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Integral Projection Models Reveal Interactive Effects of Biotic Factors and Disturbance on Plant Demography

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INTEGRAL PROJECTION MODELS REVEAL INTERACTIVE EFFECTS OF BIOTIC FACTORS AND DISTURBANCE ON PLANT DEMOGRAPHY

by

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ABSTRACT

Understanding factors limiting population growth is crucial to evaluating species persistence in changing environments. I used Integral Projection Models (IPMs) to elucidate the role of biotic interactions and disturbance on population growth rate in two plants: *Helianthemum squamatum*, a perennial endemic to gypsum habitats in central Spain, and *Liatris ohlingerae,* a long-lived perennial endemic to the Lake Wales Ridge of central Florida. In *H. squamatum*, there was a strong positive effect of trampling in the site with the highest plant density and moderate positive effects of seed addition in the site with the lowest plant density. Differences in treatment effectiveness between sites may represent a shift from seed to microsite limitation at increasing densities. Additionally, a distinct drop in population growth rate occurred in the hottest and driest year (2009-10). In *Liatris ohlingerae,* roadside populations had consistently higher population growth rates than scrub populations. A modest negative effect of time-since-fire was observed in plants that did not experience herbivory. Both habitat and time-since-fire showed distinct interactions with vertebrate herbivory, with herbivory increasing the difference in growth rate between habitats and decreasing the difference between time-since-fire classes. The direct effect of herbivory was negative in all environmental combinations except in long unburned populations. These results demonstrate the importance of considering environmental interactions when constructing population models, as well as the validity of using IPMs to assess interactions in species with differing life histories.

ACKNOWLEDGMENTS

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CHAPTER 1: INTRODUCTION

Successful conservation plans depend on understanding how life history variation interacts with environmental factors and characterizing current conditions. Herbivores and seed predators are important to the demography of many plant species. Herbivores reduce fitness by altering survival and fecundity (Crawley 1985). Alternatively, herbivores can increase plant fecundity and growth through overcompensation (Paige and Whitham 1987), compensatory growth (McNaughton 1983) and indirect effects on other species (Rooney and Waller 2003). Disturbance also is a major demographic driver of plant population dynamics. Many plant species rely on disturbances such as fire, flooding, tree falls, etc. to reduce competition and maintain suitable habitats (Hoffmann 1999, Metcalf et al. 2009). Anthropogenic habitat disturbances, such as land clearances, also can greatly affect species demography (Stephens et al. 2014).

Understanding how environmental factors affect each other is equally important. Herbivores, seed predators and disturbances interact in varied and complex ways. Changes in community structure and composition due to disturbance affect how plant species respond to herbivore pressure (Hegland et al 2010) and the probability of predation (Dahlgren and Ehrlen 2011, Stephens et al. 2014). Herbivores may change the habitat by altering nutrient cycling (Mazancourt et al 1998), or being directly responsible for disturbance (Maschinski et al. 1997). These indirect effects greatly influence demography.

Population modeling is a powerful tool to integrate various and frequently disparate responses of vital rates with environmental interactions and evaluate population growth rates (λ) (Coulson 2012). Since the introduction of the Leslie matrix (Leslie 1945), matrix based models

have become a dominant method of modeling populations, spawning a wide array of related approaches (Caswell 2003). However, all of these techniques rely on the same core concepts: individuals are divided into discrete classes (age, stage, size, etc.). Probabilities of survival, transition to another class and fecundity are calculated for each class. These probabilities are then arrayed into a matrix. Matrix models have the advantage of being able to accommodate most type of lifecycles and datasets. However, matrix models require separate parameters for each column within the matrix (Caswell 2003). This leads to a limitation in how effectively these models can address fine scale differences in lifecycle.

A more recent development in this line is the use of integral projection models (IPMs) (Easterling et al 2000). Rather than define vital rates of each matrix cell individually, IPMs use regressions to calculate changes in vital rates across a continuous variable (Ellner and Rees 2006). The resulting regressions and their error distributions are then integrated by numerical approximation and the result is discretized into a large matrix (Ellner and Rees 2007). This approach allows specification of vital rates as continuous functions (Dhalgren and Ehrlen 2009). Additionally, because matrix cells are defined by regression models of the overall data rather than data of each class, it is possible to create larger and finer scale matrices even at reduced sample sizes (Ramula et al 2009).

This thesis examines the interactive effects of biotic interactions and disturbance, on the population dynamics of two herbaceous plants: *Helianthemum squamatum* and *Liatris ohlingerae*. *Helianthemum squamatum* is a perennial herb (4-6 y life span) native to gypsum habitats in Castilla-La Mancha, central Spain. *Liatris ohlingerae* is a long-lived (>10 y) perennial herb endemic to the Lake Wales Ridge of central Florida, USA. The goals were to: (1) contribute to the understanding of how biotic interactions and disturbance affect population growth rate (2)

explore the use of integral projection models to assess these interactions in species with multi-stage life cycles, and (3) provide specific recommendations to land managers working to conserve these plants.

CHAPTER 2: CHANGES IN POPULATION DYNAMICS OF A SHORT-LIVED PERENNIAL WITH EXPERIMENTAL SEED ADDITION AND TRAMPLING

Introduction

Vital rates shift in response to environmental and demographic variation, with concomitant changes in population dynamics (Dahlgren and Ehrlén 2009, Rees and Ellner 2009). Understanding effects of multiple environmental differences and demographic structure on population dynamics is fundamental to assessing consequences of human action and changing environments and to understand species' evolutionary milieu. This knowledge is also critical for improving management, including mitigating the decline of threatened species or the expansion of invasive species and pests (Salguero-Gómez and de Kroon 2010).

Population models provide a strong framework for assessing multiple how multiple environmental factors affect vital rates as well as the overall population growth rate. Integral projection models are particularly suited to this task in cases of small sample size (Ramula et al. 2009). Both integral and matrix models also allow for the integration of both experimental and observational data (Caswell 2003). However, despite this advantage few IPM studies explicitly include experimental data (e.g., Miller et al. 2009).

Two major life history strategies have been identified for plants living in stressful, unpredictable environments such as drylands: ephemeral annuals and long-lived iteroparous plants. Annuals maximise the *avoidance* strategy, completing their life cycle before stress levels are high, but at the cost of expensive, risky re-establishment every year. Persistence depends on large seed production and dense and permanent seed banks (Pake and Venable 1996).

Iteroparous perennials optimise the *conservative* strategy, investing in vegetative tissues at the expense of reproduction (Wiegand et al. 1995; 2004). If water availability is limited annuals could fail to establish and reproduce (Aronson et al. 1992; Levine et al. 2011) and perennials could fail to survive their first stressful period (Sánchez and Peco 2007). In either case, seed availability and seedling establishment are critical for persistence in arid environments. Seed availability limitations are most likely to occur at low conspecific densities where suitable sites for germination are plentiful (Eriksson and Ehrlen 1992). At high conspecific densities, seedling completion in suitable microsites may lead to populations becoming limited by establishment (Maron and Gardner 2000).
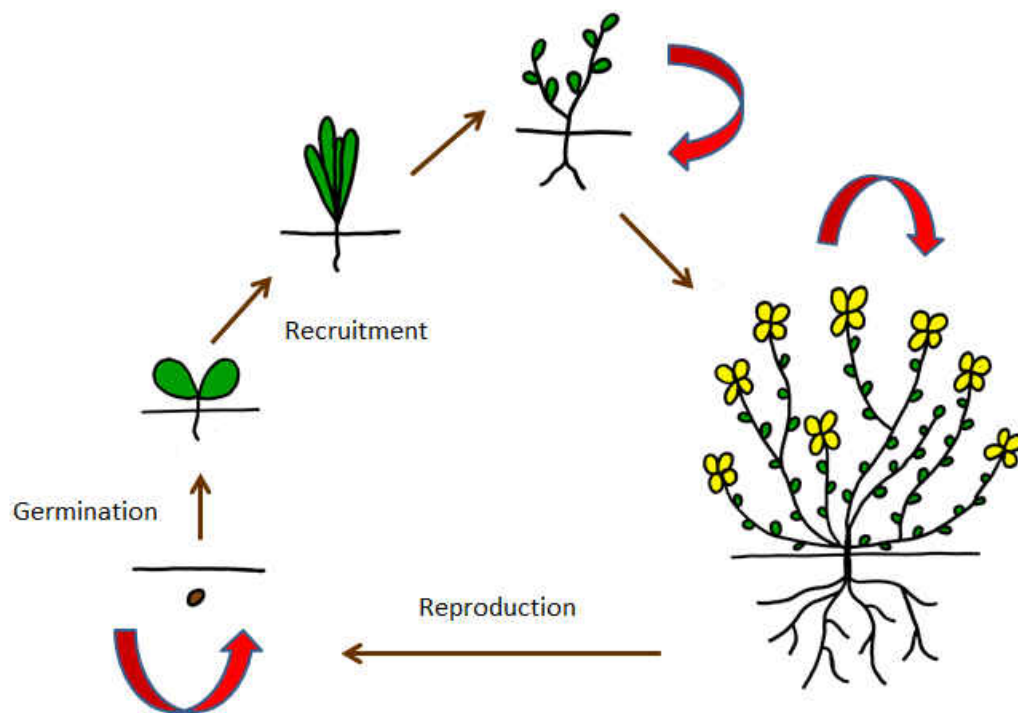
Figure 1. Diagram of the lifecycle of *Helianthemum squamatum.* Brown arrows indicate progression red arrows indicate stasis.

I evaluated the demographic consequences of seed and habitat limitation under differing weather conditions on population dynamics of the short-lived perennial *Helianthemum squamatum,* a specialist on dry gypsum soils (Figure 1). Short-lived perennials represent an intermediate life history (Agami 1987, Cody 2000, Aragón 2010). These species have an intense reproductive effort under varied conditions (Aragón 2009), a persistent seed-bank (albeit smaller than annuals) and rely on recurrent disturbance minimizing competition (Quintana-Ascencio et al. 2009). Short-lived perennials are particularly abundant in semi-arid gypsum habitats which harbour a large number of specialist and rare species (Mota et al. 2003). *Helianthemum squamatum* inhabits semi-arid Mediterranean Spain (Olano et al. 2011) and maintains high reproductive effort under different environmental conditions (Aragón et al. 2007; 2008), even at the cost of future survival (Aragón et al. 2009). Recruitment increases with seed density and is controlled by microhabitat availability for germination and establishment (Escudero et al. 1999; Escudero et al. 2005). Increases in seedling recruitment are frequently associated with perturbations, such as trampling by sheep, that reduce plant competition and create openings in hard soil crusts (Escudero et al. 2000; Escudero et al. 2005; De la Cruz et al. 2008, Quintana-Ascencio et al. 2009; Martínez-Duro et al. 2010). *Helianthemum squamatum* seeds incorporate into the soil seed bank but are short-lived (Olano et al. 2012). Consequently, *H. squamatum* has a strong dependence on frequent seed production for persistence.

I combined data from field experiments in which soil perturbation and seed densities were manipulated with a demographic modelling framework using Integral Projection Models (IPMs) (Easterling et al. 2000, Rees and Ellner 2009). Integral projection modeling is especially useful when demographic performance is controlled by a set of external and internal factors, because the continuous response structure of the model facilitates parsimonious modeling of

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factor–fate relationships (Rees and Ellner 2009). My hypothesis was that soil disturbance designed to mimick trampling by grazing sheep would have a positive effect on *H. squamatum* population dynamics by increasing safe sites for germination and establishment. Population growth may be seed limited, so seed addition may positively affect population growth rate, especially immediately after a years with reproductive failure. Recruitment relies on intense reproductive effort with weak participation of seeds in the seed bank for multiple years. Recruitment failures of gypsum endemics in years with low reproductive output have been reported (see Escudero et al. 2000 in the case of *Lepidium subulatum*). Finally, this arid-zone species is limited by water availability in some years. The demography of 15 plots of *H. squamatum* was monitored under different manipulative scenarios during three annual transitions.

Methods

Natural history and study area
Helianthemum squamatum (L.) Dum. Cours. (Cistaceae) is a small perennial shrub that occurs in the eastern half of the Iberian Peninsula. It specializes in gypsum soils, where it is a dominant species (Palacio et al., 2007). Its life span ranges from 4 to 6 y. (Olano et al. 2011), and reproduction usually occurs during May to August, beginning a year after seedling establishment (Aragón et al. 2007; Quintana-Ascencio et al. 2009). Flowers are hermaphroditic and arranged in dense inflorescences. Fruits are small capsules (3 mm diameter) generally bearing 1–7 seeds, with an average of 1.7 viable seeds per fruit (Aragón et al. 2007). Fecundity of *H. squamatum* depends on climate conditions (Aragón et al. 2008). Age structure is determined by fine-scale climate variation, with sporadic summer rainfalls being especially critical (Olano et al. 2011).

My study was conducted at Aranjuez/Sotomayor Experimental Station, 50 km south of Madrid, in central Spain (40° 4'31.94"N, 3°36'4.29"W, 600 m a.s.l.). The climate is Mediterranean and semi-arid with an average temperature of 15.8º C and mean annual precipitation of 350 mm (data from Aranjuez Meteorological Station www.aemet.es). Gypsum soils are prevalent and vegetation is dominated by gypsum plant specialists. Perennial plant cover rarely surpasses 40% and is dominated by tussocks such as *Stipa tenacissima* and shrubby gypsophytes such as *H. squamatum* and *Lepidium subulatum*. Locally abundant plants include *Centaurea hyssopifolia* and *Thymus lacaite*. Bare ground areas are covered by well-developed biological soil crusts that shelter a diverse community of cryptogams and annuals.

Experimental design

Plant demographic data were collected in 15 permanent plots during 2008-2011. Each plot was 1 m wide and long enough to include at least 100 adult individuals. Focal plant density was quite heterogeneous so plot lengths ranged between 2 and 7.5 m. Each plot was randomly assigned to one of three treatments: simulated trampling; seed addition and control. Each treatment was replicated five times. Plots were distributed in two different hills (hereafter Site 1 and Site 2) located 400 m apart but similar in terms of total plant cover, slope and orientation (i.e., south-oriented and perennial cover below 20%). Three of five plots per treatment were in Site 1 and two in Site 2. A total of 2617 established plants were sampled across all years (1537 in Site 1 and 1080 in Site 2). Density of *Helianthemum squamatum* was consistently higher in Site 1 than in Site 2 every year and for all treatments (1.02, 1.71, 1.41 times higher in 2008; 1.17, 1.65, 1.41 in 2009; and 1.50, 2.11, 1.29 in 2010 for control, trampling and seed addition, respectively, in each year).

Trampling was simulated at the end of each July by thoroughly destroying the biological soil crust with a hammer without damaging existing plants. This treatment was intended to mimic the effect of regular trampling by a sheep herd. In 2008 total seed production of plants in each plot was calculated and an equivalent number of seeds were added. The number of seeds added ranged between 1200 and 9500 seeds/m^2 according with each plot's seed production. No seeds were produced in 2009, so a constant amount of seeds, 2000 seeds/m^2, were added to the five treated plots. Finally, in 2010 900 seeds/m^2 were added in all treated plots, because insufficient seeds had been collected to reach previous years' seed additions. Seeds were added in late autumn, prior to field seed germination and after activity of granivorous ants (mainly *Messor* sp.) ceased (Sánchez et al. 2006). Seeds were homogenously distributed on the ground surface after watering plots to increase attachment of their mucilage to the ground. Seed addition treatments were performed with seeds collected from wild plants during each previous year at Aranjuez Biological Station. Capsules were aired dried and manually processed to obtain their seeds. Seeds were stored in paper bags under lab conditions before use.

Seedlings were counted in each plot within cells of 20 x 20 cm^2 in May of each year after maximal emergence and prior to summer drought mortality. Adult sampling was performed annually in late July, well after fruit ripening. Status (alive/dead) together with its two main crown diameters and number of infrutescences were recorded for each plant. Seed production was obtained from 50 infrutescences from randomly-selected plants harvested outside plots at both sites in 2008, 2010 and 2011. These data were used to estimate flowers per infrutescence and seeds per fruit.

Integral Projection Model construction

I used general linear models (GLMs) to evaluate the effect of different biotic and environmental factors on vital rates of *H. squamatum*: survival, growth, probability of reproduction and per-capita fecundity. Growth and per-capita fecundity were assessed using Gaussian distributions, while survival and probability of reproduction were modeled with binomial distributions. In all cases, the primary predictor variable was size, measured as the natural log of average crown diameter (cm). I considered four additional potential predictors: experimental treatment (control, trampling and seed addition), sampling location (sites), summer temperature (average monthly temperature from June to September) and winter-spring precipitation (total precipitation from January to May). Both climatic predictors were good surrogates of main climatic constraints for the plant: summer drought stress and water availability during the growing season (Aragón et al. 2007). Observed climatic values during the study period were representative of precipitation and temperature recorded between 1977 and 2012 (*see* Appendix A Figures 21 and 22).

I created 20 models for survival, probability of reproduction and per-capita fecundity. For growth, I used the same set of covariates for survival (Morris and Doak 2002). All the most informative models included plant size plus different combinations of predictive variables. The most informative model for each vital rate was selected with corrected Akaike Information Criterion (AICc; Burnham and Anderson 2002).

Results of GLMs were used to build an Integral Projection Model (IPM), using modified code from version 1.5 of IPMPack (Metcalf et al. 2013) in R (2.15.2, R Development Core Team) to incorporate continuous covariates. The IPM was organized into a single continuous stage that incorporated all extant non-seed plants and a single stage for the seed bank. The continuous stage was calculated using a standard IPM kernel function (Easterling et al. 2000):

$$n(y, t + 1) = \int_T^U [s(x)g(x,y) + f(x,y)]\, n(x,t)dx \tag{1}$$

where the probability function of individuals at time t+1 (n(y,t+1)) is equal to the integration of survival (s(x,y)), growth (g(x,y)) and reproduction (f(x,y)) across the possible range of sizes (T to U).

Reproduction was calculated as the product of the probability of reproduction and per-capita fecundity. I calculated number of individuals in the seed bank as the sum of seeds entering into the seed bank and seeds remaining from the previous year's seed bank (as in Ramula et al. 2009). New seedlings enter the continuous stage (i.e., individuals with aboveground biomass) with size frequencies matching an estimated normal distribution for offspring diameter (1.52 ± 0.44 cm). Resulting seeds were then split into individuals entering next year's soil seed bank (Probability=0.281) and individuals germinating next spring (Probability=0.138). Seedlings survived at a rate of 0.160. These parameters were calculated from data previously collected on this species (Caballero et al. 2003, 2005,2008a, 2008b; Quintana-Ascencio et al. 2009; Olano et al. 2012).

I calculated IPMs on subsets of each of three treatments: trampling, seed addition and control. I generated IPMs for differing climatic conditions by changing values of environmental covariates in the underlying GLMs and estimated differences in population growth rate between treatments using the dominant eigenvalue of each IPM. Confidence intervals were calculated by bootstrapping data within years and sites with 999 iterations per treatment combination.

I carried out Life Table Response Experiments (LTREs; Caswell 2001) to assess how experimental treatments on each part of the life cycle of *Helianthemum* affected the resulting deterministic rates of population growth (λ). After IPMs were discretized into 200 × 200

matrices, I assessed cell by cell differences between each treatment and the control. The resulting matrix was then multiplied by the sensitivity of the control matrix. I summed the columns of each resulting matrix to determine how plant size contributed to λ variation. For each column, I also calculated individual growth contribution as summed contributions higher than equivalent row size. Similarly, I calculated individual retrogression contributions as summed contributions of IPM elements lower than or equal to column size.

Results

GLM models

Plant survival varied as a quadratic function of plant diameter. The most informative set of covariates for survival was the interaction between treatment and site, with temperature and precipitation as additive effects (Appendix A, Table 5). Treatment effect depended on Site. In Site 1, trampling treatment had the highest survival, while survival was lowest in the control. Survival in seed addition plots was intermediate across all three years (Figure 2). In Site 2, survival in trampling and seed addition treatments were similar and higher than in the control. Survival was higher during years with moderate (209 mm) and high (273 mm) winter-spring precipitation and moderate (23.7° C) and lower (22.7° C) summer temperatures (2008, 2010) than in the year with low precipitation (100.5 mm) and temperature (24.1°C) (2009; Figure 2).
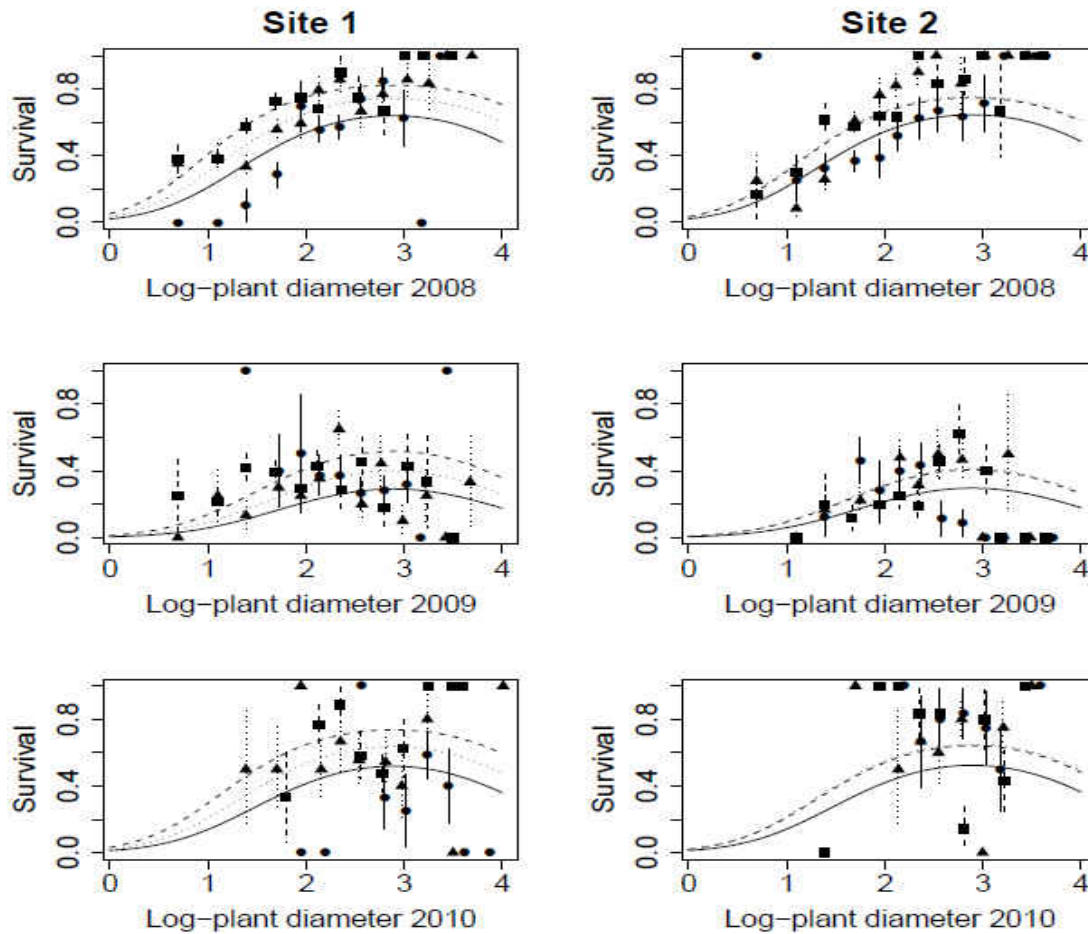
Figure 2. General linear models showing rates of survival for treatments and control across three yearly transitions for both sites. Dashed lines and squares denote trampling, dotted lines and triangles denote seed addition and solid lines and circles denote control.

Growth of plants in Site 1 control plots was slightly faster than in experimental plots, while in Site 2 all treatments had nearly identical growth (Figure 3). Variation in predicted individual growth rates between years was minimal and data did not indicate a significant decrease in the rate of growth due to drought (2009).
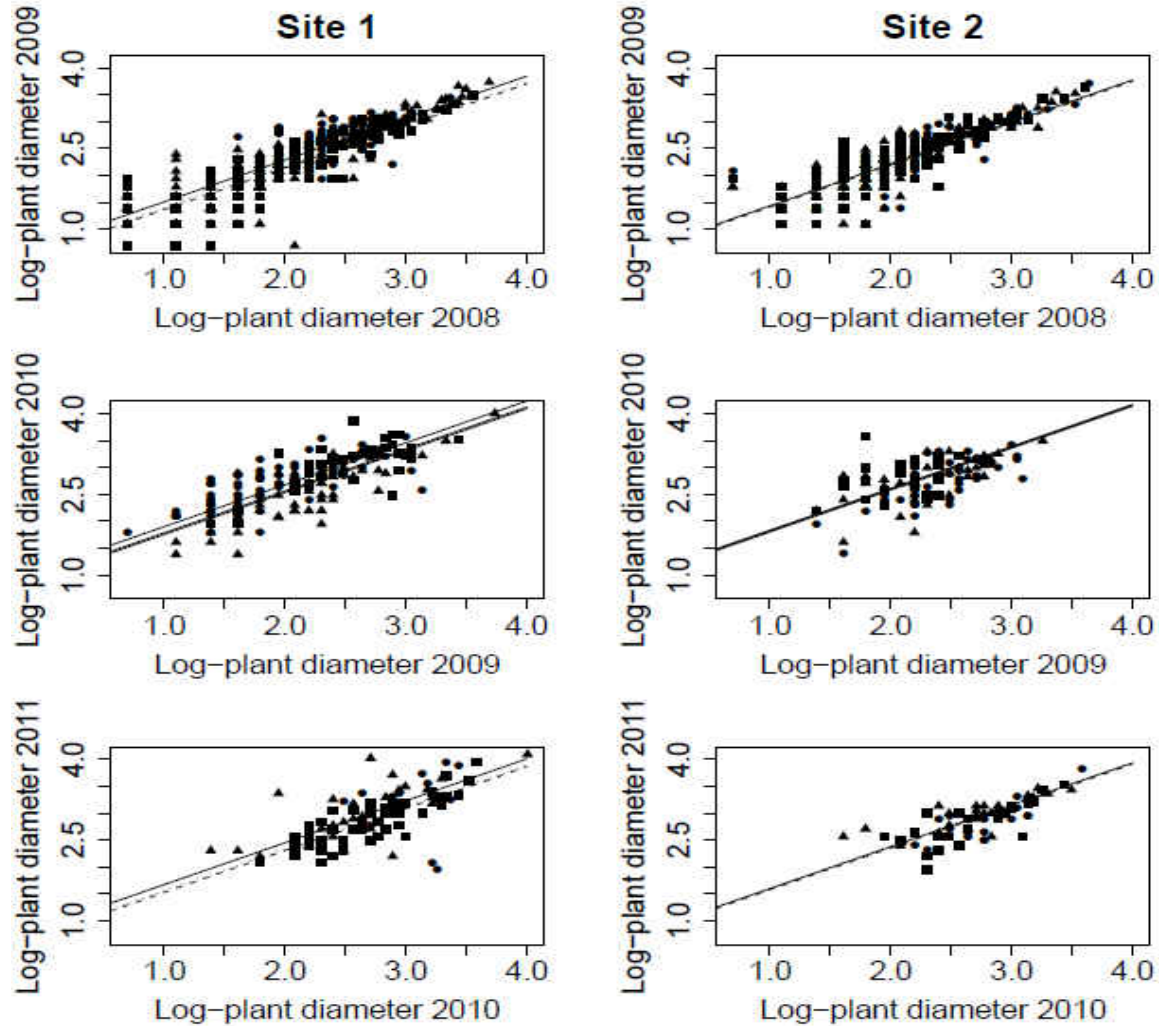
Figure 3 General linear models showing change in size for treatments and control across three yearly transitions for both sites. Dashed lines and squares denote trampling, dotted lines and triangles denote seed addition and solid lines and circles denote control.

