tsf=17					
0.449	0	0	233.90	649.69	2362.69
0.0002	0	0	0.0566	0.1573	0.5721
0	0.826	0.333	0.083	0.000	0.000
0	0.087	0.000	0.250	0.136	0.040
0	0.000	0.167	0.500	0.500	0.200
0	0.000	0.000	0.000	0.091	0.680

VITA

Satya Maliakal Witt was born on December 23, 1972, in Newton, Massachusetts, to Raena Kay and Joseph Chacko Maliakal. She grew up in Lexington, Massachusetts, and attended Hastings Elementary School, Diamond Junior High School, and Lexington High School. Her interest in plant ecology was inspired by reading Henry David Thoreau and taking long walks at Walden Woods, in Concord, Massachusetts. In 1995, Satya graduated from Brown University with a Bachelor of Arts in biology. While at Brown, she completed an honor's thesis investigating the physiological costs of elongation in *Impatiens capensis* with Dr. Johanna Schmitt. After graduation, she held internships at Harvard Forest, New England Wildflower Society, and Archbold Biological Station. At Archbold Biological Station, in Lake Placid, Florida, she learned about fire ecology and rare plant demography from Dr. Eric S. Menges, and developed a passion for the Florida scrub ecosystem. In 1997, she entered the Department of Biological Sciences at Louisiana State University, in Baton Rouge, Louisiana, and began a doctoral program under the supervision of Dr. Julie S. Denslow.