The set of covariates identified for probability of reproduction was again the interaction between treatment and site, with temperature and precipitation as additive effects (Appendix A Table 5). The probability of reproduction increased with plant size in the wettest year (2008). In the hottest and driest year (2009), no plants reproduced, but in the year of intermediate rainfall and temperature (2010), all individuals reproduced. Treatment effects differed depending on site. At Site 1, probability of reproduction was higher for the control followed by the trampling and

seed addition treatments (Figure 4). In contrast at Site 2 plants in the seed addition treatment had the highest probability of reproduction, followed by the control and trampling treatments.
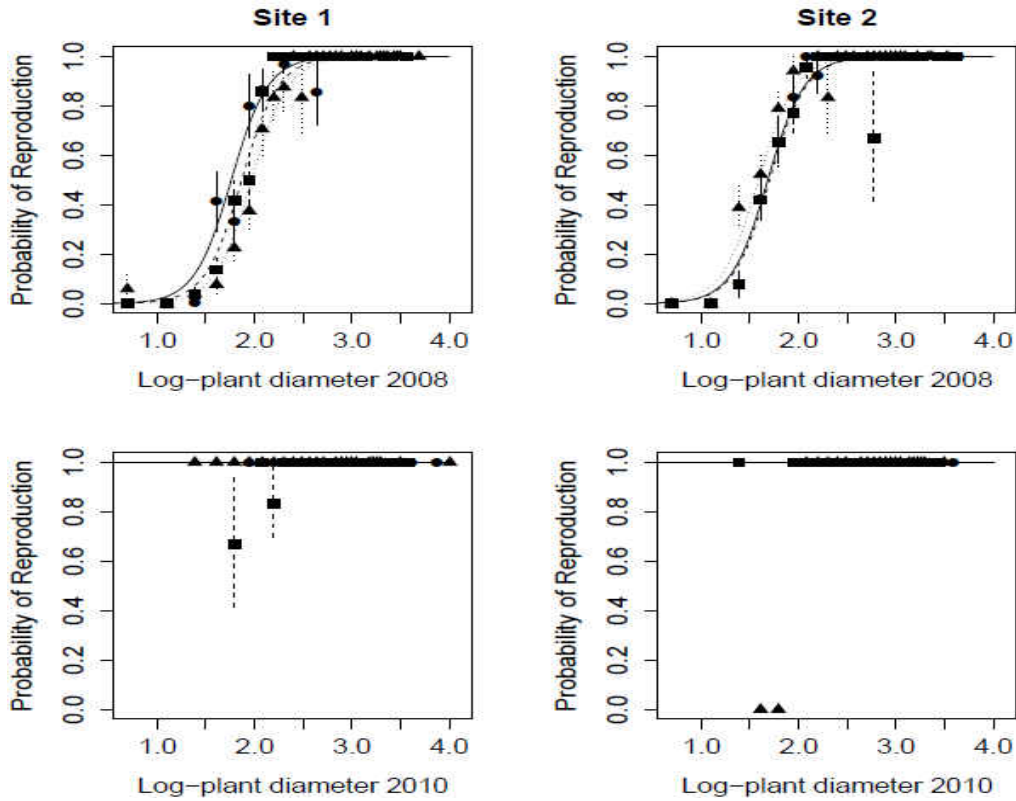
Figure 4 General linear models showing change in size for treatments and control across two yearly transitions for both sites. Probability of reproduction for 2009 was zero. Dashed lines and squares denote trampling, dotted lines and triangles denote seed addition and solid lines and circles denote control.

The most informative model for seed production was the same as for probability of reproduction (Appendix A Table 5). Seed production increased with plant size and was higher in Site 1 than in Site 2 (Figure 5). Seed production also was higher in the control than in the seed addition and trampling treatments at Site 1, whereas in Site 2 seed production in the seed addition treatment was higher than in the control and trampling treatments. Reproduction was slightly higher in the year with moderate rainfall (2010) compared to the year with the highest rainfall (2008).
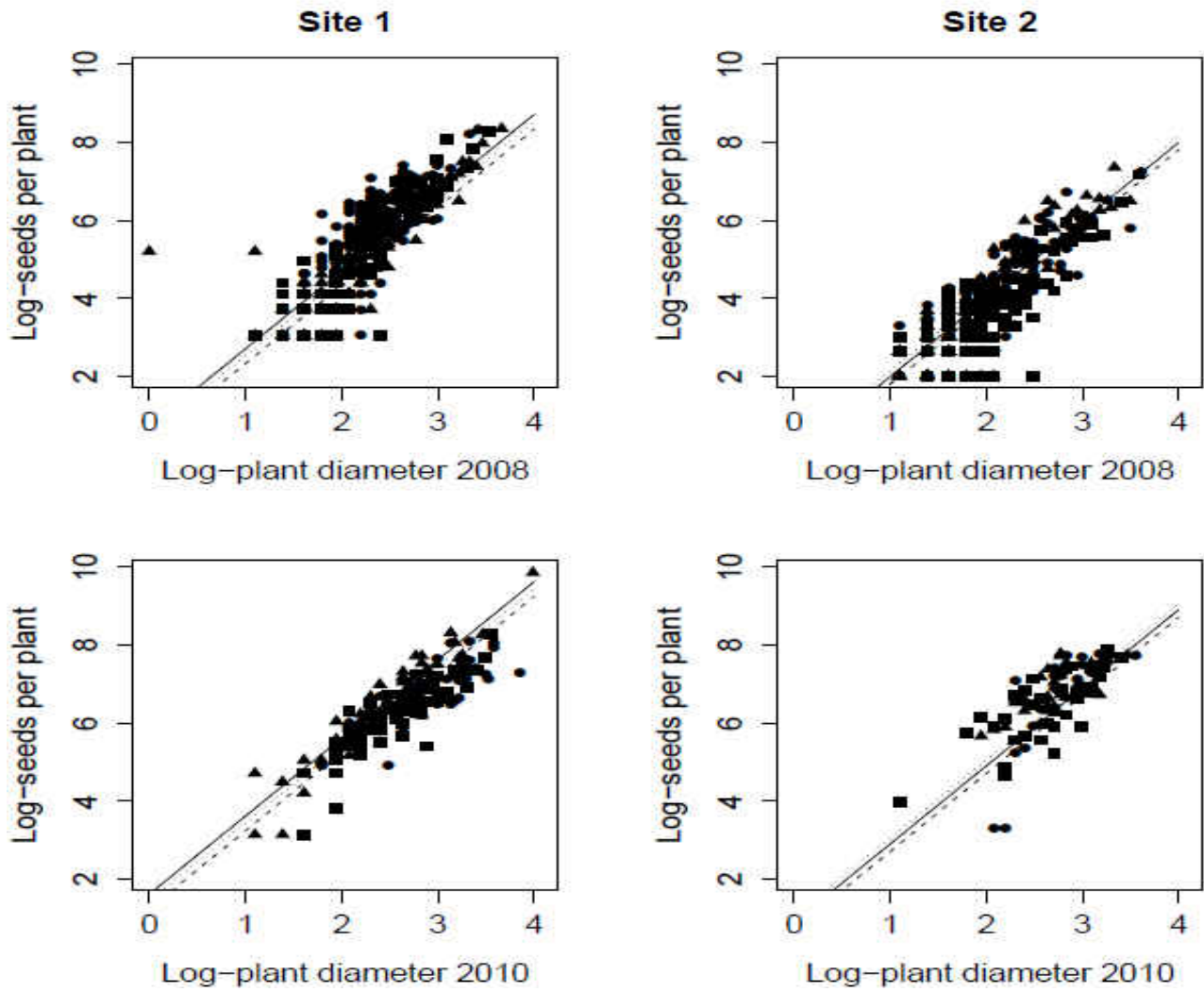
Figure 5 General linear models showing change in size for treatments and control across three yearly transitions for both sites. There was no fecundity in 2009. Dashed lines and squares denote trampling, dotted lines and triangles denote seed addition and solid lines and circles denote control.
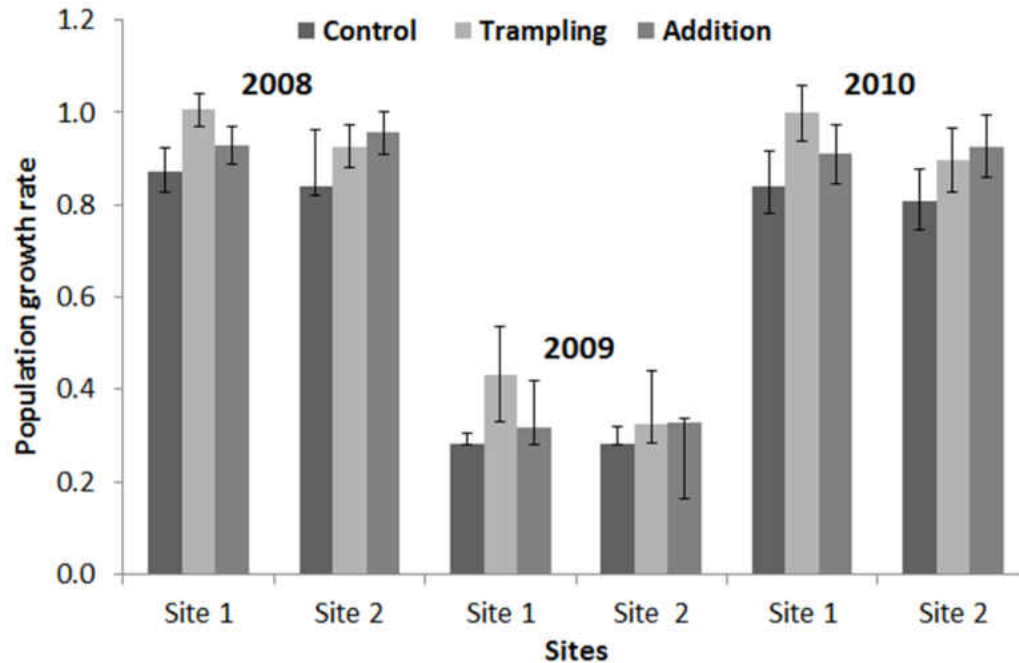
Figure 6. Deterministic population growth rates for each combination of treatment, site, and year. Error bars correspond to 95% confidence intervals calculated from bootstrapping (999 iterations).

Integral Projection Models

I used IPMs (Appendix A Figure 23) to assess demographic changes due to both experimental treatments and climate by comparing dominant eigenvalues (λ) of each treatment, site and year combination (Figure 6). Population growth rate was lower for 2009 as compared to the two years with higher precipitation for all combinations of treatment and site (non-overlapping at >95% C.I.). In Site 1, trampling treatment showed a trend across all three years for higher growth rate as compared to both seed addition treatment (2008: non-overlapping at 90% CI, 2009: non-overlapping at 70% CI, 2010: non-overlapping at 80% CI) and the control (non-overlapping at >95 % CI in all three years). In Site 2, the seed addition treatment was similar to trampling (2008: non-overlapping at 40% CI, 2009: non-overlapping at <5% CI, 2010: non-overlapping at 25% CI), and seed addition showed a somewhat higher λ than the control (2008: non-overlapping at >95% CI, 2009: non-overlapping at 75% CI, 2010: non-overlapping at 70% CI) across all three years.

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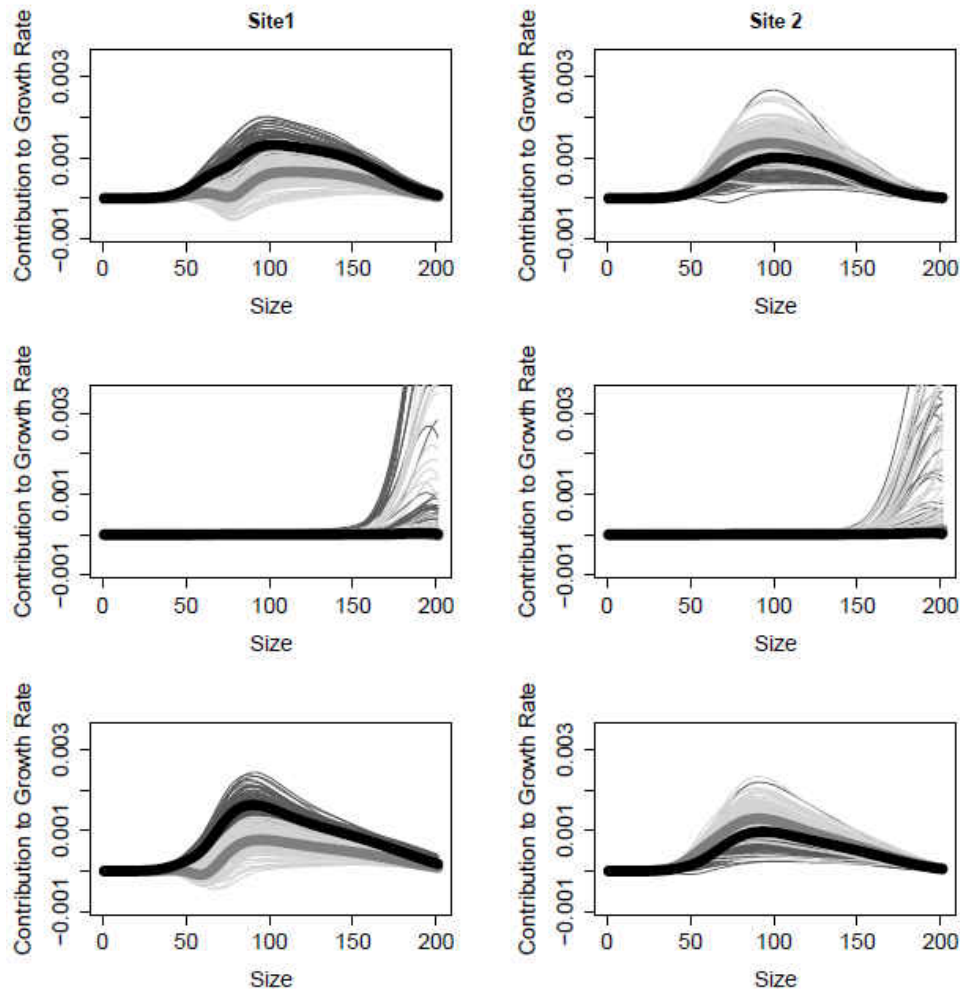
Figure 7 Changes in summed contribution by column (plant size) to population growth rate for seed addition (thick grey line) and trampling (thick black line) treatments as compared to control. Thinner lines represent 100 iterations of bootstrapping around seed addition (light grey) and trampling (dark grey). The left and right columns present Site 1 and Site 2, respectively. Rows designate differing years (Top row=2008, Middle Row=2009, Bottom row=2010).

Life Table Response Experiments

In Site 1, during annual transitions 2008-09 and 2010-11, both treatments had large positive contributions of survival and growth to variation in λ among individuals of intermediate diameter (Figure 7). The largest negative contributions came from seeds entering and persisting in the seed bank (Figure 8). In contrast, in Site 1 in 2009 the largest positive contributions of treatments came from the largest individuals (Figure 6C; notice the bootstrap CI). The largest

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negative contribution in 2009 was from individuals entering the seed bank (Figure 8). In Site 1, both treatments had more retrogression than growth in the year with moderate rainfall, but less retrogression than growth for the wet year. Contributions of both components were lower in the dry year of 2009 (Figure 9). The contribution of growth was higher for smaller individuals and negative or low for larger individuals, while the contribution of retrogression displayed the opposite pattern.
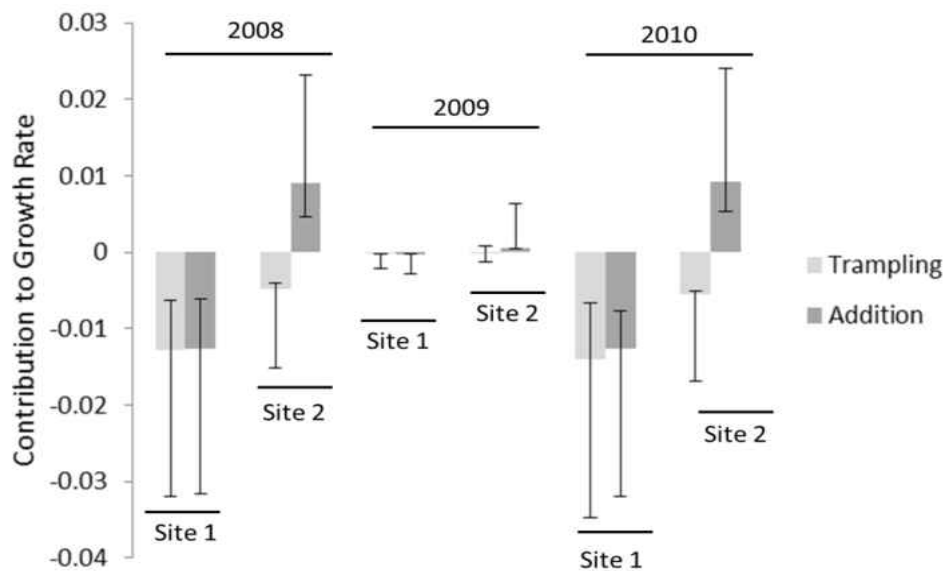
Figure 8 Seedbank contributions to population growth rate in comparison to the control. Error bars represent 95% confidence intervals calculated from bootstrapping (999 iterations)

Site 2 showed similar trends, but with several exceptions. The largest positive contributions in wet and moderately wet years (2008 and 2010) occurred at intermediate plant sizes. Seed addition had higher positive contributions to λ than trampling in all years studied (Figure 7). In Site 2, for wet and moderate years, growth had higher contribution than retrogression (Figure 9). Also, seed addition in Site 2 was the only treatment where seedbank had a positive contribution to λ compared to the control (Figure 8).

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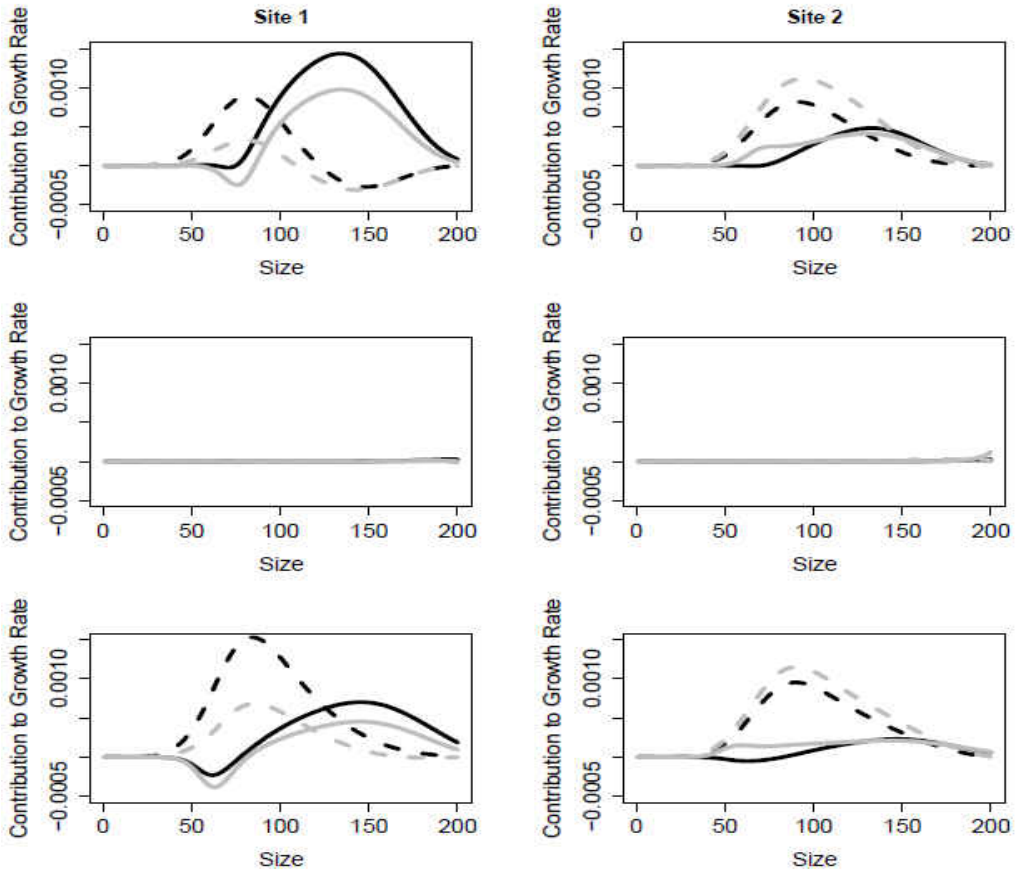
Figure 9 Changes in summed contributions by vital rate components, growth (dashed lines) and regression and stasis (solid lines), to lambda for trampling (black) and seed addition (grey) treatments. The left and right columns present Site 1 and Site 2, respectively. Rows designate differing years (Top=2008-2009, Middle=2009-2010, Bottom=2010-2011)

Discussion

The results of this study reveal the strong limiting effect of water availability on population growth rate as well as apparent density-dependent positive effects of simulated trampling and seed addition on *H. squamatum* demography. This study also reiterates the efficacy of using Integral Projection models to assess the effects of environmental variables and incorporate experimental data. Combining experimental and modeling approaches provide a link

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between causal mechanisms and population dynamics (Dahlgren and Ehrlén, 2011, Kolb, 2012, Ozgul et al., 2012, Shefferson and Roach, 2012).

Soil perturbation by trampling increased population growth rates. Positive association of *H. squamatum* establishment with bare soil crust surfaces was likely related to decreases in competition (Escudero et al. 2000, 2005, De la Cruz et al. 2008). This is further supported by the positive effects of trampling on the survival of small and medium sized individuals as well as a reduction in the importance of a multi-year seed bank. Seedling survival and growth of *H. squamatum* depends upon existence of clearings and is negatively affected by the presence of perennials and annuals (Escudero et al. 1999). In these environments, seeds of many species, including *Helianthemum squamatum,* have adhesive mechanisms that help seeds attach to soil. (Gutterman Y. and Shem-Tov, S. 1997, Engelbrecht and García-Fayos 2012).

Trampling was also shown to have a markedly stronger effect in the higher density Site 1 as compared to the lower density site 2. Trampling creates fissures through the hard physical crusts that facilitate better anchoring and recruitment (Romao and Escudero 2005). In higher densities, recruitment may be limited by the amount of suitable microsites for germination (Maron and Gardner 2000). At lower densities, seeds rather than microsite may become the limiting factor in germination success (Eriksson and Ehrlen 1992).

Seed addition improved population growth rate. *Helianthemum squamatum* has been shown to rely on high fertility for persistence and to be limited by seedling availability or establishment (Aragón et al. 2009). The increase in seed availability provided by seed addition thus helps to remove a limiting factor on population growth. This is supported by the fact that

seed addition treatments were more effected at the lower density sites, where seed limitation should be strongest (Eriksson and Ehrlen 1992, Clark et al. 2007, Waser et al. 2010).

The IPM models show strong negative effects of low water availability on both survival and reproduction, and therefore the overall population dynamics of *H. squamatum*. This effect is markedly higher than those of the trampling and seed addition. Plants in drylands are particularly limited by water availably (Crawley and Ross, 1990); lack of reproduction in the driest year I studied suggests conditions were too harsh for *H. squamatum* to maintain any reproductive effort. Additionally the increasing importance of growth transitions in the year following the drought as compared to the year preceding it suggests that years with low rainfall may have long term effects on population structure. Rates of drought may thus be a long term limiting factor on the population growth of this species.

From a conservation and management perspective, the models emphasize that conservation of these populations and associated endangered habitats requires a certain level of perturbation to minimize encroachment and competitive exclusion. This concurs with the idea that in open habitats with a long tradition of livestock grazing, moderate grazing pressure preserves rangeland productivity and biodiversity (Moret -Fernández et al. 2011). Additionally, land abandonment, a critical driver of landscape level changes in developed countries, may push species on open habitats to the verge of extinction due to encroachment and forest expansion (Gimeno et al. 2012; Olano et al. 2012). The critical role of livestock in these Mediterranean regions is also due to their ability to act as seed dispersal agents that reduce isolation between vegetation remnants in fragmented landscapes (Sánchez and Peco 2002; Pueyo et al. 2008).

This study highlights the importance of opportunistic demographic behavior displayed by a short-lived specialist, which requires openings by disturbance and under some conditions can become seed limited. Trampling had positive effects under an array of environmental conditions. Seed addition may be effective only when the effect of seed limitation exceeds the effect of microsite limitation. Low water availability also limits the fecundity of the species. It is thus critical for land managers to tailor future treatments to account for both drought risk and conspecific density.

CHAPTER 3: INTERACTIVE EFFECTS OF HERBIVORES, HABITAT AND FIRE ON THE POPULATION DYNAMICS OF A RARE PLANT ENDEMIC TO THE FLORIDA SCRUB

Introduction

Biotic interactions involving a predator or herbivore and its target species have long been identified as critical drivers of population dynamics. These interactions may besimple negative effects on population growth (Crawley 1985). However, these interactions are often more complex. These interactions may vary temporally (Austrheim et al. 2011), spatially (Pennings et al. 2005), or due to an evolved mechanism of compensating for predation pressure (Rautio et al. 2005).

The effect of fire as a mechanism for maintaining habitat structure and population dynamics in plant species is similarly well documented. Many plant species depend on fire to maintain open spaces (Thaxton and Platt 2006), promote seed germination (Crosti et al. 2006) or alter soil properties (Certini 2005). The effects of fire may not be consistent across species in the same ecosystem. This has led to the argument that pyrodiversity is an important tool for preserving biodiversity (Brockett et al. 2001), although this remains controversial (Parr and Andersen 2006).

Both of these effects often occur against a backdrop of anthropogenic disturbance. These disturbances can produce a wide range of effects depending on the nature of the disturbance as well as the species affected. Habitat disturbances such as the creation of roads may alter the competitive interactions between plant species in an ecosystem (Gelbard and Belnap 2003).

Populations existing along the edge of the disturbance may experience positive (Stephens et al. 2014) or negative (Laurance et al. 1998) consequences on population dynamics.

Despite the major direct impacts that each of these factors can have on population dynamics, it is crucial to remember that their effects do not occur in a vacuum. Indeed these factors often interact with each other to produce indirect effects on population growth. Herbivore pressure or the response of target species may change in response to changing fire regimes (Hegland et al. 2010). Anthropogenic disturbances such as roadsides may also alter the relative rates and intensity of herbivory (Kettenring et al. 2009). Herbivory itself may also serve to either increase or reduce the habitat altering effects of fire or anthropogenic disturbance (Fuhlendorf et al. 2009).

Complex life cycles may add a further layer of interactions to the study of population dynamics. Environmental factors may affect differing parts of a complex life cycle at different magnitudes or even in opposing directions (Benton et al. 2006). Species from many different taxa have life cycles consisting of stages that differ drastically in morphology or in ecosystem interactions. Understanding how differing portions of a life cycle are affected by environmental drivers is thus a crucial step in the successful management of many species.

The flexibility of matrix-based population models, such as Integral Projection Models, makes them an ideal approach for studying complex interactions. However, in spite of the benefits of assessing these interactions, only 40% of 396 recently reviewed matrix model studies in plants assessed the relative importance of life history stages, only 28% of studies looked at even a single environmental factor, and only 16% assessed biotic interactions (Crone et al. 2011). The lack of studies assessing the interactive effects of these factors thus represents a gap

in ecological understanding of population dynamics that few studies have attempted to address (e.g., Dhalgren and Ehrlen 2011).

I studied the relative importance of herbivory, time-since-fire, anthropogenic disturbance and their interactive effects on the population dynamics of an endangered endemic Florida scrub species with a complex life cycle *Liatris ohlingerae* S.F. Blake B.L. Rob. *(*Asteraceae). Florida Scrub is a focal point for conservation studies due to high endemism and habitat degradation (Abrahamson et al. 1984). *L. ohlingerae* (Scrub blazing star) is a perennial plant with a long lifespan, high survival and poor recruitment (Evans et al 2003, Weekley et al 2008). It exhibits a complex life cycle including a reproductive stage, a non-reproductive vegetative stage, and plant dormancy (Figure 10). Fire is a major disturbance in this ecosystem with many herbaceous species being favored by frequent burns (Quintana-Ascencio et al 2003, Menges and Quintana-Ascencio 2004). Fire's positive effects on demography are likely related to the maintenance of gaps and reduction of below ground competition (Hawkes and Menges 1996, Menges et al. 2008). However, *L. ohlingerae* occurrence increases slightly with time-since-fire (Miller et al. 2012). Anthropogenic disturbance in sandy roads within Florida scrub has been documented to increase fecundity and population instability in the several scrub endemics (Quintana-Ascencio et al. 2007, Schafer et al. 2010, Oakley 2013). Interactions between herbivory (mostly by white-tailed deer), time-since-fire, and roads affect *L. ohlingerae,* with higher rates of herbivory occurring in recently burned and non-roadside habitats (Kettenring et al 2009). The same study found no evidence of overcompensation (Kettenring et al 2009).
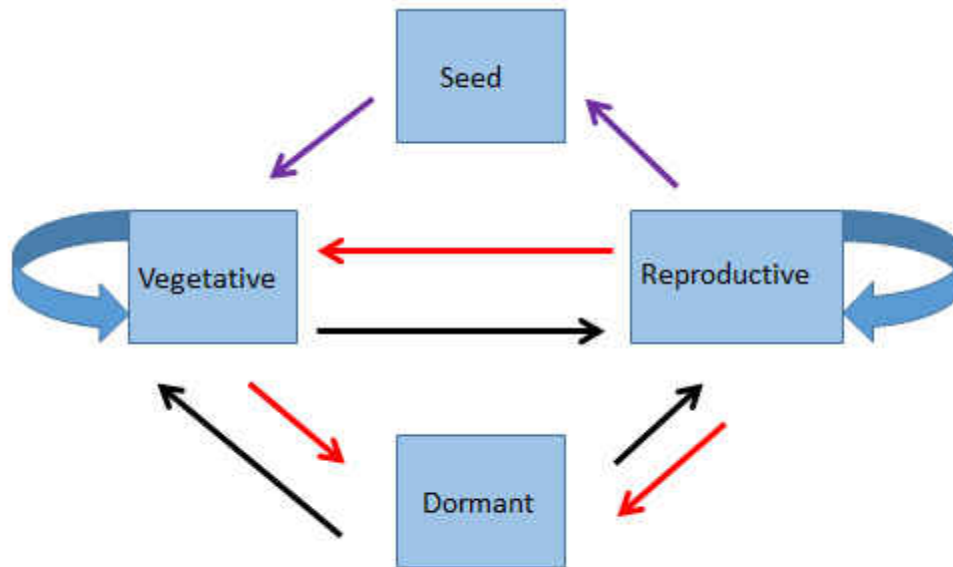
Figure 10. Life cycle diagram of *Liatris ohlingerae.* Black lines indicate progression, red lines indicated retrogressions, purple lines indicate fecundity, and blue lines indicated stasis.

I built an integral projection model for *Liatris ohlingerae* to evaluate interactive effects of herbivory, habitat and fire on population growth and underlying vital rates. I hypothesize (i) frequent disturbance and openness in roadside populations will result in more unstable demography, with higher fecundity and lower survival. (ii) because *Liatris ohlingerae* is a long lived species its population dynamics after fire will be more stable than has been documented for shorted lived herbaceous species in the same ecosystem (iii) higher rates of herbivory in roads and recently burned plots will compensate for positive demographic effects of competition with disturbance in roads and after fire.

Methods

Study Site and natural history

The study was conducted in Florida scrub primarily at Archbold Biological Station (21º11' N, 82º 21' W), Venus, FL., USA. Data from additional populations were collected at nearby sites in Gould Road Scrub and Lake Wales Ridge State Forest (Table 1). All sites occur

in the southern portion of the Lake Wales Ridge, a relict sand dune system formed from

sediment deposition in the Pleistocene (Abrahamson et al. 1984). The climate is sub-tropical and

is typically defined by a warmer rainy season and a cooler dry season. Soils are xeric, nutrient

poor and sandy. Florida Scrub is characterized by denser patches of Florida Rosemary (*Ceratiola*

ericoides), xeric oaks (*Quercus* spp.) and palmettos interspersed by open gaps including a large

number of endemic herbs (Abrahamson et al. 1984). The ratio of open patches to shrubby

patches is primarily mediated by fire frequency (Hawkes and Menges 1996). Herbivory pressure

from vertebrates, particularly white-tailed deer (*Odocoileus virginianus*), is relatively high

(Kettenring et al. 2009)

Table 1 Summary of the populations used in this study. ABS = Archbold Biological Station, LWRSF = Lake Wales
Ridge State Forest, GRS = Gould Road Scrub

Region	Site	Individual Observations	Years Measured	Habitat	Mean Herbivory Rate	2010 Time-since-fire (in yrs)
2	ABS	408	2003-2012	Scrub	0.41	25
2	ABS	756	2003-2012	Scrub	0.62	9
1	ABS	636	2000-2012	Scrub	0.54	0
1	ABS	1488	2000-2012	Scrub	0.56	42
1	ABS	900	2000-2012	Scrub	0.44	74
1	ABS	1392	2000-2012	Scrub	0.46	12
1	ABS	696	2000-2012	Scrub	0.67	2
1	ABS	1764	2000-2012	Scrub	0.54	38
1	ABS	756	2000-2012	Scrub	0.66	0
2	ABS	1068	2003-2012	Scrub	0.64	8
2	ABS	1260	2002-2012	Scrub	0.61	9
1	ABS	948	2003-2012	Roadside	0.49	Unburned
2	ABS	1020	2003-2012	Roadside	0.49	Unburned
2	ABS	852	2003-2012	Roadside	0.45	Unburned
1	ABS	2388	2003-2012	Roadside	0.52	Unburned
1	ABS	624	2003-2012	Roadside	0.35	Unburned
1	ABS	2100	2000-2012	Roadside	0.34	Unburned
1	LWRSF	8520	1997-2012	Scrub	0.47	12
1	ABS	1308	2003-2009	Scrub	0.65	7
2	GRS	336	2005-2006	Scrub	0.43	NA

Liatris ohlingerae (Asteraceae) is an herbaceous perennial endemic to the Lake Wales

Ridge. (Evans et al. 2003). Individuals form a corm from which aboveground biomass is

produced yearly (Dolan et al. 1999). Aboveground biomass dies back during winter. Flowering

scapes are developed in mature individuals in summer and its maximum lifespan exceeds 10

years (Evans et al. 2003). Individuals are self-incompatible (Evans et al. 2003) and genetic

differentiation between populations is minimal, although overall genetic diversity is fairly high

(Dolan et al. 1999). *Liatris ohlingerae* exhibits high rates of germination and likely lacks a long

term seed-bank (Weekley et al. 2008, Stephens et al. 2012). Seeds of *L. ohlingerae* also appear to

be resistant to allelopatic effects of other plants within its habitat (Weekley et al. 2008). Despite

this, recruitment of new germinants is often poor (Menges et al. 2010a). It is subject to frequent

vertebrate herbivory, particularly in recently burned areas, which has a negative effect on within-

year fecundity (Kettenring et al. 2009). Several invertebrate species predate on its seeds

(Stephens et al. 2012).

The life cycle of *Liatris ohlingerae* consists of three distinct life history stages:

vegetative, reproductive, and dormant. Vegetative individuals produce one or more grassy

rosettes in a given year. Reproductive individuals develop one or more reproductive stems

(scapes). Dormant individuals produce no above-ground biomass in a given year. All possible

transitions between these stages may occur within a given year.

Sampling design
Demographic data was collected annually in August on 20 populations of *Liatris*

ohlingerae. Sampling on populations began between 1998 for the earliest plot and 2005 for the

most recent plot. Plots were created surrounding extant populations of the species and thus

varied in size, ranging from 5 m^2 and 600 m^2. Plots were split among populations that occurred

in the interior of the scrub (scrub) and populations along the edge of unpaved, sandy roads (roadside). Populations within the scrub were further divided into three time-since-fire (TSF) categories based on unique and known burn histories: <10 y., 10-20 y, >20 y. Roadside populations were all long unburned. Populations were also broadly categorized into two groups along a north-south axis to test for the possibility of spatial variation. Average annual rainfall and temperature were obtained from Archbold Biological Station.

Within each plot, each new individual was marked with a flag and numbered tag. Data collected for each reproductive individual included total stem length, number of flowering heads, evidence of vertebrate herbivory ("topping"), and survival. Leaf number, rosette number and recorded survival were counted for each vegetative individual. Tagged individuals not found aboveground were assumed dormant, and those without aboveground biomass for at least 3 consecutive years were declared dead.

Modeling design
I constructed multiple stage integral projection models (IPMs, Easterling et al 2000, Ellner and Rees 2006) to model the full life cycle of *Liatris ohlingerae* in R (3.0.1, R Development Core Team). Because there was not variation in fire history for the roads, I constructed two separate IPMs. The Habitat Model contained all populations, while the TSF Model was based on scrub populations only. I evaluated models assessing the effect of environmental variables and their interactions on each vital rate using general linear models (GLMs). Models were ranked using AICc (Appendix B). All models of similar AICc score (see Burnham and Anderson 2002) were individually assessed. The model that produced the highest proportion of significant variables and the lowest complexity were preferred. In a case where the models differed drastically between the Habitat and TSF models, the overall (Habitat) model was

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retained. For vegetative plants, I estimated probability of survival, probabilities of transitioning to vegetative, reproductive or dormant stages, and growth. The kernel functions for vegetative individuals that remained vegetative and vegetative individuals that became reproductive were:

$$K_{vv}(X,Y) = S_v(X) * (1 - T_{vr}(X,Y)) * G_{vv}(X,Y) \tag{2}$$

$$K_{vr}(X,Y) = S_v(X) * (T_{vr}(X,Y)) * G_{vr}(X,Y) \tag{3}$$

Where K indicates the kernel of each sub-matrix, S indicates survival of an individual, T indicates the probability of transitioning between stages, and G indicates growth. The subscripts indicate the stage on which each function is being assessed. Number of leaves in vegetative individuals was modeled using either a Poisson (vegetative to vegetative) or negative binomial (reproductive to vegetative) error distribution.

I used a similar kernel for reproductive individuals but the size variable (total stem length) was modeled using a Gaussian error distribution. I estimated size-dependent fecundity of reproductive individuals. Fecundity was the product of probability of successfully producing a reproductive head (*PR1*, with binomial error), number of heads produced (with Gaussian error) and scalar quantities estimated from previous data (Stephens et al. 2012, Weekley 2008, Menges, unpublished data): number of seeds per head (F_1), pre and post dispersal seed predation (F_2, F_3) seed viability (F_4), and germination (F_5). This procedure likely represented an overestimation of successful reproduction because I did not have estimates of all possible sources of seed mortality. To compensate, I included a correction factor (F_6) that adjusts the estimated value to be more consistent with the observed number of germinants in the field. Successful germinants were assigned a vegetative size based on the observed distribution of germinant sizes. The model assumes no seedbank. The kernel functions for reproductive individuals were thus defined as:

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$$K_{rv}(X,Y)= (PR1* F_1* F_2* F_3 * F_4* F_5* F_6) + (S_r(X)*(1-T_{rr}(X,Y))*G_{rv}(X,Y)) \qquad (4)$$

$$K_{rr}(X,Y)= S_r(X)*T_{rr}(X,Y)*G_{rr}(X,Y) \qquad (5)$$

I estimated size dependent probability of entering dormancy from either reproductive (R_d) or vegetative (V_d) stages. I obtained size distributions of individuals leaving dormancy and entering either reproductive (D_r) or vegetative (D_v) stages. The probability of entering a given continuous stage from dormancy is given by scalar quantities. The probability of individuals remaining dormant (D_d) more than a year was assumed to be zero as it occurred infrequently (probability = 0.016).

The four continuous kernel functions: K_{vv}, K_{vr}, K_{rv}, K_{rr}, as well as four vectors describing dormancy transitions: D_v, D_r, V_d, R_d, and the scalar quantity D_d were concatenated to form an overall Goodman matrix (Goodman 1969)

$$\begin{Bmatrix} D_v & K_{vv} & K_{rv} \\ D_r & K_{vr} & K_{rr} \\ D_d & V_d & R_d \end{Bmatrix}$$

The dominant eigenvalue of the overall square matrix corresponds to population growth rate.

I modified the levels of environmental covariates in each vital rate function to represent differing herbivory rates, habitats, times-since-fire, and levels of precipitation in order to test the hypotheses. I calculated the effects of these changes both at the level of individual vital rates as well as the overall population growth rate

I estimated the effects of differing herbivory rates on λ by first using logistic models to assess the probability of herbivory across differing combinations of environmental variables for reproductive individuals. Non-reproductive individuals were distributed between sub-matrices representing herbivory occurrence using probabilities of herbivory per habitat for each combination of environmental factors. This resulted in four possible herbivory transitions: herbivorized in consecutive years, not herbviorized in consecutive years, transition from not herbivorized to herbivorized, and transition from herbivorized to not herbivorized. I constructed an IPM for each transition using the methods described above. I then combined all four of these matrices to form a megamatrix assessing the effects of differing rates of herbivory.

Results

Vital Rates and Herbivory Rates
The most informative model for vegetative survival included size and size^2 in the TSF and Habitat models (Table2, Table 3) as well as habitat and precipitation in the Habitat model. Survival varied with size as a concave parabola with higher survival in individuals with a small or large amount of leaves (Figures 9, 10). Survival was significantly higher in roadside plots than in scrub and in years with high precipitation.

The models defining the probability of a vegetative individual becoming a reproductive individual included size, size^2, habitat and precipitation in the Habitat Model (Table 2). Reproductive probability increased with increasing size (Figure 11). There was a significant increase in transition probability in roadside habitats as well as a marginal increase in transition probability with increased rainfall. In the TSF model, there was a non-significant increase for the

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transition probability of a vegetative individual becoming a reproductive with increasing time-since-fire (Table 3, Figure 12). The probability of vegetative models transitioning to dormant individuals included only a small decrease in dormancy with increasing size in both the Habitat and TSF models (Figures 11 and 12).
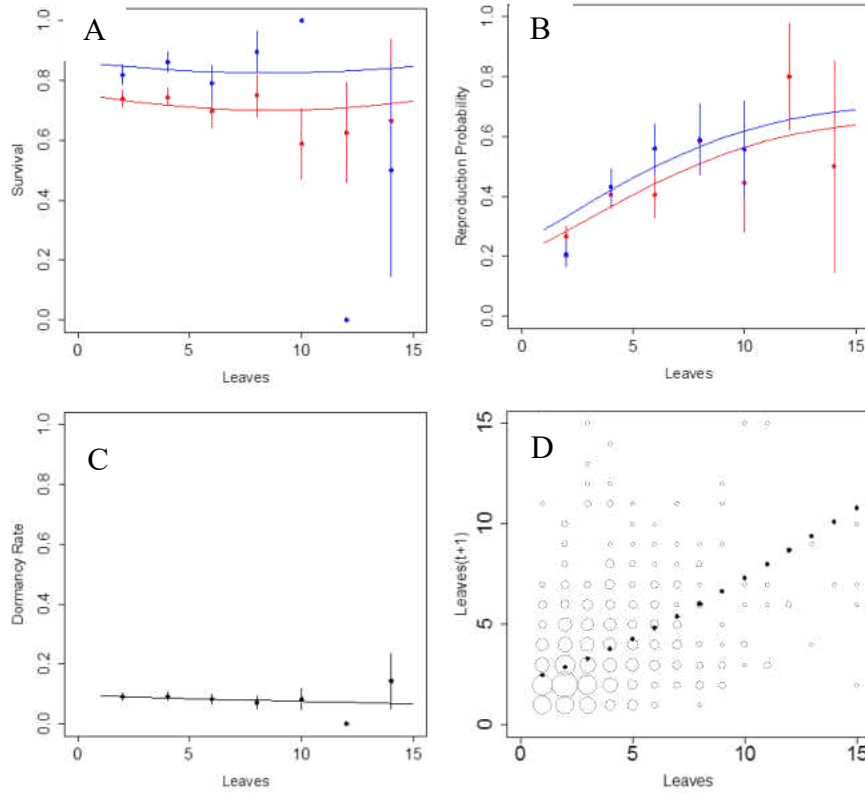
Figure 11 Figures showing (A) vegetative survival (B) vegetative reproduction probability (C) vegetative dormancy (D) vegetative to vegetative growth for the Habitat model. Red = Scrub, Blue = Roadside. Points and vertical lines in A-C indicate binned probably and errors. Points in D indicate data (light gray) and results of Poisson regression (black).

Table 2 Effect sizes of predictor variables on vital rates in Habitat Model. Significant effects are in bold. Numbers after the slash represent interactions between size^2 and environmental variables. VS=Vegetative Survival, RS=Reproductive survival, VR=Vegetative to Reproductive Transition, VD=Vegetative to Dormant Transition, RR=Reproductive to Reproductive transition, RD=Reproductive to Dormant Transition, OF=Probability of Producing a Reproductive Head. F= Number of Reproductive Heads Produced.

	Size	Size^2	Habitat	Herb	Region	Precip	Size*Habitat	Size*Herbiv	Habitat*Herb	S*H*HB
VS	**-0.066**	**0.004**	**0.704**			**0.235**				
RS	**0.417**		**0.250**	**-0.107**	**0.330**					
VR	**0.226**	**-0.007**	**0.229**			0.202				
VD	-0.025									
RR	0.018	**0.104**	**0.270**	**-0.657**					**0.525**	
RD	**-0.250**		**-0.380**	**-0.274**		**0.345**				
OF	**4.376**	**-0.235**	**0.732**	**-1.925**						
F	-0.480	**0.189**	-0.590	**-3.717**	**0.059**	**0.069**	**0.495/-0.060**	**2.176/-**	**2.268**	**-1.237/0.158**

Table 3 Effect sizes of predictor variables on vital rates in time-since-fire model. Significant effects are in bold. VS=Vegetative Survival, RS=Reproductive survival, VR=Vegetative to Reproductive Transition, VD=Vegetative to Dormant Transition, RR=Reproductive to Reproductive transition, RD=Reproductive to Dormant Transition, OF=Probability of Producing a Reproductive Head. F= Number of Reproductive Heads Produced.

	Size	Size^2	TSF	Herb	Region	Precip	Size*TSF	Size*Herb	TSF*Herb	S*TSF*HB
VS	-0.051	0.003								
RS	**0.506**				**0.409**					
VR	**0.195**	**-0.006**	0.075							
VD	-0.031									
RR	-0.069	**0.117**		-0.146						
RD	**-0.533**		-0.659	**-2.523**	**-0.311**	**0.472**	0.143	**0.665**	1.443	**-0.420**
OF	**2.855**			**-1.939**						
F	**0.673**		-0.020		-0.019					
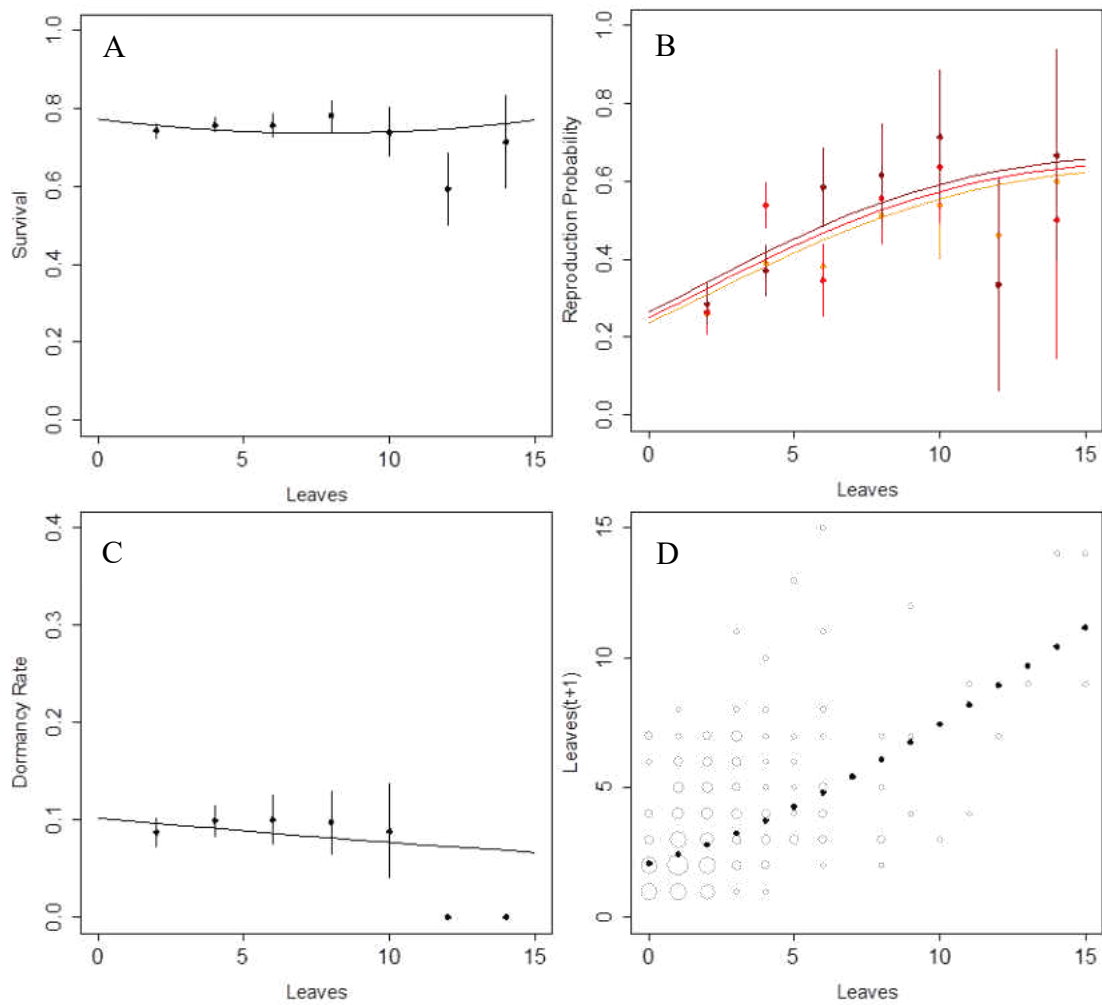
Figure 12 Figures showing (A) vegetative survival (B) vegetative reproduction probability (C) vegetative dormancy (D) vegetative to vegetative growth for the TSF model. Orange = < 10 TSF, Red = 10-20 TSF, Dark red = > 20 TSF. Points and vertical lines in A-C indicate binned probably and errors. Points in D indicate data (light gray) and results of Poisson regression (black).

Size, habitat, herbivory, and region were the most informative predictors of survival of

reproductive individuals in the Habitat Model (Table 2, Figure 13). Size and region were the

most informative for survival in the TSF Model (Table 3). Survival increased significantly with

increasing size and latitude of the region (Figure 14). Increasing rates of herbivory had a significantly negative effect on the survival of reproductive individuals.

The probability of a reproductive remaining reproductive was associated with size and size^2 and herbivory in both models as well as habitat in the Habitat Model (Table 2, Table 3, Figure 13, Figure 14).. Herbivory showed a negative relationship with reproductive probability in both models. However, in the Habitat Model, there was a significant positive interaction between habitat and herbivory. Probability of reproduction increased with size and in the roadside habitat without herbivory

The most informative variables for reproductive dormancy in the Habitat Model were size, habitat, herbivory and precipitation (Table 2, Figure 13). The rate of dormancy was significantly decreased with size, roadside habitat, and increasing herbivory. Higher precipitation significantly increased dormancy in reproductive individuals. In the TSF Model, dormancy of reproductive individuals varied with size, time-since-fire, herbivory, region, and precipitation (Table 3, Figure 14). Dormancy decreased with size, time-since-fire, herbivory and latitude and increased with higher precipitation. In addition to the additive effects, there were also positive interactions between size and time-since-fire, size and herbivory, and time-since-fire and herbivory as well as a negative three way interaction between size, time-since-fire, and herbivory.
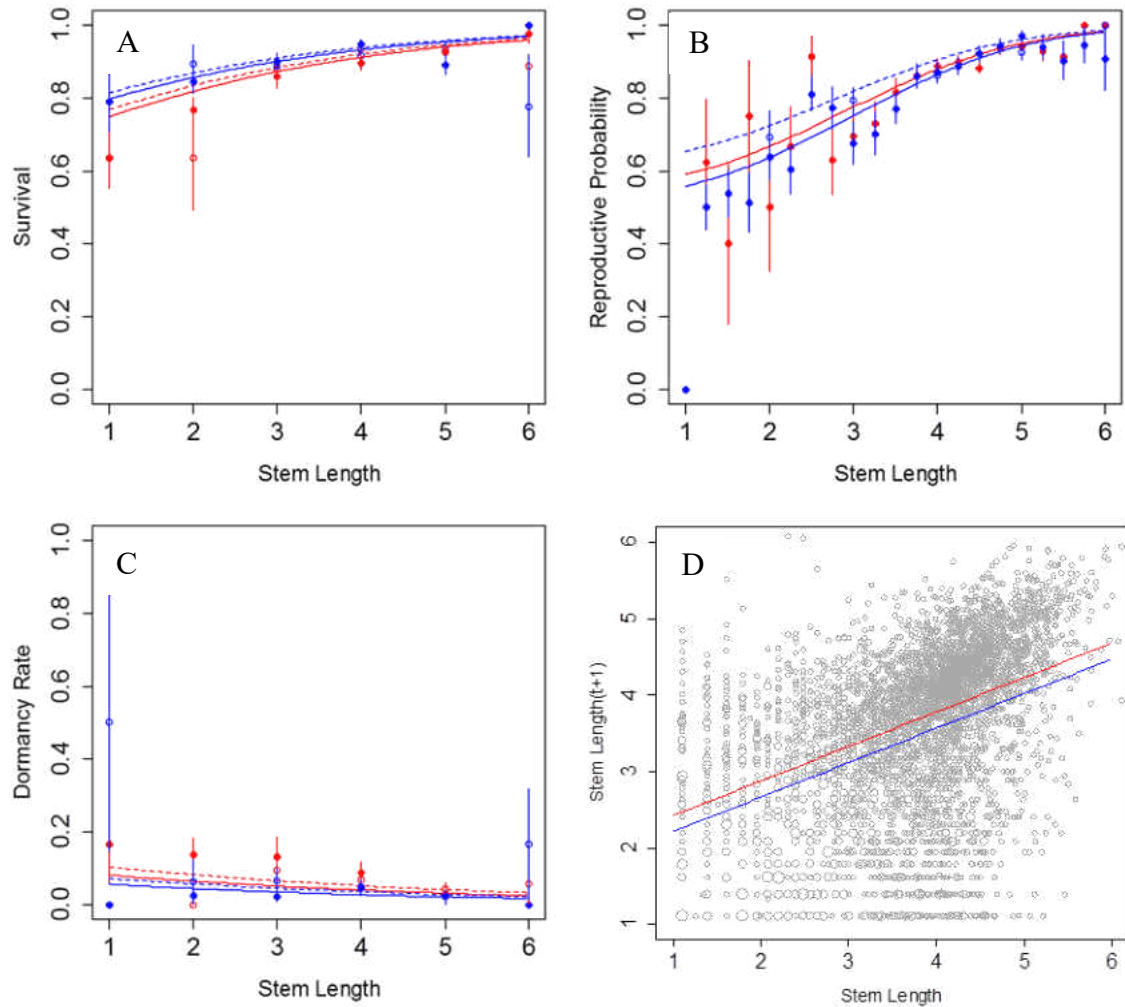
Figure 13 Figures showing (A) reproductive survival (B) reproductive reproduction probability (C) reproductive dormancy (D) reproductive to reproductive growth for the Habitat model. Red = Scrub, Blue = Roadside. Solid lines indicate herbivory, dashed lines indicate no herbivory. Points and vertical lines in A-C indicate binned probably and errors. Points in D indicate data (light gray).
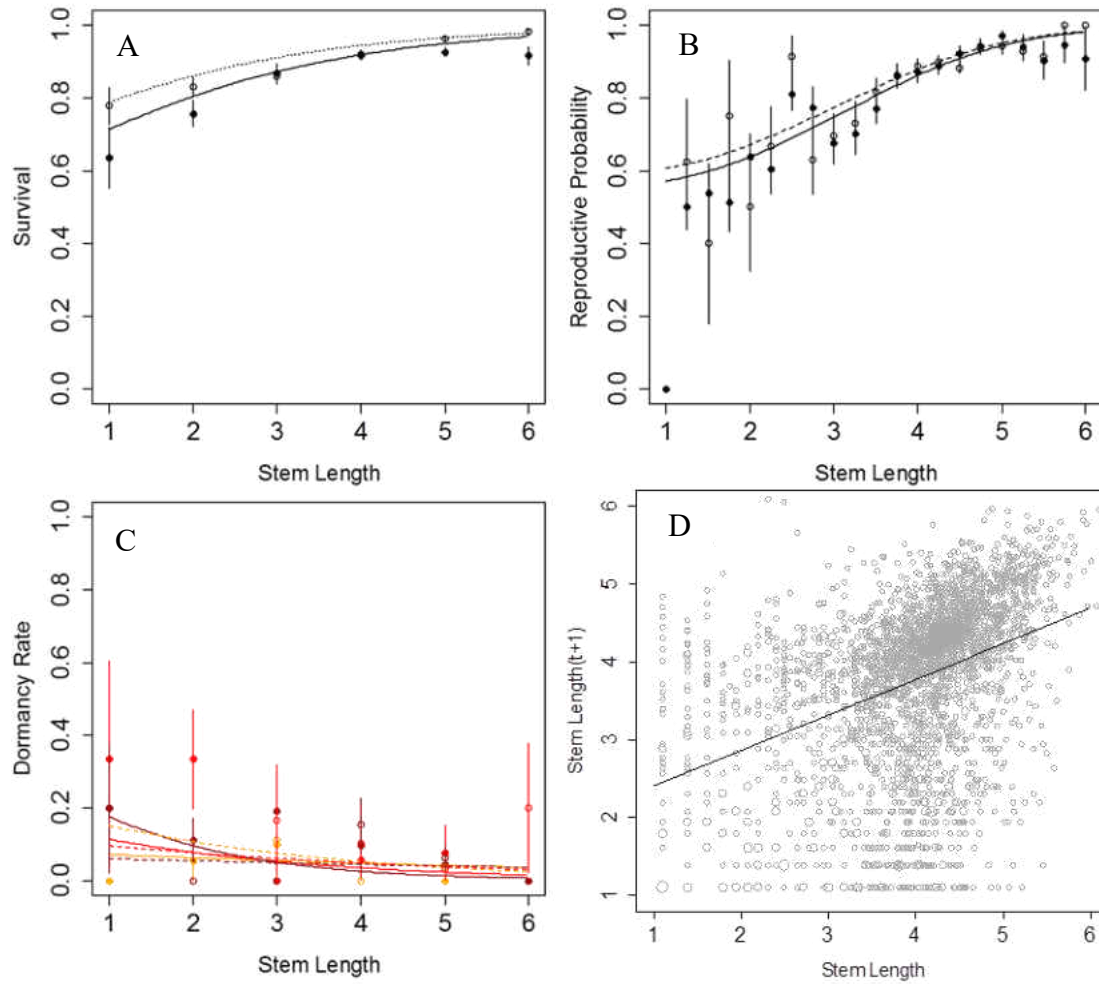
Figure 14. Figures showing (A) reproductive survival (B) reproductive reproduction probability (C) reproductive dormancy (D) reproductive to reproductive growth for the TSF model. Orange = < 10 TSF, Red = 10-20 TSF, Dark red = > 20TSF Solid lines indicate herbivory, dashed lines indicate no herbivory. Points and vertical lines in A-C indicate binned probably and errors. Points in D indicate data (light gray).

Not all reproductive individuals produced flowering heads. The probability of a

reproductive individual producing flowering heads varied with size, size^2, habitat, and herbivory

in the Habitat Model (Table 2, Figure 15) and size and herbivory in the TSF Model (Table 3,

Figure 16). The probability of successfully producing a flowering head increased with

increasing size and decreased significantly with herbivory. Roadside habitats had higher probabilities of producing reproductive heads.

The number of reproductive heads was predicted by a full factorial model of size, habitat and herbivory as well as additive effects of $size^2$, latitude and precipitation (Table 2, Figure 15). Fecundity had a quadratic increase with size, region and precipitation. Fecundity decreased interactively with higher herbivory and roadside. Two way interactions between size, habitat and herbivory were all positive, however the three-way interaction between these variables was significantly negative. In the TSF Model, fecundity was influenced by size, TSF, and region (Table 3, Figure 16). Fecundity increased with size, while decreased with increased TSF and latitude of the region.

Herbivory rates were generally high across all environmental conditions (Table 4). Roadside populations consistently experienced higher herbivory rates as compared to scrub populations. Populations with higher time-since-fire generally experienced higher herbivory, but variation was high between environmental conditions. There was no consistent pattern observed with latitude of the region or precipitation.
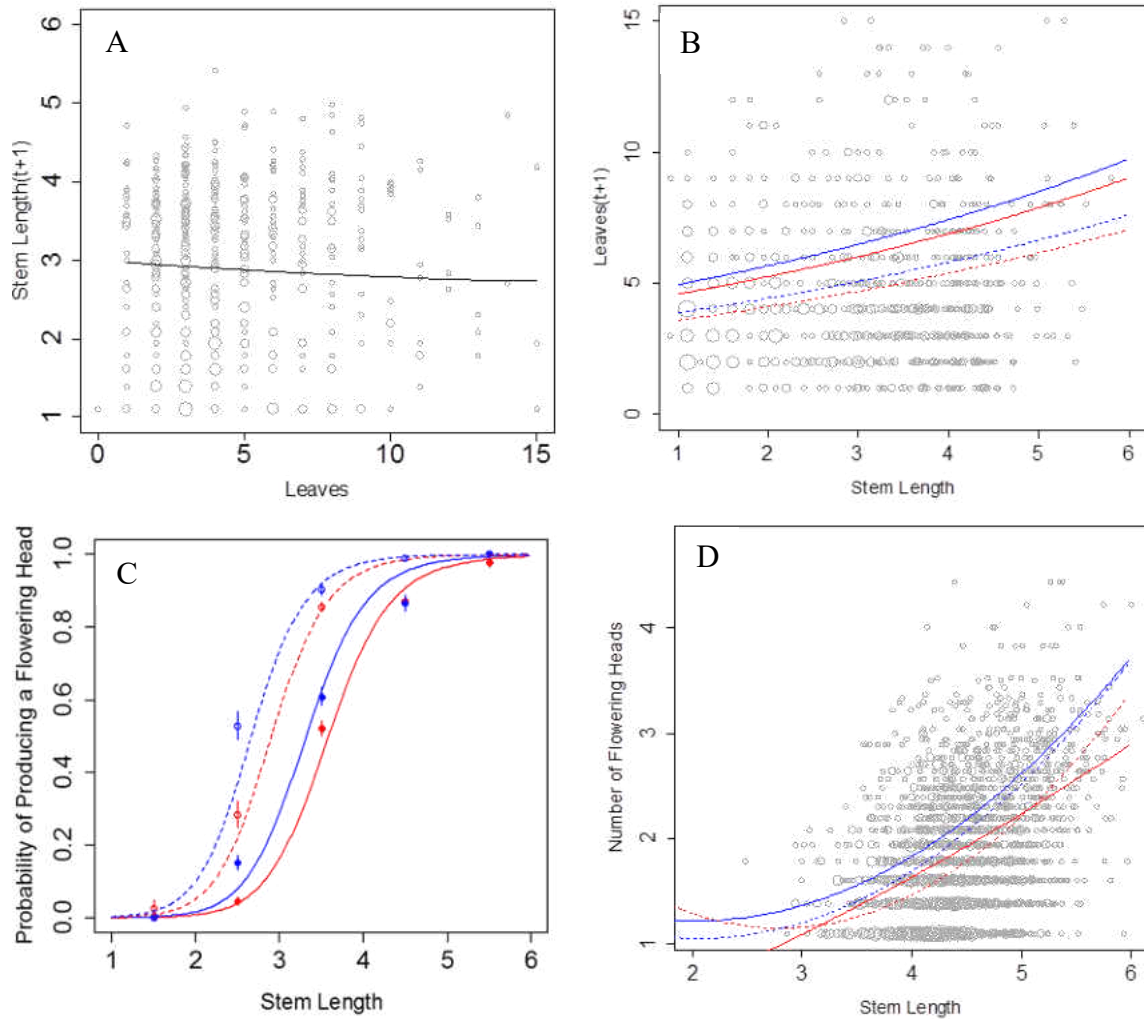
Figure 15 Figures showing (A) vegetative to reproductive growth (B) reproductive to vegetative growth (C) probability of producing a flowering head (D) number of flowering heads produced for the Habitat model. Red = Scrub, Blue = Roadside. Solid lines indicate herbivory, dashed lines indicate no herbivory. Points and vertical lines in C indicate binned probabilities and errors. Points in A, B, D indicate data (light gray).
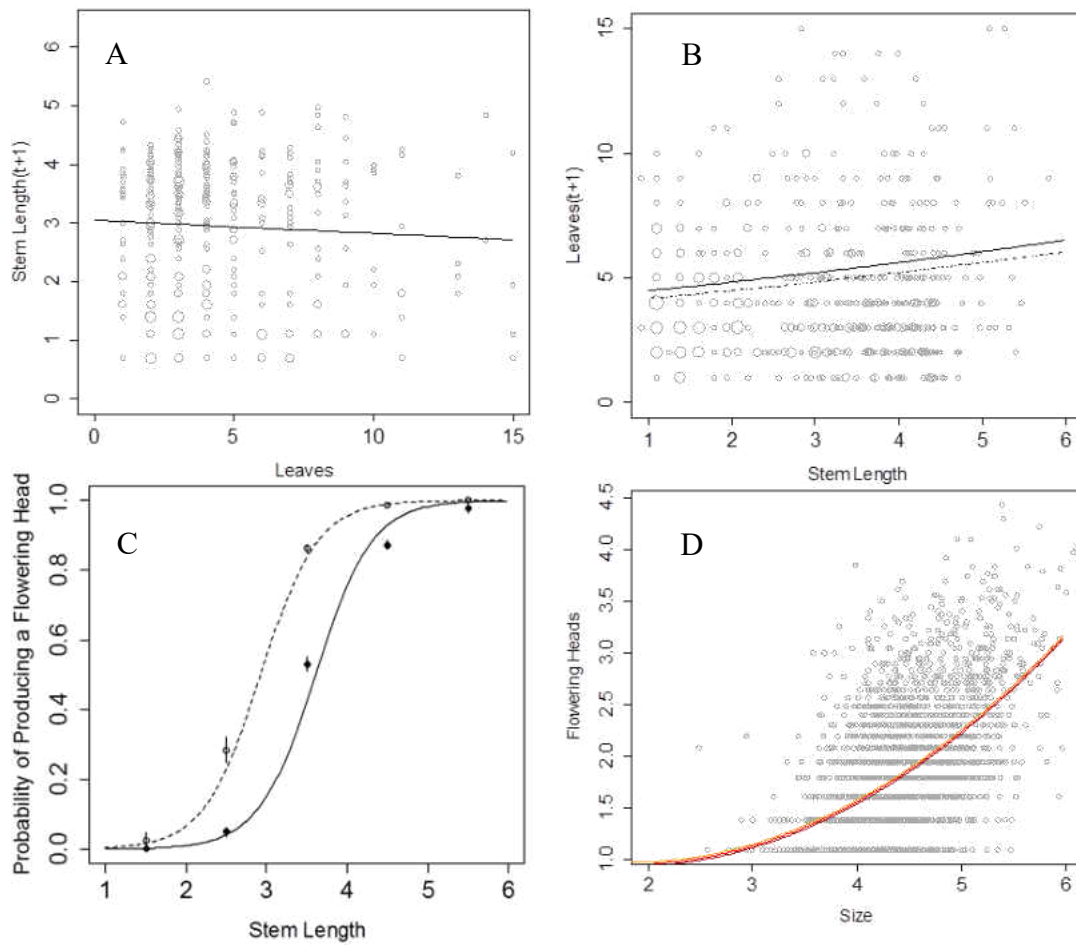
Figure 16 Figures showing (A) vegetative to reproductive growth (B) reproductive to vegetative growth (C) probability of producing a flowering head (D) number of flowering heads produced for the TSF model. Orange = <10 TSF, Red = 10-20TSF, Dark red = >20 TSF. Solid lines indicate herbivory, dashed lines indicate no herbivory. Points and vertical lines in C indicate binned probabilities and errors. Points in A, B, D indicate data (light gray).

Table 4 Herbivory rates in differing environmental conditions.

	Low Precipitation		High Precipitation	
	South	North	South	North
Roadside	0.527	0.562	0.632	0.557
Scrub	0.464	0.470	0.414	0.490
<10 TSF	0.418	0.440	0.456	0.484
10-20 TSF	0.417	0.506	0.298	0.531
>20 TSF	0.557	0.875	0.408	0.667

Population growth rate

In the Habitat Model, population growth rates ranged from 0.975 to 1.116 (Figure 17). Roadside populations exhibited higher population growth rates across all sets of environmental conditions. This trend was especially pronounced for herbivory scenarios, where differences in population growth rate between road and scrub ranged from .075 to .091 as compared to .036 to .047 in scenarios without herbivory. This is due to a strong decline in population growth rate in herbivorized scrub populations compared to a relatively modest decline in herbivorized roadside populations. Northern populations produced higher growth rates than southern populations. High precipitation also produced consistent but modest improvements in population growth rate.

In the Habitat megamatrix, roadside populations once again outperformed scrub populations across all combinations of site and rainfall, despite higher rates of herbivory (Figure 18). These differences were relatively uniform, ranging from .057 to .074. These values are intermediate between the results of the herbviorized and unherbviorized populations. Populations in northern sites were marginally better than populations in southern sites. Populations in high rainfall years had marginally higher population growth rates than those in low rainfall years.

In the Time-since-fire model, population growth rates ranged from 1.006 to 1.045 (Figure 19). In all scenarios with no herbivory, population growth rates decreased with increasing time-since-fire, although the effect was smaller than the one between habitats. The difference in population growth rate between the highest and lowest time-since-fire classes ranged from -.011 to -.016. However, herbivory virtually eliminated the difference in population growth rate due to time-since-fire. Population growth rates in recently burned populations decreased while the population growth rates in long unburned populations actually increased slightly. Northern populations experienced higher population growth rates than southern populations. High precipitation led to a small but consistent improvement in population growth rate.

In the Time-Since-Fire megamatrix, the effect of time-since-fire was extremely small across all environmental combinations (Figure 20). The differences in population growth rate ranged from .0006 to .0016. These changes were far smaller than the observed differences in performances between site (maximum difference=.022) and rainfall (maximum difference=.01). These differences are similar to the models of herbivorized individuals.
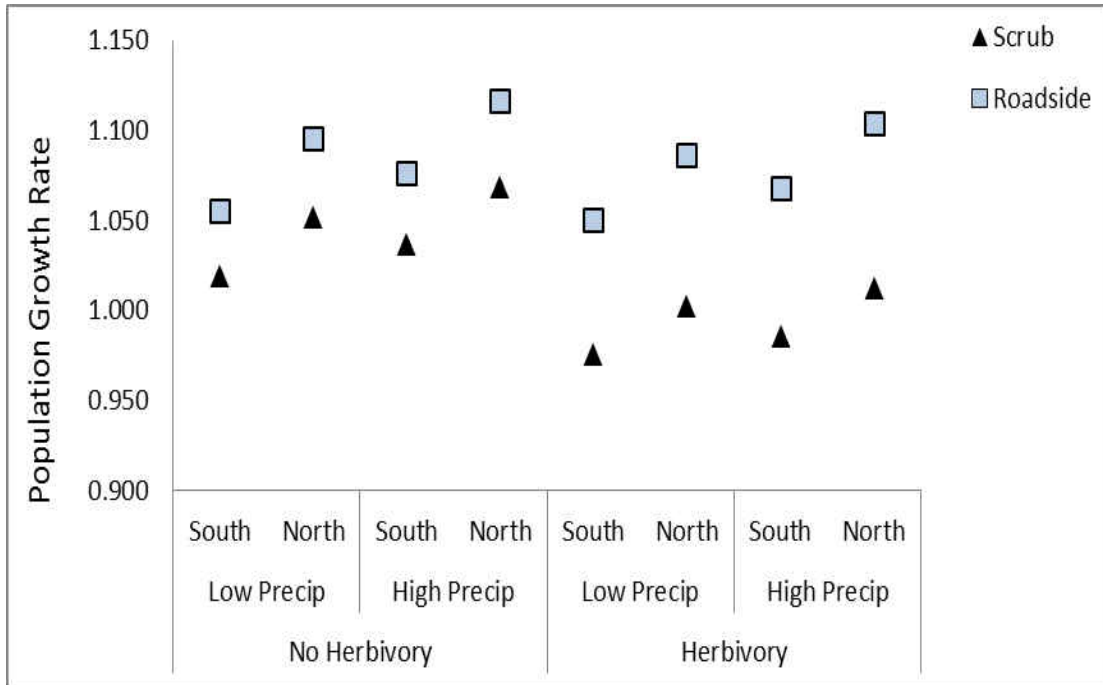
Figure 17 Figure showing the heuristic population growth rates predicted by the habitat model under varying environmental conditions.
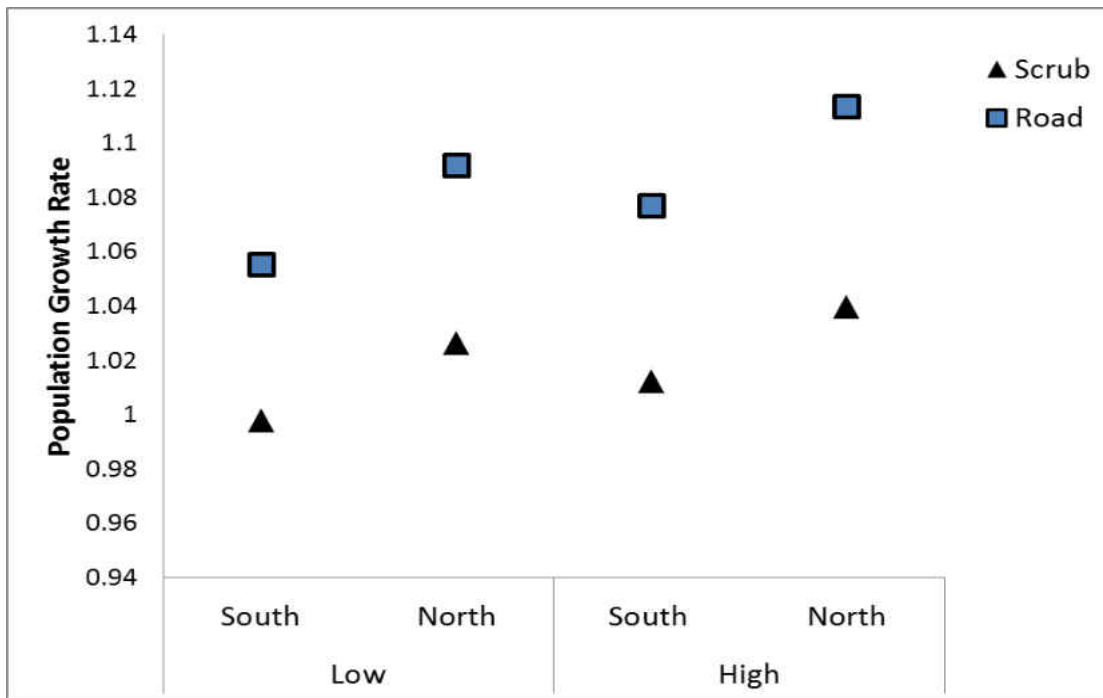
Figure 18. Figure showing the heuristic population growth rates predicted by the habitat model under varying environmental conditions.
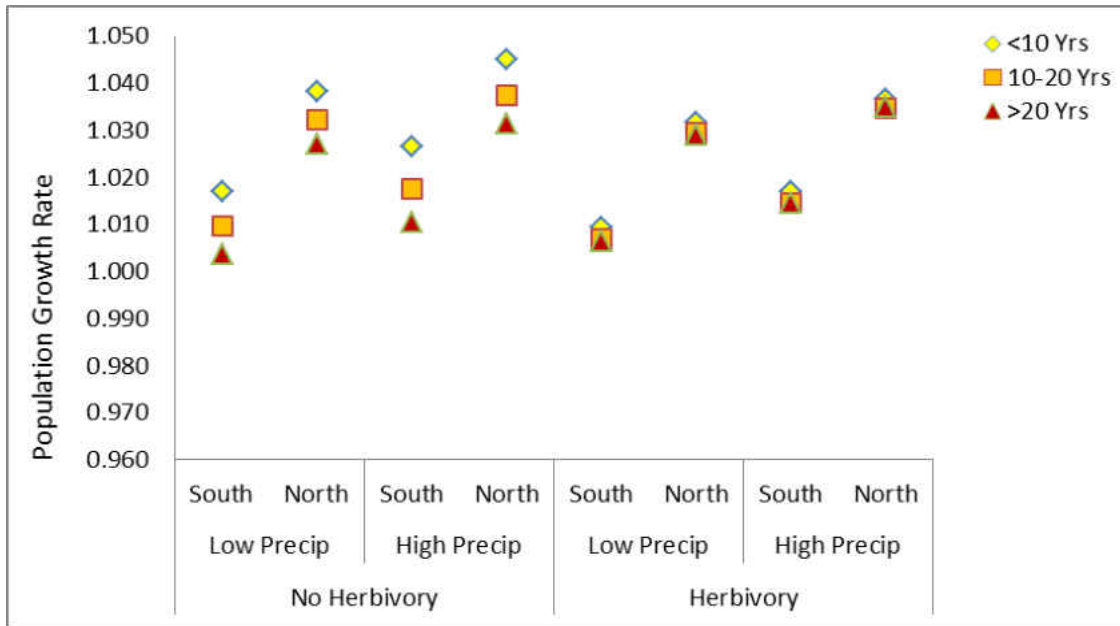
Figure 19. Figure showing the heuristic population growth rates of the herbivory mega-matrix for habitat.
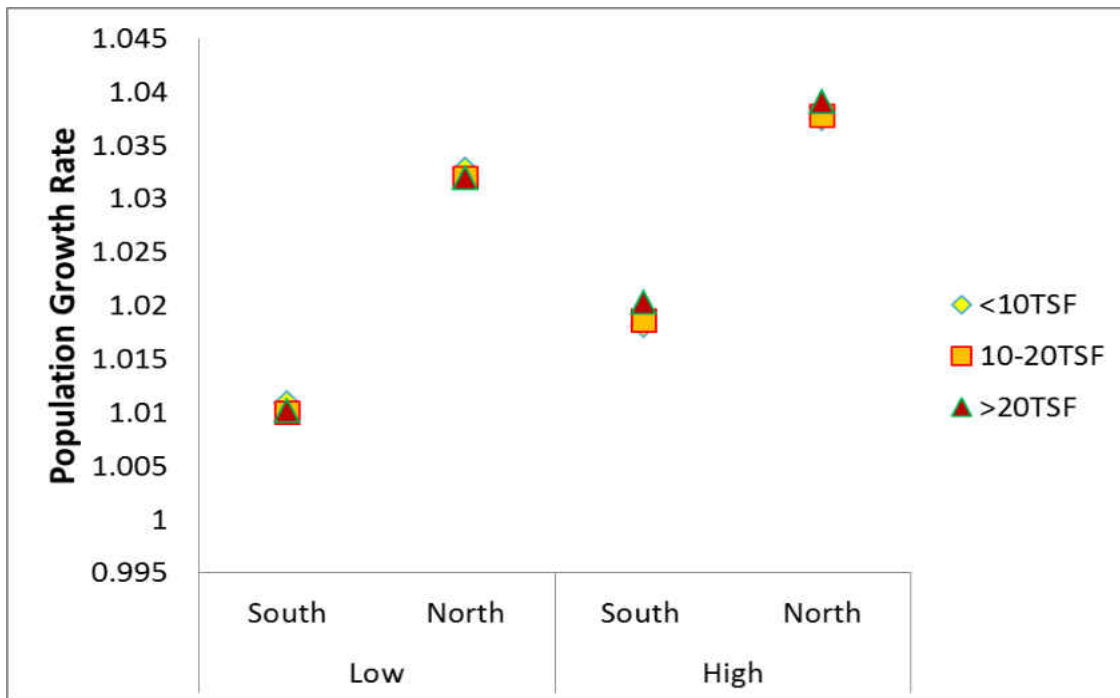
Figure 20. Figure showing the heuristic population growth rates of the herbivory mega-matrix for time-since-fire.

Discussion

Herbivory, habitat and fire have synergistic effects on plant population dynamics of the Florida endemic plant *Liatris ohlingerae*. Integral projection models reveal a uniform increase in population growth rate in roadside habitats, a small positive effect of decreasing time-since-fire, and strong interactions of both habitat and time-since-fire with vertebrate herbivory. Spatial and climatic effects played a secondary but significant role in population growth.

Contrary to the previous studies on shorter-lived scrub endemics, such as *Hypericum cumulicola* (Quintana-Ascencio et al. 2007, Oakley 2013), populations of *Liatris ohlingerae* near sandy roads experienced higher survival in both the reproductive and vegetative stage as well as slightly lower fecundity. Higher survival rates may result from decreased below-ground competition in this human disturbed habitat (Petrů and Menges 2003). A higher population growth rate was still observed in roadside populations even after accounting for higher rates of herbivory. This supports the conclusion that plants in roadside populations are able to tolerate herbivory pressure better than scrub populations. This study does not account for the increased potential of total population destruction associated with anthropogenic disturbance near roads (Menges et al. 2010).

The increased differences in population growth rate between habitats when herbivory occurs are likely due to the strong interaction observed between habitat, plant size, and herbivory on fecundity. This interaction could be due to difference in intensity of herbivory and/or a shift in the type of plants selected. Differences in herbivore choice and intensity changed with disturbance and vegetative structure in other systems (Jeffries et al 1994, von Euler et al. 2013), and may affect fecundity both negatively (Kolb 2012) and positively (Shimamoto et al. 2011).

I found little evidence of an effect of time-since-fire on the population growth rate of *L. ohlingerae*. Increasing time-since-fire had a small but consistent negative effect on population growth rate in non-herbivorized individuals. This effect was mostly due to a decrease in fecundity. However, population growth rates were similar between time-since-fire classes in herbivorized individuals. This effect was, at least in part, due to interactions between TSF, herbivory and size in determining the probability of reproductive dormancy. These results suggest that, similarly to other species (e.g. Shefferson et al. 2005), dormancy may be partially related to plant stress. When incorporating observed rates of herbivory, the results showed a similarly small effect of fire as with the model of herbivorized individuals. Current rates of herbivore pressure thus appear to mitigate whatever small effects of fire interval may be present in non-herbivorized individuals.

The lack of instability in roadside habitats and the relatively small effect of TSF are consistent with the more stable population dynamics often observed in longer-lived species (Garcia et al. 2008, Kuss et al. 2008, Dalghren and Ehrlen 2009). This supports the hypothesis that long-lived species that are not killed by fire experience far more stable populations across changes in disturbance frequency than do species with shorter life cycles. The lack of significant effect of time-since-fire in herbivorized individuals is also consistent with occurrence data in Florida rosemary patches with different times-since-fire (Miller et al. 2012). This underscores the importance of fully understanding the life-history strategies of a species as well as its interaction with the environment.

This study confirms the advantages of combining environmental interactions with a fine-scale approach to modeling (e.g. Dalghren and Ehrlen 2011). My work combines integral projection models with several interacting environmental factors. The viability of incorporating

complex life cycles into IPMs has been well studied (Ellner and Rees 2006, 2007). However, in practice most studies included one or more discrete stages with a single continuous stage rather than multiple continuous stages (e.g., Ramula et al. 2009). By incorporating multiple continuous stages with environmental interactions, this study provides a more in depth understanding of interactions between environmental factors and life history strategies.

A persistent criticism of techniques related to matrix modeling is the lack of accuracy in the predicted growth rates when compared to observed population growth rates (Crone et al. 2013). The development of IPMs has done little to solve this problem. However, this study demonstrates the usage of IPMs as an aid to understand complex environmental interactions rather than as an explicitly predictive tool. By comparing the relative effects of each environmental condition on the growth rate, it is possible to gain great insight into species-environmental interactions while avoiding the inherent weaknesses of these models.

Observed differences in *Liatris ohlingerae's* response to fire and habitat changes compared to other endemics in the same area demonstrates the folly of one-size-fits-all management strategies. Management interventions such as frequent fire which is beneficial to certain species may have neutral or even negative effects on other species (Schurbon and Fauth 2003). The results of this study support the important role of pyrodiversity as a tool for the management of the multiple conservation-relevant species of the Florida Scrub (Menges 2007). Only by maintaining heterogeneity of environmental conditions can land managers hope to conserve a diverse range of taxa in increasingly smaller amounts of land.

CHAPTER 4: CONCLUSION

Linking environmental effects to differences in vital rates provides a way to unravel mechanisms governing population dynamics (Dahlgren and Ehrlén, 2009). Both studies demonstrate previously suggested ability of integral projection models to effectively model the effects of environmental factors in species with differing and complex life cycles (Ellner and Rees 2006). Integral projection models constitute an excellent approach for tackling basic and applied ecological questions (e.g., Coulson, 2012, Bruno et al., 2011, Childs et al, 2004, Coulson et al., 2011, Dahlgren and Ehrlén, 2009). This allows the methods described in this thesis to serve as a basic methodological framework the development of models identifying population dynamics in other taxa.

Evidence for the interaction of herbivores with disturbance was present in both studies. In *Helianthemum squamatum*, simulated trampling showed that herbivores can be a direct cause of disturbance by increasing soil rugosity. This led to a notable positive effect at high density which was likely due to trampling increasing the amount of suitable microsites for germination. However at lower density, trampling was less effective than seed addition, which suggests that microsite limitation is less important at low densities (Eriksson and Ehrlen 1992).

In *Liatris ohlingerae*, rather than directly causing the disturbance, herbivore pressure interacted with two disturbances in differing ways. The relative positive effect of roadside habitat increased with herbivory, while the negative effects of time-since-fire decreased dramatically. Herbivory also reduced population growth rate in all scenarios with the exception of times-since-

fire exceeding 20 years, supporting previous work suggesting undercompensation in this species (Kettenring et al 2009).

The overall results of this thesis demonstrate both the need to consider the effects of environmental interactions on population dynamics as well as the efficacy of integral projection models in achieving this aim. These results are especially applicable to the management of threatened populations, where an accurate understanding of population dynamics can be the difference between persistence and extinction.

APPENDIX A:
SUPPLEMENTAL INFORMATION FOR CHAPTER 2
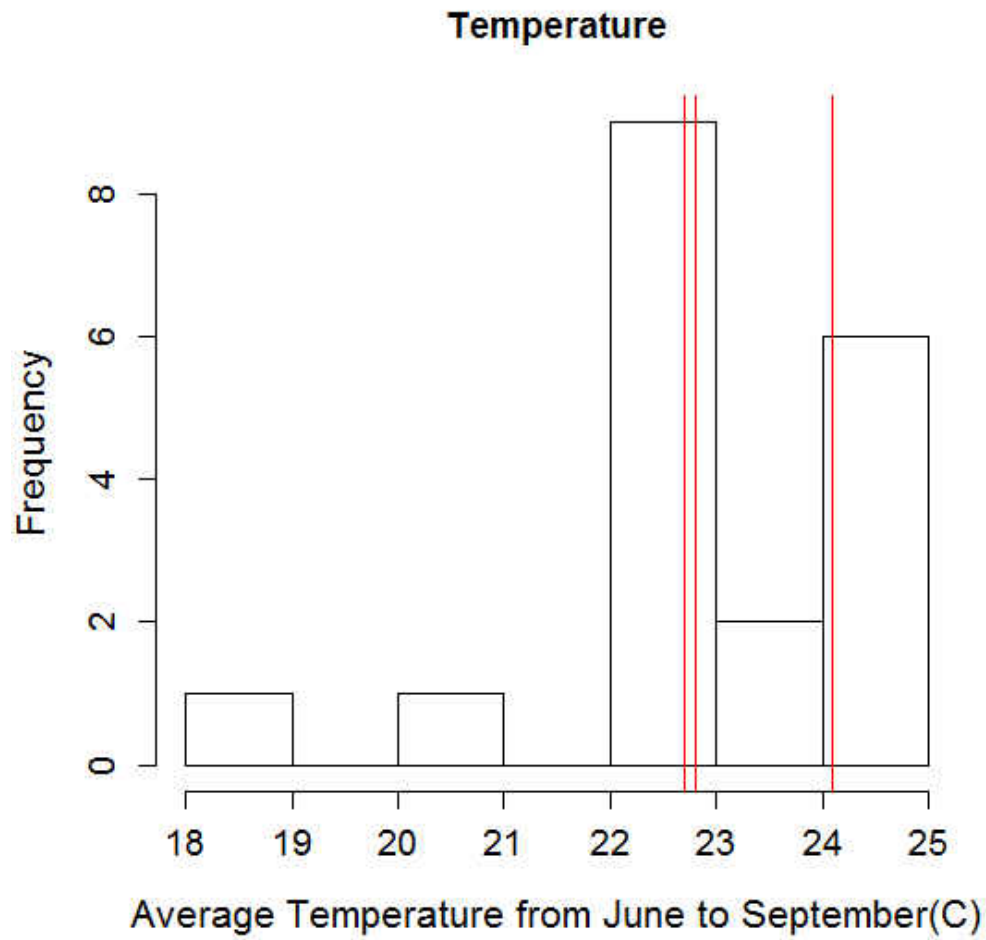
Figure 21. Histogram showing average June to September temperatures of our three study years (red lines) in comparion to historic data
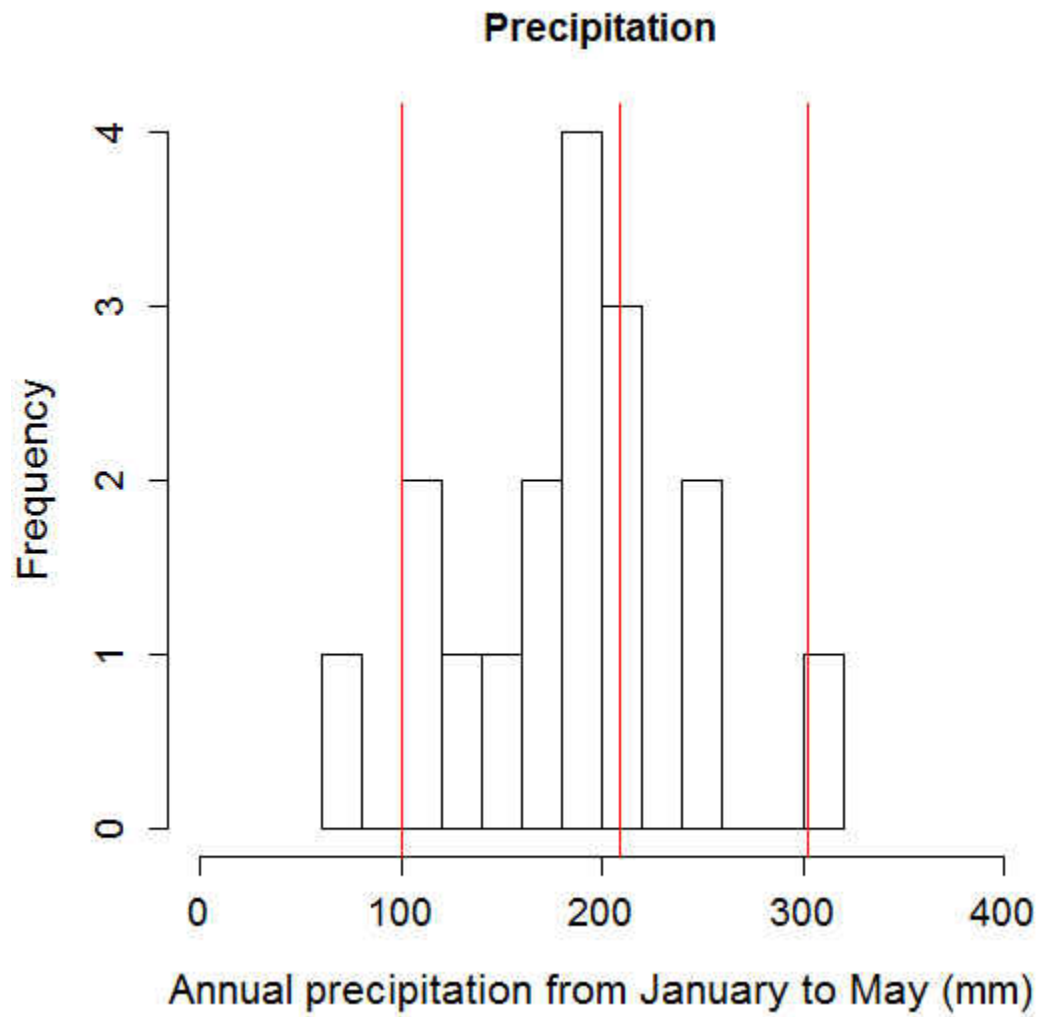
Figure 22. Histogram showing average January to May precipiation of our three study years (red lines) in comparion to historic data.

Table 5. AIC tables showing differing general linear models for survival, probability of reproduction and seeds per plant.

GLM for Survival (all years)

Models for Survival	K	AICc	Delta
Survival ~ log-diameter + logdiameter^2 + Treat* Sites + TJS + PJM	9	3353.3	0.0
Survival ~ log-diameter + logdiameter^2 + Treat + Sites + TJS + PJM	7	3355.4	2.1
Survival ~ log-diameter + logdiameter^2 + Treat* Sites + TJS	8	3357.7	4.4
Survival ~ log-diameter + logdiameter^2 + Treat* Sites *TJS*PJM	19	3359.5	6.2
Survival ~ log-diameter + logdiameter^2 + Treat + TJS	5	3360.1	6.8
Survival ~ log-diameter + logdiameter^2 + Treat + Sites + TJS	6	3360.8	7.5
Survival ~ log-diameter + logdiameter^2 + Treat*TJS	7	3362.7	9.4
Survival ~ log-diameter + logdiameter^2 + Treat* Sites *TJS	13	3362.8	9.5
Survival ~ log-diameter + logdiameter^2 + TJS	3	3403.1	49.8
Survival ~ log-diameter + logdiameter^2 + Treat + PJM	5	3408.0	54.7
Survival ~ log-diameter + logdiameter^2 + Treat + Sites + PJM	6	3409.5	56.2
Survival ~ log-diameter + logdiameter^2 + Treat* Sites + PJM	8	3410.1	56.8
Survival ~ log-diameter + logdiameter^2 + Treat*PJM	7	3411.1	57.8
Survival ~ log-diameter + logdiameter^2 + Treat* Sites *PJM	13	3413.7	60.4
Survival ~ log-diameter + logdiameter^2 + PJM	3	3432.0	78.7
Survival ~ log-diameter + logdiameter^2 + Treat	4	3569.9	216.6
Survival ~ log-diameter + logdiameter^2 + Treat + Sites	5	3571.3	218.0
Survival ~ log-diameter + logdiameter^2 + Treat* Sites	7	3571.8	218.5
Survival ~ log-diameter + logdiameter^2	2	3589.2	235.9
Survival ~ log-diameter + logdiameter^2 + Sites	3	3589.9	236.6
Survival ~ 1	1	3628.5	275.2
Treat= treatments, TJS= temperature June-September, PJM= precipitation January-May			

Summary for the most informative model for Survival

Glm (formula = survival ~ log-diameter + logdiameter^2+ Treat * Sites + TJS + PJM, family = binomial)					
Coefficients:	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	12.54	2.54	4.93	0.00	***
Log-diameter	3.08	0.39	7.96	0.00	***
logsquare	-0.53	0.09	-5.96	0.00	***
Treat 0-1	0.96	0.15	6.32	0.00	***
Treat 0-2	0.48	0.15	3.27	0.00	**
Sites 1-2	0.02	0.16	0.14	0.89	
TJS	-0.76	0.10	-7.21	0.00	***
PJM	0.00	0.00	3.35	0.00	***
Treat 0-1:Site1-2	-0.47	0.22	-2.15	0.03	*
Treat 0-2:Site1-2	0.04	0.22	0.18	0.85	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'					

GLM's for Probability of reproduction (all years)

Models for Probability of reproduction	K	AICc	Delta
Rep ~ log-diameter + Treat*Sites + TJS + PJM	9	1186.4	0.0
Rep ~ log-diameter + Treat + Sites + TJS + PJM	7	1202.8	16.3
Rep ~ log-diameter + Treat*Sites*PJM	13	1276.1	89.6
Rep ~ log-diameter + Treat*Sites + PJM	8	1306.7	120.3
Rep ~ log-diameter + Treat + Sites + PJM	6	1322.1	135.6
Rep ~ log-diameter + Treat*PJM	7	1364.5	178.0
Rep ~ log-diameter + PJM	3	1378.8	192.4
Rep ~ log-diameter + Treat + PJM	5	1379.8	193.4
Rep ~ log-diameter + Treat*Sites*TJS	13	1939.0	752.6
Rep ~ log-diameter + Treat*TJS	7	2032.2	845.7
Rep ~ log-diameter + Treat*Sites + TJS	8	2035.8	849.4
Rep ~ log-diameter + Treat + Sites + TJS	6	2046.7	860.2
Rep ~ log-diameter + TJS	3	2077.2	890.8
Rep ~ log-diameter + Treat + TJS	5	2077.9	891.4
Rep ~ log-diameter + Treat*Sites	7	3140.6	1954.2
Rep ~ log-diameter + Treat + Sites	5	3143.7	1957.2
Rep ~ log-diameter + Sites	3	3148.6	1962.2
Rep ~ log-diameter + Treat	4	3164.8	1978.4
Rep ~ log-diameter	2	3171.5	1985.0
Rep ~ 1	1	3799.3	2612.9
Treat= treatments, TJS= temperature June-September, PJM= precipitation January-May			

Summary the most informative model for probability of reproduction

Glm (formula = rep ~ logdiameter + Treat*Sites + TJS + PJM, family = binomial)					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-251.34	23.58	-10.66	< 2e-16	***
Log-diameter	5.30	0.27	19.64	< 2e-16	***
Treat 0-1	-0.57	0.28	-2.06	0.04	*
Treat 0-2	-1.10	0.28	-3.99	0.00	***
Sites 1-2	0.41	0.29	1.41	0.16	
TJS	8.78	0.91	9.66	< 2e-16	***
PJM	0.20	0.01	14.23	< 2e-16	***
Treat 0-1:Sites 1-2	0.47	0.39	1.22	0.22	
Treat 0-2:Sites 1-2	1.60	0.38	4.21	0.00	***
Signif. codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.'**					

GLM's for Seeds per plant (all years)

Model for Seeds per plant	K	AICc	Delta
Log_seed_plant ~ log-diameter + Treat*Sites + TJS + PJM	10	2593.0	0.0
Log_seed_plant ~ log-diameter + Treat + Sites + TJS + PJM	8	2599.7	6.7
Log_seed_plant ~ log-diameter + Treat* Sites + TJS	9	2616.1	23.1
Log_seed_plant ~ log-diameter + Treat + Sites + TJS	7	2622.7	29.7
Log_seed_plant ~ log-diameter + Treat*TJS	8	2772.1	179.1
Log_seed_plant ~ log-diameter + Treat + TJS	6	2776.3	183.3
Log_seed_plant ~ log-diameter + TJS	4	2803.5	210.4
Log_seed_plant ~ log-diameter + Treat* Sites + PJM	9	2811.5	218.5
Log_seed_plant ~ log-diameter + Treat + Sites + PJM	7	2816.7	223.7
Log_seed_plant ~ log-diameter + Treat* Sites	8	2837.3	244.3
Log_seed_plant ~ log-diameter + Treat + Sites	6	2842.1	249.1
Log_seed_plant ~ log-diameter + Sites	4	2853.5	260.5
Log_seed_plant ~ log-diameter + Treat*PJM	8	2935.5	342.5
Log_seed_plant ~ log-diameter + Treat + PJM	6	2952.0	359.0
Log_seed_plant ~ log-diameter + PJM	4	2959.0	366.0
Log_seed_plant ~ log-diameter + Treat	5	2979.2	386.2
Log_seed_plant ~ log-diameter	3	2985.7	392.7
Log_seed_plant ~ 1	2	4602.1	2009.1

Summary the most informative model for seeds per plant

Glm (log_seed_plant ~ log-diameter + Treat*Sites + TJS + PJM, family=gaussian)					
Coefficients:	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	-16.95	1.07	-15.90	< 2e-16	***
Log-diameter	2.00	0.04	48.00	< 2e-16	***
Treat 0-1	-0.38	0.07	-5.32	0.00	***
Treat 0-2	-0.18	0.07	-2.54	0.01	*
Sites 1-2	-0.72	0.07	-9.79	< 2e-16	***
TJS	0.75	0.05	15.50	< 2e-16	***
PJM	0.00	0.00	5.02	0.00	***
Treat 0-1:Sites 1-2	0.18	0.10	1.80	0.07	.
Treat 0-2:Sites 1-2	0.33	0.10	3.27	0.00	**
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'					
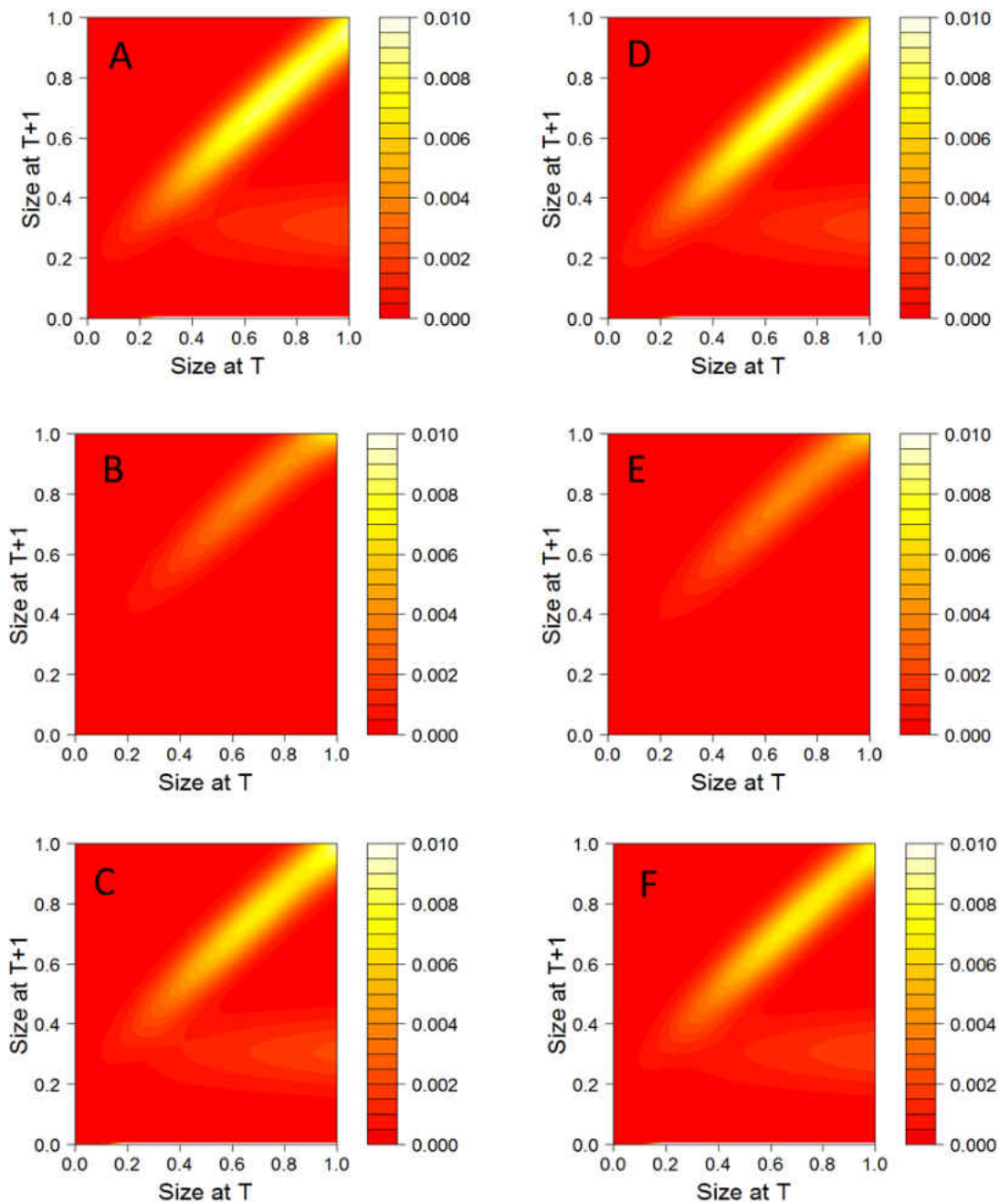
Figure 23. Overall IPM kernels for Site 1 2008-09 (A), 2009-10 (B) and 2010-11 (C) and Site 2 2008(D), 2009(E) and 2010(F). The diagonal region increasing from left to right corresponds to survival and growth. The region at the bottom-right corresponds to the seeds being produced that directly germinate within the span of the observed annual transition, thus not entering the persistent seedbank. The thin, white line at the extreme bottom of the graph corresponds to seeds entering the seedbank

APPENDIX B: SUPPLEMENTAL INFORMATION FOR CHAPTER 3

Table 6. AICc tables for vital rates in the Habitat model. Bolded models indicated selected GLMs.

Vegetative Survival	K	AICc	Delta_AICc
surv ~ leaves +leaves2 + Hab2 + Norco + Precip	6	1912.17	0.00
surv ~ leaves +leaves2+ Hab2 + Precip	**5**	**1912.71**	**0.54**
surv ~ leaves+leaves2 + Hab2 + Norco	5	1913.97	1.80
surv ~ leaves + Hab2 + Norco + Precip	5	1914.03	1.86
surv ~ leaves + Hab2 + Precip	4	1914.77	2.60
surv ~ leaves+leaves2 + Hab2	4	1914.85	2.68
surv ~ leaves + Hab2 + Norco	4	1915.32	3.15
surv ~ leaves * Hab2 + Norco + Precip	6	1915.67	3.50
surv ~ leaves +leaves2+ Hab2 + Norco + Precip +leaves:Hab2+leaves2:Hab2	8	1915.79	3.62
surv ~ leaves +leaves2 + Hab2 + Precip +leaves:Hab2+leaves2:Hab2	7	1916.21	4.04
surv ~ 1	1	6447.41	4535.24

Reproductive Survival	K	AICc	Delta_AICc
surv ~ size * Hab2 * BiHerbiv + Norco	9	3527.32	0.00
surv ~ size * Hab2 * BiHerbiv + Norco + Precip	10	3529.17	1.85
surv~size+size2+Hab2*BiHerbiv+Norco+size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+ size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	13	3530.49	3.17
surv~size+size2+Hab2*BiHerbiv+Norco+Precip+size:Hab2+size2:Hab2+size:BiHerbiv+ size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	14	3532.27	4.95
surv ~ size * Hab2 * BiHerbiv	8	3537.56	10.24
surv ~ size + Hab2 + BiHerbiv + Norco	**5**	**3538.12**	**10.80**
surv ~ size * Hab2 * BiHerbiv + Precip	9	3539.43	12.11
surv ~ size + Hab2 + BiHerbiv + Norco + Precip	6	3539.61	12.30
surv ~ size + Hab2 * BiHerbiv + Norco	6	3540.05	12.74
surv ~ size + Hab2 + BiHerbiv + Norco+ size2	6	3540.08	12.76
surv ~ 1	1	6447.41	2920.09

Vegetative to Reproductive Transition	K	AICc	Delta_AICc
ReporNext ~ leaves + Hab2 + Precip+ leaves2	**5**	**1717.05**	**0.00**
ReporNext ~ leaves + Hab2+ leaves2	4	1718.00	0.94
ReporNext ~ leaves + leaves2+ Hab2 + Precip+ leaves:Hab2+leaves2:Hab2	7	1718.44	1.39
ReporNext ~ leaves + Precip+ leaves2	4	1718.45	1.40
ReporNext ~ leaves + Hab2 + Norco + Precip+ leaves2	6	1718.74	1.68
ReporNext ~ leaves+ leaves2	3	1718.76	1.71
ReporNext ~ leaves + leaves2 + Hab2+ leaves:Hab2+leaves2:Hab2	6	1719.34	2.29
ReporNext ~ leaves + Norco+ leaves2	4	1719.54	2.48
ReporNext ~ leaves + Hab2 + Norco+ leaves2	5	1719.70	2.64
ReporNext ~ leaves + leaves2 + Hab2 + Norco + Precip+ leaves:Hab2+leaves2:Hab2	8	1720.19	3.14
ReporNext ~ 1	1	9984.50	8267.45

Vegetative Dormancy	K	AICc	Delta_AICc
dorm ~ leaves	2	842.77	0.00
dorm ~ leaves + Hab2	3	843.71	0.94
dorm ~ leaves + leaves2	3	844.56	1.79
dorm ~ leaves + Precip	3	844.78	2.00
dorm ~ leaves + Norco	3	844.78	2.00
dorm ~ leaves + Hab2 + leaves2	4	845.52	2.75
dorm ~ leaves + Hab2 + Norco	4	845.54	2.76
dorm ~ leaves * Hab2	4	845.58	2.80
dorm ~ leaves + Hab2 + Precip	4	845.72	2.95
dorm ~ leaves + Precip + leaves2	4	846.56	3.79
dorm ~ 1	1	4270.41	3427.64

Reproductive to Reproductive Transition	K	AICc	Delta AICc
ReporNext ~ size + size2 + Hab2 * BiHerbiv+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	12	4156.68	0.00
ReporNext ~ size + size2 + Hab2 * BiHerbiv + Precip+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	13	4157.20	0.52
ReporNext ~ size + size2+ Hab2 * BiHerbiv + Norco+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	13	4158.48	1.81
ReporNext ~ size + size2+ Hab2 * BiHerbiv + Norco + Precip+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	14	4159.00	2.32
ReporNext ~ size + Hab2 * BiHerbiv+ size2	**6**	**4164.00**	**7.33**
ReporNext ~ size + Hab2 * BiHerbiv + Precip+ size2	7	4164.38	7.70
ReporNext ~ size + Hab2 * BiHerbiv + Norco+ size2	7	4165.93	9.25
ReporNext ~ size + Hab2 * BiHerbiv + Norco + Precip+ size2	8	4166.31	9.63
ReporNext ~ size + Hab2 + BiHerbiv+ size2	5	4170.78	14.10
ReporNext ~ size + Hab2 + BiHerbiv + Precip+ size2	6	4171.43	14.75
ReporNext ~ 1	1	9984.50	5827.83

Reproductive Dormancy	K	AICc	Delta_AICc
dorm ~ size + Hab2 + BiHerbiv + Precip	5	2350.46	0.00
dorm ~ size + Hab2 * BiHerbiv + Precip	6	2350.72	0.26
dorm ~ size + Hab2 + BiHerbiv + Precip + size2	6	2352.08	1.62
dorm ~ size + Hab2 + BiHerbiv + Norco + Precip	6	2352.10	1.64
dorm ~ size + Hab2 * BiHerbiv + Norco + Precip	7	2352.30	1.85
dorm ~ size + Hab2 * BiHerbiv + Precip + size2	7	2352.39	1.94
dorm ~ size * Hab2 * BiHerbiv + Precip	9	2353.31	2.85
dorm ~ size + Hab2 + BiHerbiv + Norco + Precip + size2	7	2353.77	3.31
dorm ~ size + Hab2 * BiHerbiv + Norco + Precip + size2	8	2354.03	3.57
dorm ~ size * Hab2 * BiHerbiv + Norco + Precip	10	2354.78	4.32
dorm ~ 1	1	4270.41	1919.95

Probability of Producing a Flowering Head	K	AICc	DeltaAICc
srep ~ size + size2 + Hab2 * BiHerbiv+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	12	3803.86	0.00
srep ~ size + size2+ Hab2 * BiHerbiv + Norco + size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	13	3805.58	1.73
srep ~ size + size2+ Hab2 * BiHerbiv + Precip+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	13	3805.83	1.97
srep ~ size + size2+ Hab2 * BiHerbiv + Norco + Precip+ size:Hab2+size2:Hab2+size:BiHerbiv+size2:BiHerbiv+size:BiHerbiv:Hab2+size2:BiHerbiv:Hab2	14	3807.57	3.71
srep ~ size + Hab2 + BiHerbiv + size2	**5**	**3810.34**	**6.48**
srep ~ size + Hab2 + BiHerbiv + Norco + size2	6	3811.85	7.99
srep ~ size + Hab2 * BiHerbiv + size2	6	3812.18	8.32
srep ~ size + Hab2 + BiHerbiv + Precip + size2	6	3812.33	8.47
srep ~ size * Hab2 * BiHerbiv	8	3813.36	9.50
srep ~ size + Hab2 * BiHerbiv + Norco + size2	7	3813.68	9.82
srep ~ 1	1	9107.51	5303.65

Number of Flowering Heads Produced	K	AICc	DeltaAICc
heads ~ sizef + sizef2+ Hab2f * BiHerbivf + Norcof + PrecipF + sizef:Hab2f+sizef2:Hab2f+sizef:BiHerbivf+sizef2:BiHerbivf+sizef:BiHerbivf:Hab2f+sizef2:BiHerbivf:Hab2f	**15**	**10041.5**	**0.00**
heads ~ sizef + sizef2+ Hab2f * BiHerbivf + PrecipF+ sizef:Hab2f+sizef2:Hab2f+sizef:BiHerbivf+sizef2:BiHerbivf+sizef:BiHerbivf:Hab2f+sizef2:BiHerbivf:Hab2f	14	10046.3	4.78
heads ~ sizef + sizef2+ Hab2f * BiHerbivf + Norcof+ sizef:Hab2f+sizef2:Hab2f+sizef:BiHerbivf+sizef2:BiHerbivf+sizef:BiHerbivf:Hab2f+sizef2:BiHerbivf:Hab2f	14	10049.8	8.25
heads ~ sizef + sizef2+ Hab2f * BiHerbivf + sizef:Hab2f+sizef2:Hab2f+sizef:BiHerbivf+sizef2:BiHerbivf+sizef:BiHerbivf:Hab2f+sizef2:BiHerbivf:Hab2f	13	10054.9	13.36
heads ~ sizef + Hab2f + BiHerbivf + Norcof + PrecipF + sizef2	8	10058.4	16.91
heads ~ sizef * Hab2f * BiHerbivf + Norcof + PrecipF	11	10059.1	17.59
heads ~ sizef + Hab2f * BiHerbivf + Norcof + PrecipF + sizef2	9	10060.4	18.89
heads ~ sizef + Hab2f + BiHerbivf + PrecipF + sizef2	7	10063.2	21.68
heads ~ sizef * Hab2f * BiHerbivf + PrecipF	10	10064.0	22.46
heads ~ sizef + Hab2f * BiHerbivf + PrecipF + sizef2	8	10065.1	23.61
heads ~ 1	2	12598.4	2556.92

Table 7. AICc tables for vital rates in the TSF model. Bolded models indicated selected GLMs. Red models indicate cases in which habitat model was retained.

Vegetative Survival	K	AICc	Delta_AICc
surv1 ~ leaves1+ leaves12	**3**	**1465.30**	**0.00**
surv1 ~ leaves1 + leaves12+ Precip1	4	1465.33	0.03
surv1 ~ leaves1 + leaves12+ TSF1 + Norco1 + Precip1	6	1465.66	0.36
surv1 ~ leaves1	2	1465.77	0.48
surv1 ~ leaves1+ leaves12 + Norco1	4	1465.89	0.59
surv1 ~ leaves1 + leaves12+ TSF1 + Norco1	5	1465.90	0.60
surv1 ~ leaves1 + Precip1	3	1466.16	0.86
surv1 ~ leaves1 + TSF1 + Norco1	4	1466.19	0.89
surv1 ~ leaves1 + Norco1	3	1466.29	0.99
surv1 ~ leaves1 + TSF1 + Norco1 + Precip1	5	1466.30	1.00
surv1 ~ 1	1	4612.81	3147.52

Vegetative to Reproductive Transition	K	AICc	Delta_AICc
ReporNext1 ~ leaves1 +leaves12+ TSF1 + Norco1 + leaves1:TSF1+leaves12:TSF1	7	1156.08	0.00
ReporNext1 ~ leaves1 +leaves12+ TSF1+ leaves1:TSF1+leaves12:TSF1	**6**	**1157.37**	**1.29**
ReporNext1 ~ leaves1 +leaves12+ TSF1 + Norco1 + Precip1+ leaves1:TSF1+leaves12:TSF1	8	1157.66	1.57
ReporNext1 ~ leaves1 +leaves12+ TSF1 + Precip1+ leaves1:TSF1+leaves12:TSF1	7	1158.92	2.84
ReporNext1 ~ leaves1 +leaves12+ Norco1	4	1163.19	7.10
ReporNext1 ~ leaves1+leaves12	3	1165.07	8.99
ReporNext1 ~ leaves1 +leaves12+ TSF1 + Norco1	5	1165.14	9.06
ReporNext1 ~ leaves1 +leaves12+ TSF1 + Norco1 + Precip1	6	1166.13	10.04
ReporNext1 ~ leaves1 +leaves12+ Precip1	4	1166.22	10.14
ReporNext1 ~ leaves1 +leaves12+ TSF1	4	1166.33	10.25
ReporNext1 ~ 1	1	6610.50	5454.42

Vegetative Dormancy	K	AICc	Delta_AICc
dorm1 ~ leaves1	**2**	**599.48**	**0.00**
dorm1 ~ leaves1 + Norco1	3	599.67	0.18
dorm1 ~ leaves1 + Precip1	3	600.87	1.39
dorm1 ~ leaves1 + Norco1 + Precip1	4	600.98	1.50
dorm1 ~ leaves1 + TSF1 + Norco1	4	601.01	1.52
dorm1 ~ leaves1 + TSF1	3	601.49	2.01
dorm1 ~ leaves1+leaves12	3	601.50	2.01
dorm1 ~ leaves1 +leaves12+ Norco1	4	601.68	2.20
dorm1 ~ leaves1 + TSF1 + Norco1 + Precip1	5	602.45	2.97
dorm1 ~ leaves1 + TSF1 + Precip1	4	602.87	3.39
dorm1 ~ 1	1	3023.14	2423.66

Reproductive Survival	K	AICc	Delta_AICc
surv1 ~ size1 + Norco1	**3**	**2404.36**	**0.00**
surv1 ~ size1 + TSF1 + BiHerbiv1 + Norco1	5	2404.71	0.35
surv1 ~ size1 +size12+ Norco1	4	2405.79	1.43
surv1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Norco1	6	2406.15	1.79
surv1 ~ size1 + TSF1 * BiHerbiv1 + Norco1	6	2406.36	2.00
surv1 ~ size1 + TSF1 + BiHerbiv1 + Norco1 + Precip1	6	2406.48	2.12
surv1 ~ size1 +size12+ TSF1 * BiHerbiv1+Norco1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	12	2407.24	2.88
surv1 ~ size1 +size12+ TSF1 * BiHerbiv1 + Norco1	7	2407.81	3.45
surv1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1 + Norco1	7	2407.87	3.51
surv1 ~ size1 + TSF1 * BiHerbiv1 + Norco1 + Precip1	7	2408.17	3.81
surv1 ~ 1	1	4612.81	2208.45

Reproductive to Reproductive Transition	K	AICc	Delta_AICc
ReporNext1 ~ size1 +size12+ BiHerbiv1+size1:BiHerbiv1+size12:BiHerbiv1	**6**	**2916.75**	**0.00**
ReporNext1 ~ size1 +size12+ TSF1 * BiHerbiv1+Norco1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	12	2922.29	5.54
ReporNext1 ~ size1 +size12+ TSF1 * BiHerbiv1+ Precip1+ Norco1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	13	2922.46	5.71
ReporNext1 ~ size1 +size12+ TSF1 * BiHerbiv1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	11	2922.88	6.13
ReporNext1 ~ size1 +size12+ TSF1 * BiHerbiv1+Precip1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	12	2923.05	6.30
ReporNext1 ~ size1 +size12+ BiHerbiv1	4	2928.57	11.82
ReporNext1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Norco1	6	2930.00	13.25
ReporNext1 ~ size1 +size12+ TSF1 + BiHerbiv1	5	2930.21	13.46
ReporNext1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1 + Norco1	7	2930.29	13.54
ReporNext1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1	6	2930.50	13.75
ReporNext1 ~ 1	1	6610.50	3693.75

Reproductive Dormancy	K	AICc	Delta_AICc
dorm1 ~ size1 * TSF1 * BiHerbiv1 + Norco1 + Precip1	**10**	**1722.51**	**0.00**
dorm1 ~ size1 + TSF1 + BiHerbiv1 + Norco1 + Precip1	6	1722.66	0.15
dorm1 ~ size1 + Precip1	3	1723.21	0.69
dorm1 ~ size1 + TSF1 + BiHerbiv1 + Precip1	5	1724.18	1.67
dorm1 ~ size1 * TSF1 * BiHerbiv1 + Precip1	9	1724.48	1.97
dorm1 ~ size1 + TSF1 * BiHerbiv1 + Norco1 + Precip1	7	1724.50	1.98
dorm1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1 + Norco1	7	1724.67	2.15
dorm1 ~ size1 +size12+ Precip1	4	1725.20	2.69
dorm1 ~ size1 + TSF1 * BiHerbiv1 + Precip1	6	1726.06	3.55
dorm1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1	6	1726.19	3.67
dorm1 ~ 1	1	3023.14	1300.63

Probability of Producing a Flowering Head	K	AICc	Delta_AICc
srep1 ~ size1 +size12+ TSF1 * BiHerbiv1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	11	2193.79	0.00
srep1 ~ size1 * TSF1 * BiHerbiv1	8	2194.37	0.58
srep1 ~ size1 +size12+ TSF1 * BiHerbiv1+Norco1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	12	2194.80	1.01
srep1 ~ size1 +size12+ TSF1 * BiHerbiv1+Precip1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	12	2195.25	1.46
srep1 ~ size1 +size12+ BiHerbiv1+size1:BiHerbiv1+size12:BiHerbiv1	6	2195.36	1.57
srep1 ~ size1 * TSF1 * BiHerbiv1 + Norco1	9	2195.59	1.80
srep1 ~ size1 * TSF1 * BiHerbiv1 + Precip1	9	2195.84	2.05
srep1 ~ size1 +size12+ TSF1 * BiHerbiv1+ Precip1+ Norco1+ size1:TSF1+size12:TSF1+size1:BiHerbiv1+size12:BiHerbiv1+ size1:BiHerbiv1+TSF1+size12:TSF1:BiHerbiv1	13	2196.13	2.34
srep1 ~ size1 * BiHerbiv1	4	2196.87	3.08
srep1 ~ size1 * TSF1 * BiHerbiv1 + Norco1 + Precip1	10	2196.95	3.16
srep1 ~ size1 +size12+ BiHerbiv1	4	2197.66	3.87
srep1 ~ size1 +size12+ TSF1 + BiHerbiv1	5	2199.66	5.87
srep1 ~ size1 +size12+ TSF1 * BiHerbiv1	6	2200.86	7.07
srep1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Norco1	6	2200.99	7.20
srep1 ~ size1 +size12+ TSF1 + BiHerbiv1 + Precip1	6	2201.14	7.35
srep1 ~ size1 + BiHerbiv1	**3**	**2201.90**	**8.11**
srep1 ~ 1	1	5655.63	3461.84

Number of Flowering Heads Produced	K	AICc	Delta_AICc
heads1 ~ size1f +size1f2+ TSF1f * BiHerbiv1f + Norco1f+ size1f:TSF1f+size1f2:TSF1f+size1f:BiHerbiv1f+size1f2:BiHerbiv1f+ size1f:BiHerbiv1f+size1f2:TSF1f:BiHerbiv1f	13	1424.80	0.00
heads1 ~ size1f +size1f2+ TSF1f * BiHerbiv1f + Norco1f + Precip1F+ size1f:TSF1f+size1f2:TSF1f+size1f:BiHerbiv1f+size1f2:BiHerbiv1f+ size1f:BiHerbiv1f+size1f2:TSF1f:BiHerbiv1f	14	1426.13	1.33
heads1 ~ size1f+ size1f2+ TSF1f+ Norco1f	**6**	**1429.41**	**4.61**
heads1 ~ size1f +size1f2+ TSF1f + BiHerbiv1f + Norco1f	7	1431.46	6.66
heads1 ~ size1f +size1f2+ TSF1f + BiHerbiv1f + Norco1f + Precip1F	8	1432.87	8.06
heads1 ~ size1f +size1f2+ TSF1f * BiHerbiv1f + Norco1f	8	1433.48	8.68
heads1 ~ size1f +size1f2+ TSF1f * BiHerbiv1f + Norco1f + Precip1F	9	1434.89	10.08
heads1 ~ size1f + TSF1f+ Norco1f	5	1436.50	11.70
heads1 ~ size1f + TSF1f + BiHerbiv1f + Norco1f	6	1438.55	13.75
heads1 ~ size1f + TSF1f + BiHerbiv1f + Norco1f + Precip1F	7	1440.05	15.25
heads1 ~ 1	2	1912.82	88.02

APPENDIX C: R CODE FOR CHAPTER 2

Script to build an IPM for Helianthemum incorporating a discrete stage,
Multiple covariates, and an LTRE assessing the effects of trampling and seed addition

###Curator: Matthew Tye

###With input from Pedro Quintana-Ascencio
###Partially based on functions in IPMpack version 1.5 (Jess Metcalf, Rob Salguero-Gomez,
###Sean McMahon, ###Eelke Jongejans, Cory Merow)

###Last Updated: February 5, 2013
#Clean memory
rm(list=ls(all=TRUE))

```
#########################################################################
####Functions for continuous covariates#################################
#########################################################################
##Altering the IPMpack functions to accept non-factor covariates#####
##The functions are nearly identical to the regular IPMpack functions except
##The lines requiring a covariate to be a factor are removed

makecontsurvobj<-function (dataf, Formula = surv ~ size + size2)
{
  dataf <- subset(dataf, is.na(dataf$surv) == FALSE)
  if (length(dataf$offspringNext) > 0)
    dataf <- subset(dataf, !dataf$offspringNext %in% c("sexual",
                                      "clonal"))
  dataf$size2 <- dataf$size^2
  dataf$size3 <- dataf$size^3
  if (length(grep("expsize", as.character(Formula))) > 0)
    dataf$expsize <- exp(dataf$size)
  if (length(grep("logsize", as.character(Formula))) > 0)
    dataf$logsize <- log(dataf$size)
  if ("covariate" %in% unlist(strsplit(as.character(Formula),
                        "[+-\\* ]")) & length(dataf$covariate) > 0) {
    dataf$covariate <- dataf$covariate
    levels(dataf$covariate) <- 1:length(unique(dataf$covariate))
  }
  if ("covariateNext" %in% unlist(strsplit(as.character(Formula),
                          "[+-\\* ]")) & length(dataf$covariateNext) > 0) {
    dataf$covariateNext <- dataf$covariateNext
    levels(dataf$covariateNext) <- 1:length(unique(dataf$covariateNext))
  }
```

```
if (length(intersect(all.vars(Formula), colnames(dataf))) <
  length(all.vars(Formula)))
  print("warning: not all variables in the formula are present in dataf; model cannot be fit")
 fit <- glm(Formula, family = binomial, data = dataf)
 sv1 <- new("survObj")
 sv1@fit <- fit
 return(sv1)
}




makecontgrowthobj<-function (dataf, Formula = sizeNext ~ size, regType = "constantVar",
               Family = "gaussian")
{
 dataf <- subset(dataf, is.na(dataf$size) == FALSE & is.na(dataf$sizeNext) ==
  FALSE)
 if (length(dataf$offspringNext) > 0)
   dataf <- subset(dataf, !dataf$offspringNext %in% c("sexual",
                                    "clonal"))
 if (length(grep("incr", as.character(Formula))) > 0 & length(dataf$incr) ==
  0) {
  print("building incr as sizeNext - size")
  dataf$incr <- dataf$sizeNext - dataf$size
 }
 if (length(grep("logincr", as.character(Formula))) > 0 &
  length(dataf$logincr) == 0) {
  print("building logincr as log(sizeNext - size) - pre-build if this is not appropriate")
  dataf$logincr <- log(dataf$sizeNext - dataf$size)
 }
 if (length(grep("incr", as.character(Formula))) > 0) {
  if (sum(!is.na(dataf$incr) & dataf$surv == 0, na.rm = TRUE) >
    0) {
    print("measures of growth exist where individual has died (surv==0); replacing these with
NA")
    dataf$incr[dataf$surv == 0] <- NA
  }
 }
 if (length(grep("sizeNext", as.character(Formula))) > 0) {
  if (sum(!is.na(dataf$sizeNext) & dataf$surv == 0, na.rm = TRUE) >
    0) {
    print("measures of growth exist where individual has died (surv==0); replacing these with
NA")
    dataf$sizeNext[dataf$surv == 0] <- NA
  }
 }
 if (length(grep("logincr", as.character(Formula))) > 0) {
```

```r
  if (sum(!is.na(dataf$logincr) & dataf$surv == 0, na.rm = TRUE) >
    0) {
    print("measures of growth exist where individual has died (surv==0); replacing these with
NA")
    dataf$logincr[dataf$surv == 0] <- NA
  }
}
dataf$size2 <- dataf$size^2
dataf$size3 <- dataf$size^3
if (length(grep("expsize", as.character(Formula))) > 0)
  dataf$expsize <- exp(dataf$size)
if (length(grep("logsize", as.character(Formula))) > 0)
  dataf$logsize <- log(dataf$size)
if ("covariate" %in% unlist(strsplit(as.character(Formula),
                          "[+-\\* ]")) & length(dataf$covariate) > 0) {
  dataf$covariate <- dataf$covariate
  levels(dataf$covariate) <- 1:length(unique(dataf$covariate))
}
if ("covariateNext" %in% unlist(strsplit(as.character(Formula),
                             "[+-\\* ]")) & length(dataf$covariateNext) > 0) {
  dataf$covariateNext <- dataf$covariateNext
  levels(dataf$covariateNext) <- 1:length(unique(dataf$covariateNext))
}
if (length(intersect(all.vars(Formula), colnames(dataf))) <
  length(all.vars(Formula)))
  print("warning: not all variables in the formula are present in dataf; model cannot be fit")
if (Family == "gaussian") {
  if (regType == "constantVar") {
    fit <- lm(Formula, data = dataf)
  }
  else {
    if (regType == "declineVar") {
      require(nlme)
      fit.here <- gls(Formula, na.action = na.omit,
                weights = varExp(form = ~fitted(.)), data = dataf)
      fit <- list(coefficients = fit.here$coefficients,
              sigmax2 = summary(fit.here)$sigma^2, var.exp.coef =
as.numeric(fit.here$modelStruct$varStruct[1]),
              fit = fit.here)
    }
  }
}
else {
  if (regType != "constantVar")
    print("Warning: your regType is ignored because a non-gaussian model is fitted using glm")
  if (Family == "negbin") {
```

```
      fit <- glm.nb(Formula, data = dataf)
      fit.here <- list()
      fit.here[[1]] <- glm.convert(fit)
      fit.here[[2]] <- fit$theta
      fit.here[[3]] <- fit
    }
    else {
      fit <- glm(Formula, data = dataf, family = Family)
      fit.here <- fit
    }
  }
  if (length(grep("sizeNext", as.character(Formula))) > 0) {
    if (class(fit)[1] == "lm") {
      gr1 <- new("growthObj")
      gr1@fit <- fit
      gr1@sd <- summary(fit)$sigma
    }
    else {
      if (class(fit.here)[1] == "gls") {
        gr1 <- new("growthObjDeclineVar")
        gr1@fit <- fit
      }
      else {
        if (class(fit)[1] == "glm") {
          if (Family == "poisson") {
            gr1 <- new("growthObjPois")
            gr1@fit <- fit
          }
          else {
            print("unidentified object class")
          }
        }
        else {
          if (class(fit)[1] == "negbin") {
            gr1 <- new("growthObjNegBin")
            gr1@fit <- fit.here
          }
        }
      }
    }
  }
  else {
    if (length(grep("incr", as.character(Formula))) > 0 &
      length(grep("logincr", as.character(Formula))) ==
      0) {
      if (class(fit)[1] == "lm") {
```

```
    gr1 <- new("growthObjIncr")
    gr1@fit <- fit
    gr1@sd <- summary(fit)$sigma
  }
  else {
   if (class(fit.here)[1] == "gls") {
     gr1 <- new("growthObjIncrDeclineVar")
     gr1@fit <- fit
   }
   else {
     print("undefined object class")
   }
  }
 }
}
 else {
  if (length(grep("logincr", as.character(Formula))) >
    0) {
   if (class(fit)[1] == "lm") {
     gr1 <- new("growthObjLogIncr")
     gr1@fit <- fit
     gr1@sd <- summary(fit)$sigma
   }
   else {
    if (class(fit.here)[1] == "gls") {
      gr1 <- new("growthObjLogIncrDeclineVar")
      gr1@fit <- fit
    }
    else {
      print("undefined object class")
    }
   }
  }
 }
}
 return(gr1)
}




makecontfecobj <- function (dataf, fecConstants = data.frame(NA), Formula = list(fec ~
  size), Family = "gaussian", Transform = "none", meanOffspringSize = NA,
               sdOffspringSize = NA, offspringSplitter = data.frame(continuous = 1),
```

```
                    vitalRatesPerOffspringType = data.frame(NA), fecByDiscrete =
data.frame(NA),
                    offspringSizeExplanatoryVariables = "1")
{
  if (class(Formula) == "list") {
    if (class(Formula[[1]]) != "formula")
      stop("Error - the entries in your Formula list should be of class 'formula': e.g. fec~size
without quotation marks")
  }
  else {
    if (class(Formula) != "formula")
      stop("Error - the Formula entry should by of class 'formula' or a list of such entries:  e.g.
fec~size without quotation marks")
    Formula <- list(Formula)
  }
  if (length(dataf$stage) == 0) {
    dataf$stage <- rep("continuous", nrow(dataf))
    dataf$stage[is.na(dataf$size)] <- NA
    dataf$stage <- as.factor(dataf$stage)
  }
  if (length(dataf$stageNext) == 0) {
    dataf$stageNext <- rep("continuous", nrow(dataf))
    dataf$stageNext[dataf$surv == 0] <- "dead"
    dataf$stageNext <- as.factor(dataf$stageNext)
  }
  stages <- names(tapply(c(levels(dataf$stage), levels(dataf$stageNext)),
                  c(levels(dataf$stage), levels(dataf$stageNext)), length))
  stages <- stages[stages != "dead"]
  if ((sum(names(offspringSplitter) %in% stages)/length(offspringSplitter)) <
    1) {
    stages <- c(stages, names(offspringSplitter))
    print("Warning - the variable names in your offspringSplitter data.frame are not all part of the
levels of stage or stageNext in your data file. This could be because of an mismatch in stage
names, or because you included discrete stages in offspringSplitter that are not in the data file but
wchich you will introduce in makeDiscreteTrans (in which case you can ignore this warning).")
  }
  stages <- unique(stages)
  stages <- c(stages[stages != "continuous"], "continuous")
  dummy <- rep(0, length(stages))
  names(dummy) <- stages
  dummy <- as.data.frame(t(as.matrix(dummy)))
  for (i in names(offspringSplitter)) dummy[i] <- offspringSplitter[i]
  offspringSplitter <- dummy
  if (ncol(offspringSplitter) > 1 & (ncol(offspringSplitter) -
    1) != ncol(fecByDiscrete)) {
```

```
    print("Warning - offspring splitter indicates more than just continuous stages. No fecundity by
the discrete stages supplied in fecByDiscrete; assumed that is 0")
    fecByDiscrete <- offspringSplitter[, 1:(ncol(offspringSplitter) -
      1)]
    fecByDiscrete[] <- 0
  }
  if (sum(offspringSplitter) != 1) {
    print("Warning - offspring splitter does not sum to 1. It is now rescaled to sum to 1.")
    offspringSplitter <- offspringSplitter/sum(offspringSplitter)
  }
  if ("covariate" %in% unlist(strsplit(as.character(Formula),
                              "[+-\\* ]")) & length(dataf$covariate) > 0) {
    dataf$covariate <- dataf$covariate
    levels(dataf$covariate) <- 1:length(unique(dataf$covariate))
  }
  if ("covariateNext" %in% unlist(strsplit(as.character(Formula),
                                  "[+-\\* ]")) & length(dataf$covariateNext) > 0) {
    dataf$covariateNext <- dataf$covariateNext
    levels(dataf$covariateNext) <- 1:length(unique(dataf$covariateNext))
  }
  f1 <- new("fecObj")
  dataf$size2 <- dataf$size^2
  dataf$size3 <- dataf$size^3
  if (length(grep("expsize", unlist(as.character(Formula)))) >
    0)
    dataf$expsize <- exp(dataf$size)
  if (length(grep("logsize", unlist(as.character(Formula)))) >
    0)
    dataf$logsize <- log(dataf$size)
  if (length(Formula) > length(Family)) {
    misE <- (length(Family) + 1):length(Formula)
    print(c("number of families not the same as the number of Formula supplied, using default of
`gaussian' for missing ones which are:",
        Formula[[misE]], ". (which might be exactly what you want)"))
    Family <- c(Family, rep("gaussian", length(Formula) -
      length(Family)))
  }
  if (length(Formula) > length(Transform)) {
    misE <- (length(Transform) + 1):length(Formula)
    print(c("number of transforms not the same as the number of fecundity columns in the data
file, using default of `none' for missing ones which are:",
        Formula[[misE]], ". (which might be exactly what you want)"))
    Transform <- c(Transform, rep("none", length(Formula) -
      length(Transform)))
  }
  fecNames <- rep(NA, length(Formula))
```

```
  for (i in 1:length(Formula)) {
   fecNames[i] <- all.vars(Formula[[i]])[1]
   if (Transform[i] == "exp")
     dataf[, fecNames[i]] <- exp(dataf[, fecNames[i]])
   if (Transform[i] == "log")
     dataf[, fecNames[i]] <- log(dataf[, fecNames[i]])
   if (Transform[i] == "sqrt")
     dataf[, fecNames[i]] <- sqrt(dataf[, fecNames[i]])
   if (Transform[i] == "-1")
     dataf[, fecNames[i]] <- dataf[, fecNames[i]] - 1
   dataf[!is.finite(dataf[, fecNames[i]]), fecNames[i]] <- NA
   if (length(intersect(all.vars(Formula[[i]]), colnames(dataf))) <
     length(all.vars(Formula[[i]])))
     print("warning: not all variables in the formula are present in dataf; model cannot be fit")
   f1@fitFec[[i]] <- glm(Formula[[i]], family = Family[i],
                  data = dataf)
  }
  if (offspringSplitter$continuous > 0) {
   if (is.na(meanOffspringSize[1]) | is.na(sdOffspringSize[1])) {
    if (length(dataf$offspringNext) == 0) {
      offspringData <- subset(dataf, is.na(dataf$stage) &
       dataf$stageNext == "continuous")
      if (nrow(offspringData) == 0)
       stop("Error - no offspring size data are given: these can be given through either the
meanOffspringSize and sdOffspringSize slots, or through individual data added to your data file
(with stage equals NA, or a offspringNext column indicating 'sexual' offspring)")
    }
    else {
      offspringData <- subset(dataf, dataf$offspringNext ==
       "sexual" & dataf$stageNext == "continuous")
      if (nrow(offspringData) == 0)
       stop("Error - no offspring size data are given: these can be given through either the
meanOffspringSize and sdOffspringSize slots, or through individual data added to your data file
(with stage equals NA, or a offspringNext column indicating 'sexual' offspring)")
    }
    f1@offspringRel <- lm(paste("sizeNext~", offspringSizeExplanatoryVariables,
                   sep = ""), data = offspringData)
    f1@sdOffspringSize <- summary(f1@offspringRel)$sigma
   }
   else {
    f1@offspringRel <- lm(rep(meanOffspringSize[1], 21) ~
     1)
    f1@sdOffspringSize <- sdOffspringSize
   }
  }
  if (sum(dim(vitalRatesPerOffspringType) == c(1, 1)) < 2) {
```

```r
  if ((sum(vitalRatesPerOffspringType == 0, na.rm = T) +
    sum(vitalRatesPerOffspringType == 1, na.rm = T)) <
    (ncol(vitalRatesPerOffspringType) * nrow(vitalRatesPerOffspringType)))
    stop("Error - in vitalRatesPerOffspringType data.frame only 0's and 1's are allowed: a 1
indicates that a fecundity rate applies to that offspring type. ")
  if (sum(rownames(vitalRatesPerOffspringType) == c(fecNames,
                                    names(fecConstants))) < (length(Formula) +
length(fecConstants)))
    stop("Error - the row names in vitalRatesPerOffspringType should consist of (in order) the
names of the fec columns in the dataset and then the names of the fecConstants.")
 }
 else {
   vitalRatesPerOffspringType <- as.data.frame(matrix(1,
                                    ncol = length(offspringSplitter), nrow = length(Formula) +
                                      length(fecConstants)), row.names = c(fecNames,
                                            names(fecConstants)))
   vitalRatesPerOffspringType <- subset(vitalRatesPerOffspringType,
                         dimnames(vitalRatesPerOffspringType)[[1]] != "NA.")
   names(vitalRatesPerOffspringType) <- names(offspringSplitter)
 }
 if (length(f1@sdOffspringSize) > 0) {
   if (is.na(f1@sdOffspringSize)) {
     print("Warning - could not estimate parameters for the distribution of offspring size; defaults
must be supplied for meanOffspringSize and sdOffspringSize; you will not be able to construct
an IPM without these values.")
   }
 }
 f1@fecNames <- fecNames
 f1@fecConstants <- fecConstants
 f1@offspringSplitter <- offspringSplitter
 f1@vitalRatesPerOffspringType <- vitalRatesPerOffspringType
 f1@fecByDiscrete <- fecByDiscrete
 f1@Transform <- Transform
 return(f1)
}
###############   END CONTINUOUS COVARIATE FUNCTIONS

#set directory and load libraries
#dir="C:/Users/matt/Dropbox/PQA Lab/Ana"
#setwd(dir)

library(IPMpack)
library(popbio)

d <- read.csv("IMP data Merari.csv", header=TRUE, sep=",", na.strings="NA", dec=".",
strip.white=TRUE)
```

###The two numeric covariates represent continuous covariates (Temp, Precip) while the two factors represent discrete covariates(Trampling, Ladder)

```
d$covariate<-as.numeric(d$PEM)
d$covariate2<-as.numeric(d$TJS)
d$covariate3<-as.factor(d$Ladera)
d$covariate4<-as.factor(d$Trat)
d$size<-log(d$Size+1)
d$sizeNext<-log(d$SizeNext+1)


###Setting up the bootstrapping runs for each subset of covariates##########
part1 <- subset(d,(d$covariate2 > 22.6 & d$covariate2<22.7) & d$covariate3==1)
part2 <- subset(d,(d$covariate2 > 24) & d$covariate3==1)
part3 <- subset(d,(d$covariate2 > 23 & d$covariate2<24) & d$covariate3==1)
part4 <- subset(d,(d$covariate2 > 22.6 & d$covariate2<22.7) & d$covariate3==2)
part5 <- subset(d,(d$covariate2 > 24) & d$covariate3==2)
part6 <- subset(d,(d$covariate2 > 23 & d$covariate2<24) & d$covariate3==2)


x1<-length(part1$size)
x2<-length(part2$size)
x3<-length(part3$size)
x4<-length(part4$size)
x5<-length(part5$size)
x6<-length(part6$size)



####Defining Blank Arrays
n_iter <- 1000
lambda_boot <- array(0,c(n_iter,9))
colsum28AC<-array(0,c(n_iter,201))
colsum28TC<-array(0,c(n_iter,201))
colsum29AC<-array(0,c(n_iter,201))
colsum29TC<-array(0,c(n_iter,201))
colsum21AC<-array(0,c(n_iter,201))
colsum21TC<-array(0,c(n_iter,201))

rowsum28AC<-array(0,c(n_iter,201))
rowsum28TC<-array(0,c(n_iter,201))
rowsum29AC<-array(0,c(n_iter,201))
rowsum29TC<-array(0,c(n_iter,201))
rowsum21AC<-array(0,c(n_iter,201))
rowsum21TC<-array(0,c(n_iter,201))

rowsum<-array(0,c(n_iter,201))
colnames(lambda_boot) <-c("2008 Control", "2008 Trampling", " 2008 Addition","2009 Control", "2009 Trampling", " 2009 Addition","2010 Control", "2010 Trampling", " 2010 Addition")
```

```
bootclasses1 <- lapply(1:n_iter, function(i) part1[sample(x1, x1, replace=T), ])
bootclasses2 <- lapply(1:n_iter, function(i) part2[sample(x2, x2, replace=T), ])
bootclasses3 <- lapply(1:n_iter, function(i) part3[sample(x3, x3, replace=T), ])
bootclasses4 <- lapply(1:n_iter, function(i) part4[sample(x4, x4, replace=T), ])
bootclasses5 <- lapply(1:n_iter, function(i) part5[sample(x5, x5, replace=T), ])
bootclasses6 <- lapply(1:n_iter, function(i) part6[sample(x6, x6, replace=T), ])


for (j in 1:n_iter) {
boot1 <- as.data.frame(bootclasses1[j])
boot2 <- as.data.frame(bootclasses2[j])
boot3 <- as.data.frame(bootclasses3[j])
boot4 <- as.data.frame(bootclasses4[j])
boot5 <- as.data.frame(bootclasses5[j])
boot6 <- as.data.frame(bootclasses6[j])
boot <- rbind(boot1,boot2,boot3,boot4,boot5,boot6,deparse.level = 1)


d <- boot

#########################################################################


####Defining scalar quantities
fec4<-.16
goSB <- .281
staySB <- .281
germ<-.138
dead<-.580
fec3<-germ
##This section is based on the Hypericum script and I'm not sure it is entirely necessecary, but it
seems to be working
d <- d[,c("surv","size","sizeNext","rep","sem_plant", "covariate", "covariate2", "covariate3",
"covariate4")]

d$stageNext <- d$stage <- "continuous"
d$stage[is.na(d$size)] <- NA
d$stageNext[d$surv==0] <- "dead"
d$number <- 1


sb1 <-
data.frame(stage=c("seedbank","seedbank","continuous"),stageNext=c("seedbank","continuous",
"seedbank"),surv=1,size=NA,sizeNext=NA,rep=NA,sem_plant=NA,number=c(staySB,(1-
staySB)*fec3*fec4,1), covariate=NA, covariate2=NA, covariate3=NA, covariate4=NA)
```

```
sb1<-sb1[1:3,]
d <- rbind(d,sb1)
d$stage <- as.factor(d$stage)
d$stageNext <- as.factor(d$stageNext)


#####Creating survival growth and fecundity objects
##A few of these functions still don't work with multiple covariates but they are just
##diagnostic and plotting functions so I'm not concerned about it at the moment

g <- makecontgrowthobj(dataf=d,
Formula=sizeNext~size+covariate+covariate2+covariate3*covariate4)

s<- makecontsurvobj(d, Formula=
surv~size+size2+covariate+covariate2+covariate3*covariate4)


d$fec1<-d$rep
d$fec2<-log(d$sem_plant+1)

f <- makecontfecobj(d, Formula=c(fec1~size+covariate+covariate2+covariate3*covariate4,
fec2~size+covariate+covariate2+covariate3*covariate4),
            Family=c("binomial", "gaussian"),
            Transform=c("none", "none"),
            fecConstants=data.frame(fec3=fec3,fec4=fec4),
            meanOffspringSize=1.52, ## agregue el valor
            sdOffspringSize=0.4377, ## agregue el valor
            vitalRatesPerOffspringType=data.frame(seedbank=c(1,1,0,0),
            continuous=c(1,1,1,1),
            row.names=c("fec1","fec2","fec3","fec4")),
                        offspringSplitter=data.frame(seedbank=goSB,continuous=(1-
goSB)),
            offspringSizeExplanatoryVariables=1)

##makeDiscreteTrans has been giving me some trouble and I am still not certain this is correct
dto<-makeDiscreteTrans(d)
dto@discreteTrans[1,1]<-staySB
dto@discreteTrans[2,1]<-germ
dto@discreteTrans[3,1]<-dead
dto@discreteTrans[1,2]<- 0
dummy<-as.matrix(f@offspringRel$coefficients[1])
dimnames(dummy)<-list(1,"seedbank")
dto@meanToCont<-as.matrix(dummy,dimnames=c(1,"seedbank"))
dummy<-as.matrix(f@sdOffspringSize)
dimnames(dummy)<-list(1,"seedbank")
dto@sdToCont<-as.matrix(dummy,dimnames=c(1,"seedbank"))
```

```
########Creates separate P and F matricies based on the control(c), trample(1), and
addition(2)#########
### 2008= 209.10, 22.6921739

PmatrixC <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                    growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))
Pmatrix1 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                    growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))
Pmatrix2 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                    growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))
FmatrixC <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))

Fmatrix1 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))

Fmatrix2 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(209.10,length(200^2))),
covariate2=(rep(22.6921739,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))

IPMC<- PmatrixC+FmatrixC

IPM1<- Pmatrix1+Fmatrix1

IPM2<- Pmatrix2+Fmatrix2

####Calculates sensitivity of the control IPM#####
SIPMC<-sens(IPMC)

###Creates difference and contribution matricies for the 2 treatments###
```

```
Difference1 <- IPM1-IPMC
Difference2<-  IPM2-IPMC
Contribution1 = Difference1*SIPMC
Contribution2 = Difference2*SIPMC
###Graphs lambda values for each treatment#####
lambda_boot[j,1]<-Re(eigen(IPMC)$value[1])
lambda_boot[j,2]<-Re(eigen(IPM1)$value[1])
lambda_boot[j,3]<-Re(eigen(IPM2)$value[1])
colsum28TC[j,]<-colSums(Contribution1)
colsum28AC[j,]<-colSums(Contribution2)
rowsum28TC[j,]<-rowSums(Contribution1)
rowsum28AC[j,]<-rowSums(Contribution2)



###################################################################################
#######################################


### 2009
PmatrixC <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                 growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))
Pmatrix1 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                 growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))
Pmatrix2 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                 growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))
FmatrixC <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))

Fmatrix1 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))

Fmatrix2 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(100.5,length(200^2))),
```

covariate2=(rep(24.1061947,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))

IPMC<- PmatrixC+FmatrixC

IPM1<- Pmatrix1+Fmatrix1

IPM2<- Pmatrix2+Fmatrix2

####Calculates sensitivity of the control IPM#####
SIPMC<-sens(IPMC)

###Creates difference and contribution matricies for the 2 treatments###
Difference1 <- IPM1-IPMC
Difference2<- IPM2-IPMC
Contribution1 = Difference1*SIPMC
Contribution2 = Difference2*SIPMC

###Graphs lambda values for each treatment#####
lambda_boot[j,4]<-Re(eigen(IPMC)$value[1])
lambda_boot[j,5]<-Re(eigen(IPM1)$value[1])
lambda_boot[j,6]<-Re(eigen(IPM2)$value[1])
colsum29TC[j,]<-colSums(Contribution1)
colsum29AC[j,]<-colSums(Contribution2)
rowsum29TC[j,]<-rowSums(Contribution1)
rowsum29AC[j,]<-rowSums(Contribution2)
##
###

#######Creates separate P and F matricies based on the control(0), trample(1), and
addition(2)#########
2010= 272.9, 23.65905
PmatrixC <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))
Pmatrix1 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))
Pmatrix2 <- createIPMPmatrix(nBigMatrix=200,minSize= 0, maxSize=4,
                growObj=g, survObj=s,discreteTrans=dto, correction="constant",
chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),

```
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))
FmatrixC <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(0))))

Fmatrix1 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(1))))

Fmatrix2 <- createIPMFmatrix(fecObj=f, minSize=0, maxSize=5, nBigMatrix=200,
correction="constant",chosenCov=data.frame(covariate=(rep(272.9,length(200^2))),
covariate2=(rep(23.65905,length(200^2))), covariate3=(covariate=as.factor(2)),
covariate4=(covariate=as.factor(2))))

IPMC<- PmatrixC+FmatrixC

IPM1<- Pmatrix1+Fmatrix1

IPM2<- Pmatrix2+Fmatrix2

####Calculates sensitivity of the control IPM#####
SIPMC<-sens(IPMC)

###Creates difference and contribution matricies for the 2 treatments###
Difference1 <- IPM1-IPMC
Difference2<-  IPM2-IPMC
Contribution1 = Difference1*SIPMC
Contribution2 = Difference2*SIPMC

###Graphs lambda values for each treatment#####
lambda_boot[j,7]<-Re(eigen(IPMC)$value[1])
lambda_boot[j,8]<-Re(eigen(IPM1)$value[1])
lambda_boot[j,9]<-Re(eigen(IPM2)$value[1])
colsum21TC[j,]<-colSums(Contribution1)
colsum21AC[j,]<-colSums(Contribution2)
rowsum21TC[j,]<-rowSums(Contribution1)
rowsum21AC[j,]<-rowSums(Contribution2)
}

##Creates .CSV Files for each bootstrap run
write.table(colsum21TC,file="colsum21TC_2.csv",sep=",",row.names=F)
write.table(colsum21AC,file="colsum21AC_2.csv",sep=",",row.names=F)
write.table(rowsum21TC,file="rowsum21TC_2.csv",sep=",",row.names=F)
```

```
write.table(rowsum21AC,file="rowsum21AC_2.csv",sep=",",row.names=F)

write.table(colsum29TC,file="colsum29TC_2.csv",sep=",",row.names=F)
write.table(colsum29AC,file="colsum29AC_2.csv",sep=",",row.names=F)
write.table(rowsum29TC,file="rowsum29TC_2.csv",sep=",",row.names=F)
write.table(rowsum29AC,file="rowsum29AC_2.csv",sep=",",row.names=F)

write.table(colsum28TC,file="colsum28TC_2.csv",sep=",",row.names=F)
write.table(colsum28AC,file="colsum28AC_2.csv",sep=",",row.names=F)
write.table(rowsum28TC,file="rowsum28TC_2.csv",sep=",",row.names=F)
write.table(rowsum28AC,file="rowsum28AC_2.csv",sep=",",row.names=F)

write.table(lambda_boot,file="lambda_boot_2.csv",sep=",",row.names=F)
```

APPENDIX D: R CODE FOR CHAPTER 3

```
####################################################################
#Script to build a deterministic Liatris model consisting of          #
#three stages (Dormant, Reproductive, Vegetative)                     #
#and the transions between them                                       #
#Curated by Matthew Tye                                               #
#With input from Rob Salguero-Gomez                                   #
#and Pedro Quintana-Ascencio                                          #
#Last Updated: 3/14/2014                                              #
####################################################################

#Clean memory
rm(list=ls(all=TRUE))
getwd()
#set directory and load libraries
dir="C:/Users/matt/Dropbox/PQA Lab/Thesis/Liatris models"
setwd(dir)
library(MASS)

h.mat <- array(0,c(226,226,2))
for (q in 1:2) {

#load dataset and define variables to be used later
d <- read.csv("Liatrisdata.csv", header=TRUE, sep=",", na.strings="NA", dec=".",
strip.white=TRUE)
#variable definition
leaves   <-d$Leaves
LeavesNext<-d$LeavesNext
leaves2<-leaves^2
size     <-log(d$StemLength+1)
sizeNext <-log(d$SizeNext+1)   #logarithmic
heads<-log(d$Heads+1) #logarithmic
heads<-heads[d$Heads>0]
size2<-size^2
surv<-d$SurvNext
dorm<-d$DormNext
ReporNext<-d$ReporNext

#Fecundity Constants
seedsperhead<-40
SeedViability<-.8916     #Stephens et al Am. Mid. Nat. 2012
PreDSeedPred<-.78          #Liatrisdata
PostDSeedPred<-.628        #Stephens et al Am. Mid. Nat. 2012
germination<-.247         #LODEM03
establishment<-.003     #Correction factor

#Dummy vectors and matricies to be filled later
```

```
vsize<-seq(1,25,1)
vsize2<-vsize^2
rsize<-seq(0,7,7/200)
rsize<-rsize[1:200]
rsize2<-rsize^2
gxyv<-matrix(0,25,25)
gxyrv<-matrix(0,200,25)
n <- 200
gxyvr<-matrix(0,25,n)
minsize<-0
maxsize<-6


#Definition of covariates
covariate<-d$Hab2              #Time Since Fire
covariate2<-d$BiHerbiv              #Vertebrate Herbivory (0,1)
covariate3<-d$Norco         #Splits population into a Northern and Southern Group
covariate4<-d$Precip


#Levels for each variable altering these variables will change model outputs
hab<-2
herb <- (q-1)                  #levels(0,1)
pop<-2                              #levels(1,2)
rain<-2

#Histograms of variables
#windows()
par(mfrow=c(1,3))
hist(leaves)
hist(size)
hist(sizeNext)
table(covariate)

#Defining creates a binary variable for succesful production of heads
d$srep<-1:length(d$Heads)
d$srep[d$Heads>0]<-1
d$srep[d$Heads==0]<-0
d$srep[is.na(d$Heads)]<-NA
srep<-d$srep



#######################################################################
####Defining survival, growth, and transtion probability between        ####
####                    continuous stages                               ####
#######################################################################
```

```
## probability of a vegetative becoming reproductive
pvr <-glm(ReporNext~leaves+leaves2+covariate+covariate4, family="binomial")
summary(pvr)
cf.tvr <-pvr$coefficients
predpvr<-predict(pvr, list(leaves=vsize, leaves2=vsize2, covariate4=rep(rain,length(vsize)),
covariate=rep(hab,length(vsize))), type="response")
#windows()
plot(leaves, ReporNext)
lines(vsize,predpvr, col="blue")
lines(vsize,(1-predpvr), col="blue")

## Vegetative growth to vegetative
growthveg <-glm(LeavesNext~leaves+leaves2, family=poisson)
summary(growthveg)


cf.vg <-growthveg$coefficients
predgv<-predict(growthveg, list(leaves=vsize,leaves2=vsize2), type="response")


tp <- table(leaves[leaves<25],LeavesNext[leaves<25])
dtp <- dim(tp)
lvs <- unique(leaves[leaves<25 & !is.na(leaves)])
lvsn <- unique(LeavesNext[LeavesNext<25 & !is.na(LeavesNext)])
olvs <- order(lvs)
lvs <- lvs[olvs]
olvsn <- order(lvsn)
lvsn <-lvsn[olvsn]

plot(leaves, LeavesNext, type = "n", xlim=c(0,15), ylim=c(0,15))
for (i in 1: dtp[1]){
  for( j in 1: dtp[2]) {
    points(lvs[i],lvsn[j], pch=16, cex = (tp[i,j])^(1/2.5), col="black" )
    }
    }



lvvvv<-leaves[!is.na(leaves) & !is.na(LeavesNext)]
points(vsize,predgv, col="blue", pch=16)
plot(t(tp))


for (i in 1:25){gxyv[,i]<-(dpois(vsize,predgv[i]))}
#windows()
```

```
plot(gxyv[4,],type="l", col="red")
image(t(gxyv))


## Vegetative survival
psurvv <-glm(surv~leaves + leaves2+ covariate + covariate4, family=binomial)
summary(psurvv)

cf.vs <-psurvv$coefficients
predsurvv<-predict(psurvv, list(leaves=vsize, leaves2=vsize2, covariate=rep(hab, length(vsize)),
covariate4=rep(rain,length(vsize))), type="response")
#windows()
plot(leaves, surv)
lines(vsize,predsurvv, col="blue")

# survival vegetative function sxv(x)
sxv<-function(x, hab, rain) {
        xbeta<-cf.vs[1]+cf.vs[2]*x +cf.vs[3]*(x^2)+cf.vs[4]*hab+cf.vs[5]*rain  ####
        return(exp(xbeta)/(1+exp(xbeta)))
}

## probability of a reproductive remaining reproductive
prr <-glm(ReporNext ~ size +size2+covariate+ covariate2+covariate:covariate2 ,
family=binomial)
summary(prr)
cf.trr <-prr$coefficients
predprr<-predict(prr, list(size=rsize, size2=rsize2, covariate=rep(hab,length(rsize)),
covariate2=rep(herb,length(rsize))),type="response")
plot(size, d$ReporNext, type="n")
lines(rsize,predprr, col="red")
lines(rsize,(1-predprr), col="blue")

## Reproductive survival
psurvr<-glm(surv~size+covariate+covariate2+covariate3, family=binomial)
summary(psurvr)
cf.rs <-psurvr$coefficients
predsurvr<-predict(psurvr, list(size=rsize, covariate=rep(hab,length(rsize)),
covariate2=rep(herb,length(rsize)), covariate3=rep(pop,length(rsize))), type="response")
plot(size,surv)
lines(rsize,predsurvr, col="black")


# survival reproductive function sxr(x)
sxr<-function(x,pop,herb,hab) {
        xbeta<-cf.rs[1]+cf.rs[2]*x+cf.rs[3]*hab+cf.rs[4]*herb+cf.rs[5]*pop
        return(exp(xbeta)/(1+exp(xbeta)))
```

```
}

## Reproductive growth to reproductive
growthrep <-lm(sizeNext~size+ covariate)
summary(growthrep)
predgr<-predict(growthrep, list(size=rsize, covariate=rep(hab,length(rsize))), type="response")
plot(size,sizeNext)
sizeres<-size[!is.na(size) & !is.na(sizeNext) ]
lines(rsize,predgr, col="blue")
cf.rg <-growthrep$coefficients
r1 <- growthrep$residuals
pz <-(r1)^2

s1 <- size[size< 7 & size > -1 & !is.na(size) & !is.na(sizeNext) & !is.na(covariate)]
c1 <- covariate[size< 7 & size > -1 & !is.na(size) & !is.na(sizeNext) & !is.na(covariate)]
grres <-glm(pz~s1+c1)
summary(grres)
cf.varr <-grres$coefficients
res.varg <- summary(growthrep)$sigma

## Reproductive growth function g(x,y) reproductive to reproducive
gxyr <-function(x,y, hab) {
        mux<-cf.rg[1]+cf.rg[2]*x+ cf.rg[3]*hab       ####
    sigmax2<-cf.varr[1]+cf.varr[2]*x+ cf.varr[3]*hab  # Variable variance
        sigmax<-sqrt(sigmax2)
        fac1<-sqrt(2*pi)*sigmax;
        fac2<-((y-mux)^2)/(2*sigmax2);
    return(exp(-fac2)/fac1)
}

pg <-function(x,y, hab) { return(gxyr(x,y, hab))}             ####

## Reproductive growth to vegetative
growthrepveg <-glm.nb(LeavesNext~size+covariate+covariate2+covariate3)
summary(growthrepveg)
cf.vrg <-growthrepveg$coefficients
predgrv<-predict(growthrepveg, list(size=rsize,covariate=rep(hab,length(rsize)),
covariate2=rep(herb,length(rsize)),covariate3=rep(pop,length(rsize))), type="response")
plot(size,d$LeavesNext)
points(rsize,predgrv, col="black",pch=16)
for (i in 1:200){gxyrv[i,]<-(dnbinom(size=3.2453,x=vsize,mu=predgrv[i]))}
plot(gxyrv[20,],type="l")
image(gxyrv)

## Vegetative growth to reproductive
growthvegrep <-lm(sizeNext~leaves+leaves2)                    ###
```

```
summary(growthvegrep)
predgvr<-predict(growthvegrep, list(leaves=vsize, leaves2=vsize2), type="response")
plot(leaves,sizeNext, xlim=c(0,15))
lines(vsize,predgvr, col="blue")

cf.vrg <-growthvegrep$coefficients
vr1 <- growthvegrep$residuals
pzv <-(vr1)^2
l1<-leaves[!is.na(leaves) & !is.na(sizeNext) ]
l2<-leaves2[!is.na(leaves) & !is.na(sizeNext)]
grvres <-glm(pzv~l1+l2)
summary(grvres)
cf.varvr <-grvres$coefficients
res.vargv <- summary(growthvegrep)$sigma

## Reproductive growth function g(x,y) vegetative to reproducive
gxyvr <-function(x,y) {
        mux<-cf.vrg[1]+cf.vrg[2]*x+cf.vrg[3]*(x^2)
  sigmax2<-cf.varvr[1]+cf.varvr[2]*x+cf.varvr[3]*(x^2)   # Variable variance
        sigmax<-sqrt(sigmax2)
        fac1<-sqrt(2*pi)*sigmax;
        fac2<-((y-mux)^2)/(2*sigmax2);
    return(exp(-fac2)/fac1)
}

pgv <-function(x,y) { return(gxyvr(x,y))}

# upper and lower integration limits
        L<-minsize; U<-1*maxsize
# boundary points b and mesh points y
        b<-L+c(0:n)*(U-L)/n
        y<-0.5*(b[1:n]+b[2:(n+1)])
    h <- y[2]-y[1]

##################
####Fecundity   ####
##################

###Probaibilty that a reproductive individual produces a non-zero number of seed heads

repsuccess<-glm(srep~size+size2+covariate+covariate2, family=binomial)
summary(repsuccess)
predrs<-predict(repsuccess, list(size=rsize,size2=rsize2,
covariate=rep(hab,length(rsize)),covariate2=rep(herb,length(rsize))), type="response")
plot(size,srep,type="n")
lines(rsize,predrs)
```

```
cf.rsx<-repsuccess$coefficients
repsx<-function(x,hab,herb) {
        xbeta<-cf.rsx[1]+cf.rsx[2]*x+cf.rsx[3]*(x^2)+cf.rsx[4]*hab+cf.rsx[5]*herb
        return(exp(xbeta)/(1+exp(xbeta)))
}

#Redifining variables to only individuals with non-zero fecundity
sizef<-size[d$Heads>0]
sizef2<-sizef^2

covariatef<-covariate[d$Heads>0]
covariatef2<-covariate2[d$Heads>0]
covariatef3<-covariate3[d$Heads>0]
covariatef4<-covariate4[d$Heads>0]


##Number of seed heads produced
feclm<-glm(heads ~ sizef + sizef2+ covariatef * covariatef2 + covariatef3 + covariatef4 +
sizef:covariatef+sizef2:covariatef+sizef:covariatef2+sizef2:covariatef2+sizef:covariatef2:covaria
tef+sizef2:covariatef2:covariatef, family=gaussian)
summary(feclm)
cf.fec <-feclm$coefficients
res.fec <- summary(feclm)$sigma

##Predicted values from the above equation
predfec<-predict(feclm, list(sizef=rsize, sizef2=rsize2,
covariatef=rep(hab,length(rsize)),covariatef2=rep(herb,
length(rsize)),covariatef3=rep(pop,length(rsize)), covariatef4=rep(rain,length(rsize))),
type="response")
plot(sizef,heads)
lines(rsize,predfec, col="red")
##Multiplying predicted fecundity time fecundity constants defined earlier in the script
predfec<-
exp(predfec)*seedsperhead*germination*establishment*SeedViability*PreDSeedPred*PostDSee
dPred


##Distribution of germinant sizes
germleaves<-d$Leaves[d$stage==1&!is.na(d$Leaves)]
germsize<-mean(germleaves)
germdistrib<-dpois(vsize,germsize)

##Defining and filling the "f matrix" portion of reproductive to vegetative.
Mfrv1<-matrix(0,25,200)
for (i in 1:25){Mfrv1[i,]<-germdistrib[i]}
for (i in 1:200){Mfrv1[,i]<-Mfrv1[,i]*predfec[i]*predrs[i]}
```

```
#######################
#####Dormancy#########
#######################

###Probability of being dormant given that an individual was reproductive
repdorm<-glm(dorm~size+covariate+covariate2+covariate3+covariate4, family=binomial)
summary(repdorm)
predrd<-predict(repdorm, list(size=rsize,covariate=rep(hab,length(rsize)),
covariate2=rep(herb,length(rsize)), covariate3=rep(pop,length(rsize)),
covariate4=rep(rain,length(rsize))), type="response")

plot(size,dorm)
lines(rsize,predrd, col="red")

###Probability of being dormant given that an individual was vegetative
vegdorm<-glm(dorm~leaves, family=binomial)
summary(vegdorm)
predvd<-predict(vegdorm, list(leaves=vsize), type="response")
plot(leaves,dorm, xlim=c(0,25), ylim=c(0,1))
lines(vsize,predvd)

Notdormv<-1-predvd
Notdormr<-1-predrd

#Calculating dormancy rates from data (probability or remaing dormant multiple years
#assumed to be zero)
dormtab<-table(d$stage,d$LYStage)
dv<-(dormtab[4,1]+dormtab[4,2])/(dormtab[4,1]+dormtab[4,2]+dormtab[4,3])
dr<-dormtab[4,3]/(dormtab[4,1]+dormtab[4,2]+dormtab[4,3])
dd<-0

#Calculating size distribution of individuals exiting dormancy to vegetative stage
dormsizev<-(leaves[d$LYDorm==1])
dormsizev<-dormsizev[!is.na(dormsizev)]
hist(dormsizev)
dsvmean<-mean(dormsizev)
dsvvec<-dpois(vsize,dsvmean)
preddv<-dsvvec*dv

#Calculating size distribution of individuals exiting dormancy to reproductive stage
dormsizer<-size[d$LYDorm==1]
dormsizer<-dormsizer[!is.na(dormsizer)]
hist(dormsizer)
dsrmean<-mean(dormsizer)
dsrsd<-sd(dormsizer)
dsrvec<-dnorm(rsize, mean=dsrmean, sd=dsrsd)
```

```
dsrvec<-dsrvec/sum(dsrvec)
preddr<-dsrvec*dr
preddr[201]<-0
################################################################
#########Defining matrices and Kernel functions        ###########
################################################################

# loop to construct the matrix for reproductive growth
        rgmat<-matrix(0,n,n)
        for (i in 1:n){
                for(j in 1:n){
                        rgmat[i,j]<-pg(y[i],y[j], hab)
                }
        }
image(rgmat)


# loop to construct the matrix for reproductive to vegetative size
    rgmatv<-matrix(0,25,n)
        for (i in 1:25){
                for(j in 1:n){
                        rgmatv[i,j]<-pgv(i,y[j])
                }
        }
image(rgmatv)


##Combining survival and transitional probabilites
tvv <- (1-predpvr)*sxv(vsize,hab,rain)
trv <- (1-predprr)*sxr(rsize,pop, hab, herb)


##Functions to be used in defining vegetative and reproductive kernel fuctions
pxyrr<-function(x,y,pop,hab,herb) {return(sxr(x,pop, hab,herb)*gxyr(x,y,hab))}
pxyvr<-function(x,y,hab,rain) {return(sxv(x, hab,rain)*gxyvr(x,y))}
########## THE KERNEL K(y,x) for reproductive to reproductive

Kyxrr <-function(y,x,pop, hab,herb) {
        xeval<-max(x,minsize)
        xeval<-min(xeval,maxsize)
        yeval<-max(y,minsize)
        yeval<-min(yeval,maxsize)
    return(pxyrr(xeval,yeval,pop,hab,herb))
        }
```

```
############### Defining a reproductive to reproductive matrix
bigmatrix<-function(n,pop,hab,herb) {
# upper and lower integration limits
        L<-minsize; U<-1*maxsize


# boundary points b and mesh points y
        b<-L+c(0:n)*(U-L)/n
        y<-0.5*(b[1:n]+b[2:(n+1)])
    h <- y[2]-y[1]

# loop to construct the matrix
        M<-matrix(0,n,n)
        for (i in 1:n){
                for(j in 1:n){
                        M[i,j]<-predprr[i]*Kyxrr(y[i],y[j],pop, hab,herb)
                }
        }
        M<-M*h
        return(list(matrix=M,meshpts=y))
}

Mb1 <- bigmatrix(200, pop, hab, herb)
Mrr <- Mb1$matrix

########### THE KERNEL K(y,x) for vegetative to vegetative

Mvv<-matrix(0,25,25)
for(i in 1:25){Mvv[,i]<-tvv[i]*gxyv[,i]}

########### THE KERNEL K(y,x) for reproductive to vegetative

Mrv<-matrix(0,200,25)
for(i in 1:200){Mrv[i,]<-trv[i]*gxyrv[i,]}

########### THE KERNEL K(y,x) for vegetative to reproductive

Kyxvr <-function(x,y, hab, rain) {
        yeval<-max(y,minsize)
        yeval<-min(yeval,maxsize)
    return(pxyvr(x,yeval, hab, rain))
        }

############### Matrix for vegetative to reproductive
bigmatrix<-function(n) {
# upper and lower integration limits
```

```
        L<-minsize; U<-1*maxsize

# boundary points b and mesh points y
        b<-L+c(0:n)*(U-L)/n
        y<-0.5*(b[1:n]+b[2:(n+1)])
    h <- y[2]-y[1]

# loop to construct the matrix
        M<-matrix(0,25,n)
        for (i in 1:25){
                for(j in 1:n){
                        M[i,j]<-(predpvr[i])*Kyxvr(i,y[j], hab, rain)
                }
        }
        M<-M*h
        return(list(matrix=M,meshpts=y))
}

Mb <- bigmatrix(200)
Mvr <- Mb$matrix




###images of newly created matricies
par(mfrow=c(2,2))

image(t(Mrr))
image(t(Mvv))
image(Mrv)
image(Mvr)
dim(Mrr)
dim(Mvv)
dim(Mrv)
dim(Mvr)

#combining the survival/growth and fecundity matricies for reproductive to vegetative.
mrv1<-Mrv+t(Mfrv1)
for (i in 1:25){Mvv[i,]<-Mvv[i,]*Notdormv[i]}
for (i in 1:25){Mvr[i,]<-Mvr[i,]*Notdormv[i]}
for (i in 1:200){Mrr[i,]<-Mrr[i,]*Notdormr[i]}
for (i in 1:200){Mrv[i,]<-Mrv[i,]*Notdormr[i]}

##############################
####OVERALL MATRIX#######
##############################
```

```
###Adding dormancy vectors to continuous stage matricies
Mrr<-rbind(predrd,Mrr)
Mvr<-cbind(predvd,Mvr)
Mvr<-rbind(preddr,Mvr)
Mvv<-cbind(preddv,Mvv)
dim(Mrr)
dim(Mvr)
dim(Mvr)
dim(Mvv)

###Binding all stages together
upper<-rbind(Mrr,t(mrv1))
dim(upper)
image(t(upper^(1/5)))

lower<-rbind(t(Mvr),Mvv)
dim(lower)
image(t(lower^(1/5)))

###Overall matrix
overall<-cbind(lower,upper)
par(mfrow=c(1,1))
image(t(overall^(1/5)))
eigen(overall)$values[1]
h.mat[,,q] <- overall   } # end of matrices loop




overallNH <- h.mat[,,1]
eigen(overallNH)$values[1]
overallWH <-  h.mat[,,2]
eigen(overallWH)$values[1]
d.mat <- dim(overallWH)

par(mfrow=c (2,2))
### simplest case "constant probabilities of herbivory"

table(d$BiHerbiv)/length(d$BiHerbiv[!is.na(d$BiHerbiv)])
phh <- 0.4968979
phn <- 1-phh
pnh <- 0.5031021
pnn <- 1-pnh
p.h <- c(rep(phh,d.mat[1]),rep(phn,d.mat[1]))
p.n <- c(rep(pnh,d.mat[1]),rep(pnn,d.mat[1]))
```

```
################################################################
### observed probability of herbivory


size   <-log(d$StemLength+1)
size2  <- size^2
x <- seq(min(size[!is.na(size)]),max(size[!is.na(size)]),0.03288235)

#######################Defining the Non-herbiv-herbiv transition####################
BiHerbiv0 <-d$BiHerbiv[d$LYBiHerbiv==0]
size0    <- size[d$LYBiHerbiv==0]
covariate0<-covariate[d$LYBiHerbiv==0]
size02 <- size0^2
covariate30<-covariate3[d$LYBiHerbiv==0]
covariate40<-covariate4[d$LYBiHerbiv==0]

model1 <- glm(BiHerbiv0 ~ size0,data=d,family=binomial)
summary(model1)
model2 <- glm(BiHerbiv0 ~size0  + size02+covariate0+covariate30+covariate40
,family=binomial)
summary(model2)
y <- predict(model2, list(size0=x, size02 =x^2,
covariate0=rep(hab,length(x)),covariate30=rep(pop,length(x)),
covariate40=rep(rain,length(x))),type="response")
plot(x,y,ylim=c(0,1),type="l",col="blue")
x.c <- seq(min(size0[!is.na(size0) & !is.na(BiHerbiv0)]),max(size0[!is.na(size0) &
!is.na(BiHerbiv0)]),0.5)
class.size <- cut(size0,x.c)
class.size <- class.size
herb.class <- as.data.frame(table(class.size,BiHerbiv0))
prob.herb <- herb.class[12:22,3]/(herb.class[1:11,3]+herb.class[12:22,3])
points(seq(0.6,5.6,0.5),prob.herb)


p.n <- c(y,rep(phh,26),(1-y),rep(phn,26))



################################################
 
#######################defining the Herbiv-Herbiv Transition####################
BiHerbiv1 <-d$BiHerbiv[d$LYBiHerbiv==1]
size1    <- size[d$LYBiHerbiv==1]
size12 <- size1^2
covariate1<-covariate[d$LYBiHerbiv==1]
covariate31<-covariate3[d$LYBiHerbiv==1]
covariate41<-covariate4[d$LYBiHerbiv==1]
```

```
model1 <- glm(BiHerbiv1 ~ size1,data=d,family=binomial)
summary(model1)
model2 <- glm(BiHerbiv1 ~size1 + size12+ covariate1+covariate31+covariate41
,data=d,family=binomial)
summary(model2)
y <- predict(model2, list(size1=x, size12 =x^2, covariate1=rep(hab,length(x)),
covariate31=rep(pop,length(x)), covariate41=rep(rain,length(x))),type="response")
plot(x,y,ylim=c(0,1),type="l",col="blue")
x.c <- seq(min(size1[!is.na(size1) & !is.na(BiHerbiv1)]),max(size1[!is.na(size1) &
!is.na(BiHerbiv1)]),0.5)
class.size <- cut(size1,x.c)
class.size <- class.size
herb.class <- as.data.frame(table(class.size,BiHerbiv1))
prob.herb <- herb.class[14:24,3]/(herb.class[2:12,3]+herb.class[14:24,3])
points(seq(0.5,5.5,0.5),prob.herb)


p.h <- c(y,rep(phh,26),(1-y),rep(phn,26))


#######################Constructing overall megamatrix#####################

big.matrix_upper <- rbind(overallWH,overallNH)
big.matrix_upper <- p.h*big.matrix_upper
big.matrix_lower <- p.n*rbind(overallNH,overallWH)
big.matrix_lower <-big.matrix_lower
big.matrix <- cbind(big.matrix_upper,big.matrix_lower)
dim(big.matrix)
eigen(big.matrix)$values[1]
image(t(big.matrix^(1/5)))
```

```
############################################################
##Script to build a deterministic Liatris model consisting of          ##
##three stages (Dormant, Reproductive, Vegetative)                      ##
##and the transions between them                                        ##
##Curated by Matthew Tye                                                 ##
##With Input from Rob Salguero-Gomez                                     ##
##and Pedro Quintana-Ascencio                                            ##
##Last Updated: 3/14/2014                                                ##
############################################################

#Clean memory
rm(list=ls(all=TRUE))

#set directory and load libraries
dir="C:/Users/matt/Dropbox/PQA Lab/Thesis/Liatris models"
setwd(dir)
library(MASS)
h.mat <- array(0,c(226,226,2))
for (q in 1:2) {
#load dataset and define variables to be used later
d <- read.csv("Liatrisdata.csv", header=TRUE, sep=",", na.strings="NA", dec=".",
strip.white=TRUE)
TSFcat<-d$TSFcat
#variable definition
leaves   <-d$Leaves
leaves<- leaves[!is.na(TSFcat)]
LeavesNext<-d$LeavesNext
LeavesNext<-LeavesNext[!is.na(TSFcat)]
leaves2<-leaves^2
size    <-log(d$StemLength+1)
size<- size[!is.na(TSFcat)]  #logarithmic
sizeNext <-log(d$SizeNext+1)   #logarithmic
sizeNext<-sizeNext[!is.na(TSFcat)]
heads<-log(d$Heads+1) #logarithmic
heads<-heads[!is.na(TSFcat)]
size2<-size^2
surv<-d$SurvNext
surv<-surv[!is.na(TSFcat)]
dorm<-d$DormNext
dorm<-dorm[!is.na(TSFcat)]
ReporNext<-d$ReporNext
ReporNext<-ReporNext[!is.na(TSFcat)]

#Fecundity Constants
seedsperhead<-40
SeedViability<-.8916     #Stephens et al Am. Mid. Nat. 2012
```

```
PreDSeedPred<-.78        #LiatrisData
PostDSeedPred<-.628      #Stephens et al Am. Mid. Nat. 2012
germination<-.247        #LODEM03
establishment<-.003              #Correction Factor

#Dummy vectors and matricies to be filled later
vsize<-seq(1,25,1)
vsize2<-vsize^2
rsize<-seq(0,7,7/200)
rsize<-rsize[1:200]
rsize2<-rsize^2
gxyv<-matrix(0,25,25)
gxyrv<-matrix(0,200,25)
n <- 200
gxyvr<-matrix(0,25,n)
minsize<-0
maxsize<-6


#Definition of covariates
covariate<-d$TSFcat  [!is.na(TSFcat)]            #Time Since Fire
covariate2<-d$BiHerbiv[!is.na(TSFcat)]          #Vertebrate Herbivory (0,1)
covariate3<-d$Norco          [!is.na(TSFcat)]   #Splits population into a Northern and
Southern Group
covariate4<-d$Precip[!is.na(TSFcat)]


#Levels for each variable altering these variables will change model outputs
TSF<-3
herb<-(q-1)
pop<-2                                          #levels(1,2)
rain<-2

#Histograms of variables
#windows()
par(mfrow=c(1,3))
hist(leaves)
hist(size)
hist(sizeNext)
table(covariate)

#Defining creates a binary variable for succesful production of heads
d$srep<-1:length(d$Heads)
d$srep[d$Heads>0]<-1
d$srep[d$Heads==0]<-0
d$srep[is.na(d$Heads)]<-NA
```

```
srep<-d$srep
srep<-srep[!is.na(TSFcat)]

#########################################################################
####Defining survival, growth, and transtion probability between####
####                                  continuous stages                          ####
#########################################################################

## probability of a vegetative becoming reproductive
#pvr <-glm(ReporNext~leaves+leaves2+covariate+covariate:leaves+covariate:leaves2,
family="binomial")
pvr <-glm(ReporNext~leaves+leaves2+covariate, family="binomial")

summary(pvr)
cf.tvr <-pvr$coefficients
predpvr<-predict(pvr, list(leaves=vsize, leaves2=vsize2, covariate=rep(TSF,length(vsize))),
type="response")
#windows()
plot(leaves, ReporNext)
lines(vsize,predpvr, col="blue")
lines(vsize,(1-predpvr), col="blue")

## Vegetative growth to vegetative
growthveg <-glm(LeavesNext~leaves+leaves2, family=poisson)
summary(growthveg)


cf.vg <-growthveg$coefficients
predgv<-predict(growthveg, list(leaves=vsize,leaves2=vsize2), type="response")


tp <- table(leaves[leaves<25],LeavesNext[leaves<25])
dtp <- dim(tp)
lvs <- unique(leaves[leaves<25 & !is.na(leaves)])
lvsn <- unique(LeavesNext[LeavesNext<25 & !is.na(LeavesNext)])
olvs <- order(lvs)
lvs <- lvs[olvs]
olvsn <- order(lvsn)
lvsn <-lvsn[olvsn]

plot(leaves, LeavesNext, type = "n", xlim=c(0,15), ylim=c(0,15))
for (i in 1: dtp[1]){
  for( j in 1: dtp[2]) {
    points(lvs[i],lvsn[j], pch=16, cex = (tp[i,j])^(1/2.5), col="black" )
  }
}
```

```
lvvvv<-leaves[!is.na(leaves) & !is.na(LeavesNext)]
points(vsize,predgv, col="blue", pch=16)
plot(t(tp))


for (i in 1:25){gxyv[,i]<-(dpois(vsize,predgv[i]))}
#windows()
plot(gxyv[4,],type="l", col="red")
image(t(gxyv))


## Vegetative survival
psurvv <-glm(surv~leaves + leaves2, family=binomial)
summary(psurvv)

cf.vs <-psurvv$coefficients
predsurvv<-predict(psurvv, list(leaves=vsize, leaves2=vsize2), type="response")
#windows()
plot(leaves, surv)
lines(vsize,predsurvv, col="blue")

# survival vegetative function sxv(x)
sxv<-function(x) {
  xbeta<-cf.vs[1]+cf.vs[2]*x +cf.vs[3]*(x^2)  ####
  return(exp(xbeta)/(1+exp(xbeta)))
}

## probability of a reproductive remaining reproductive
prr<-glm(ReporNext ~ size +size2+ covariate2,family=binomial)
summary(prr)
cf.trr <-prr$coefficients
predprr<-predict(prr, list(size=rsize, size2=rsize2,
covariate2=rep(herb,length(rsize))),type="response")
plot(size, ReporNext, type="n")
lines(rsize,predprr, col="pink")
lines(rsize,(1-predprr), col="blue")

## Reproductive survival
psurvr<-glm(surv~size+covariate3, family=binomial)
summary(psurvr)
cf.rs <-psurvr$coefficients
predsurvr<-predict(psurvr, list(size=rsize, covariate3=rep(pop,length(rsize))), type="response")
plot(size,surv)
```

```
lines(rsize,predsurvr, col="red")


# survival reproductive function sxr(x)
sxr<-function(x,pop) {
  xbeta<-cf.rs[1]+cf.rs[2]*x+cf.rs[3]*pop
  return(exp(xbeta)/(1+exp(xbeta)))
}

## Reproductive growth to reproductive
growthrep <-lm(sizeNext~size)
summary(growthrep)
predgr<-predict(growthrep, list(size=rsize), type="response")
plot(size,sizeNext)
sizeres<-size[!is.na(size) & !is.na(sizeNext) ]
lines(rsize,predgr, col="blue")
cf.rg <-growthrep$coefficients
r1 <- growthrep$residuals
pz <-(r1)^2

s1 <- size[size< 7 & size > -1 & !is.na(size) & !is.na(sizeNext) & !is.na(covariate3)]
grres <-glm(pz~s1)
summary(grres)
cf.varr <-grres$coefficients
res.varg <- summary(growthrep)$sigma

## Reproductive growth function g(x,y) reproductive to reproducive
gxyr <-function(x,y) {
  mux<-cf.rg[1]+cf.rg[2]*x        ####
  sigmax2<-cf.varr[1]+cf.varr[2]*x   # Variable variance
  sigmax<-sqrt(sigmax2)
  fac1<-sqrt(2*pi)*sigmax;
  fac2<-((y-mux)^2)/(2*sigmax2);
  return(exp(-fac2)/fac1)
}

pg <-function(x,y) { return(gxyr(x,y))}                ####

## Reproductive growth to vegetative
growthrepveg <-glm.nb(LeavesNext~size+covariate3)
summary(growthrepveg)
cf.vrg <-growthrepveg$coefficients
predgrv<-predict(growthrepveg, list(size=rsize,covariate3=rep(pop,length(rsize))),
type="response")
plot(size,LeavesNext)
points(rsize,predgrv, col="red",pch=16)
```

```
for (i in 1:200){gxyrv[i,]<-(dnbinom(size=3.393,x=vsize,mu=predgrv[i]))}
plot(gxyrv[20,],type="l")
image(gxyrv)

## Vegetative growth to reproductive
growthvegrep <-lm(sizeNext~leaves)                    ###
summary(growthvegrep)
predgvr<-predict(growthvegrep, list(leaves=vsize), type="response")
plot(leaves,sizeNext, xlim=c(0,15))
lines(vsize,predgvr, col="blue")

cf.vrg <-growthvegrep$coefficients
vr1 <- growthvegrep$residuals
pzv <-(vr1)^2
l1<-leaves[!is.na(leaves) & !is.na(sizeNext) ]
grvres <-glm(pzv~l1)
summary(grvres)
cf.varvr <-grvres$coefficients
res.vargv <- summary(growthvegrep)$sigma

## Reproductive growth function g(x,y) vegetative to reproducive
gxyvr <-function(x,y) {
  mux<-cf.vrg[1]+cf.vrg[2]*x
  sigmax2<-cf.varvr[1]+cf.varvr[2]*x   # Variable variance
  sigmax<-sqrt(sigmax2)
  fac1<-sqrt(2*pi)*sigmax;
  fac2<-((y-mux)^2)/(2*sigmax2);
  return(exp(-fac2)/fac1)
}

pgv <-function(x,y) { return(gxyvr(x,y))}

# upper and lower integration limits
L<-minsize; U<-1*maxsize
# boundary points b and mesh points y
b<-L+c(0:n)*(U-L)/n
y<-0.5*(b[1:n]+b[2:(n+1)])
h <- y[2]-y[1]

#################
####Fecundity####
#################

###Probaibilty that a reproductive individual produces a non-zero number of seed heads
repsuccess<-glm(srep~size+covariate2, family=binomial)
summary(repsuccess)
```

```
predrs<-predict(repsuccess, list(size=rsize,covariate2=rep(herb,length(rsize))), type="response")

plot(size,srep, type="n")
lines(rsize,predrs, col="red")


cf.rsx<-repsuccess$coefficients
repsx<-function(x,TSF,herb) {
  xbeta<-cf.rsx[1]+cf.rsx[2]*x+cf.rsx[3]*herb
  return(exp(xbeta)/(1+exp(xbeta)))
}

#Redifining variables to only individuals with non-zero fecundity
sizef<-size[heads>1]
headsf<-heads[heads>1]
sizef2<-sizef^2

covariatef<-covariate
covariatef2<-covariate2
covariatef3<-covariate3
covariatef4<-covariate4

covariatef<-covariatef[heads>1]
covariatef2<-covariatef2[heads>1]
covariatef3<-covariatef3[heads>1]
covariatef4<-covariatef4[heads>1]
####
##Number of seed heads produced
feclm<-glm(headsf~sizef+sizef2+covariatef+covariatef3, family=gaussian)

summary(feclm)
cf.fec <-feclm$coefficients
res.fec <- summary(feclm)$sigma

##Predicted values from the above equation
predfec<-predict(feclm, list(sizef=rsize, sizef2=rsize2,
covariatef=rep(TSF,length(rsize)),covariatef3=rep(pop,length(rsize))), type="response")

plot(sizef,headsf, xlim=c(1,6))
lines(rsize,predfec, col="red")
##Multiplying predicted fecundity time fecundity constants defined earlier in the script
predfec<-
exp(predfec)*seedsperhead*germination*establishment*SeedViability*PreDSeedPred*PostDSee
dPred
```

```
##Distribution of germinant sizes
germleaves<-d$Leaves[d$stage==1&!is.na(d$Leaves)]
germsize<-mean(germleaves)
germdistrib<-dpois(vsize,germsize)

##Defining and filling the "f matrix" portion of reproductive to vegetative.
Mfrv1<-matrix(0,25,200)
for (i in 1:25){Mfrv1[i,]<-germdistrib[i]}
for (i in 1:200){Mfrv1[,i]<-Mfrv1[,i]*predfec[i]*predrs[i]}
#####################
#####Dormancy########
#####################

###Probability of being dormant given that an individual was reproductive
repdorm<-glm(dorm~size*covariate*covariate2+covariate3+covariate4, family=binomial)
summary(repdorm)
predrd<-predict(repdorm, list(size=rsize,covariate=rep(TSF,length(rsize)),
covariate2=rep(herb,length(rsize)), covariate3=rep(pop,length(rsize)),
covariate4=rep(rain,length(rsize))), type="response")
plot(size,dorm)
lines(rsize,predrd, col="red")

###Probability of being dormant given that an individual was vegetative
vegdorm<-glm(dorm~leaves, family=binomial)
summary(vegdorm)
predvd<-predict(vegdorm, list(leaves=vsize), type="response")
plot(leaves,dorm, xlim=c(0,25), ylim=c(0,1))
lines(vsize,predvd)

Notdormv<-1-predvd
Notdormr<-1-predrd

#Calculating dormancy rates from data (probability or remaing dormant multiple years
#assumed to be zero)
dormtab<-table(d$stage,d$LYStage)
dv<-(dormtab[4,1]+dormtab[4,2])/(dormtab[4,1]+dormtab[4,2]+dormtab[4,3])
dr<-dormtab[4,3]/(dormtab[4,1]+dormtab[4,2]+dormtab[4,3])
dd<-0

#Calculating size distribution of individuals exiting dormancy to vegetative stage
dormsizev<-(leaves[d$LYDorm==1])
dormsizev<-dormsizev[!is.na(dormsizev)]
hist(dormsizev)
dsvmean<-mean(dormsizev)
dsvvec<-dpois(vsize,dsvmean)
preddv<-dsvvec*dv
```

```
#Calculating size distribution of individuals exiting dormancy to reproductive stage
dormsizer<-size[d$LYDorm==1]
dormsizer<-dormsizer[!is.na(dormsizer)]
hist(dormsizer)
dsrmean<-mean(dormsizer)
dsrsd<-sd(dormsizer)
dsrvec<-dnorm(rsize, mean=dsrmean, sd=dsrsd)
dsrvec<-dsrvec/sum(dsrvec)
preddr<-dsrvec*dr
preddr[201]<-0
##############################################################
##########Defining matrices and Kernel functions###########
##############################################################

# loop to construct the matrix for reproductive growth
rgmat<-matrix(0,n,n)
for (i in 1:n){
  for(j in 1:n){
    rgmat[i,j]<-pg(y[i],y[j])
  }
}
image(rgmat)


# loop to construct the matrix for reproductive to vegetative size
rgmatv<-matrix(0,25,n)
for (i in 1:25){
  for(j in 1:n){
    rgmatv[i,j]<-pgv(i,y[j])
  }
}
image(rgmatv)


##Combining survival and transitional probabilites
tvv <- (1-predpvr)*sxv(vsize)
trv <- (1-predprr)*sxr(rsize,pop)


##Functions to be used in defining vegetative and reproductive kernel fuctions
pxyrr<-function(x,y,pop) {return(sxr(x,pop)*gxyr(x,y))}
pxyvr<-function(x,y) {return(sxv(x)*gxyvr(x,y))}
########### THE KERNEL K(y,x) for reproductive to reproductive

Kyxrr <-function(y,x,pop) {
```

```
  xeval<-max(x,minsize)
  xeval<-min(xeval,maxsize)
  yeval<-max(y,minsize)
  yeval<-min(yeval,maxsize)
  return(pxyrr(xeval,yeval,pop))
}



############### Defining a reproductive to reproductive matrix
bigmatrix<-function(n,pop) {
  # upper and lower integration limits
  L<-minsize; U<-1*maxsize


  # boundary points b and mesh points y
  b<-L+c(0:n)*(U-L)/n
  y<-0.5*(b[1:n]+b[2:(n+1)])
  h <- y[2]-y[1]

  # loop to construct the matrix
  M<-matrix(0,n,n)
  for (i in 1:n){
    for(j in 1:n){
      M[i,j]<-predprr[i]*Kyxrr(y[i],y[j],pop)
    }
  }
  M<-M*h
  return(list(matrix=M,meshpts=y))
}

Mb1 <- bigmatrix(200, pop)
Mrr <- Mb1$matrix

########### THE KERNEL K(y,x) for vegetative to vegetative

Mvv<-matrix(0,25,25)
for(i in 1:25){Mvv[,i]<-tvv[i]*gxyv[,i]}

########### THE KERNEL K(y,x) for reproductive to vegetative

Mrv<-matrix(0,200,25)
for(i in 1:200){Mrv[i,]<-trv[i]*gxyrv[i,]}

########### THE KERNEL K(y,x) for vegetative to reproductive

Kyxvr <-function(x,y) {
```

```
  yeval<-max(y,minsize)
  yeval<-min(yeval,maxsize)
  return(pxyvr(x,yeval))
}

############### Matrix for vegetative to reproductive
bigmatrix<-function(n) {
  # upper and lower integration limits
  L<-minsize; U<-1*maxsize

  # boundary points b and mesh points y
  b<-L+c(0:n)*(U-L)/n
  y<-0.5*(b[1:n]+b[2:(n+1)])
  h <- y[2]-y[1]

  # loop to construct the matrix
  M<-matrix(0,25,n)
  for (i in 1:25){
    for(j in 1:n){
      M[i,j]<-(predpvr[i])*Kyxvr(i,y[j])
    }
  }
  M<-M*h
  return(list(matrix=M,meshpts=y))
}

Mb <- bigmatrix(200)
Mvr <- Mb$matrix




###images of newly created matricies
par(mfrow=c(2,2))

image(t(Mrr))
image(t(Mvv))
image(Mrv)
image(Mvr)
dim(Mrr)
dim(Mvv)
dim(Mrv)
dim(Mvr)

#combining the survival/growth and fecundity matricies for reproductive to vegetative.
mrv1<-Mrv+t(Mfrv1)
for (i in 1:25){Mvv[i,]<-Mvv[i,]*Notdormv[i]}
```

```
for (i in 1:25){Mvr[i,]<-Mvr[i,]*Notdormv[i]}
for (i in 1:200){Mrr[i,]<-Mrr[i,]*Notdormr[i]}
for (i in 1:200){Mrv[i,]<-Mrv[i,]*Notdormr[i]}

###############################
####OVERALL MATRIX###########
###############################

###Adding dormancy vectors to continuous stage matricies
Mrr<-rbind(predrd,Mrr)
Mvr<-cbind(predvd,Mvr)
Mvr<-rbind(preddr,Mvr)
Mvv<-cbind(preddv,Mvv)
dim(Mrr)
dim(Mvr)
dim(Mvr)
dim(Mvv)

###Binding all stages together
upper<-rbind(Mrr,t(mrv1))
dim(upper)
image(t(upper^(1/5)))

lower<-rbind(t(Mvr),Mvv)
dim(lower)
image(t(lower^(1/5)))

###Overall matrix
overall<-cbind(lower,upper)
par(mfrow=c(1,1))
image(t(overall^(1/5)))
eigen(overall)$values[1]
h.mat[,,q] <- overall   } # end of matrices loop




overallNH <- h.mat[,,1]
eigen(overallNH)$values[1]
overallWH <-  h.mat[,,2]
eigen(overallWH)$values[1]
d.mat <- dim(overallWH)

par(mfrow=c (2,2))
### simplest case "constant probabilities of herbivory"
```

```
table(d$BiHerbiv)/length(d$BiHerbiv[!is.na(d$BiHerbiv)])
phh <- 0.4968979
phn <- 1-phh
pnh <- 0.5031021
pnn <- 1-pnh
p.h <- c(rep(phh,d.mat[1]),rep(phn,d.mat[1]))
p.n <- c(rep(pnh,d.mat[1]),rep(pnn,d.mat[1]))


############################################################
### observed probability of herbivory


size  <-log(d$StemLength+1)
size2 <- size^2
x <- seq(min(size[!is.na(size)]),max(size[!is.na(size)]),0.03288235)


####################Defining the Non-herbiv-herbiv transition#######################
BiHerbiv0 <-d$BiHerbiv[d$LYBiHerbiv==0]
size0    <- size[d$LYBiHerbiv==0]
covariate0<-covariate[d$LYBiHerbiv==0]
size02 <- size0^2
covariate30<-covariate3[d$LYBiHerbiv==0]
covariate40<-covariate4[d$LYBiHerbiv==0]

model1 <- glm(BiHerbiv0 ~ size0,data=d,family=binomial)
summary(model1)
model2 <- glm(BiHerbiv0 ~size0  + size02+covariate0+covariate30+covariate40
,family=binomial)
summary(model2)
y <- predict(model2, list(size0=x, size02 =x^2,
covariate0=rep(TSF,length(x)),covariate30=rep(pop,length(x)),
covariate40=rep(rain,length(x))),type="response")
plot(x,y,ylim=c(0,1),type="l",col="blue")
x.c <- seq(min(size0[!is.na(size0) & !is.na(BiHerbiv0)]),max(size0[!is.na(size0) &
!is.na(BiHerbiv0)]),0.5)
class.size <- cut(size0,x.c)
class.size <- class.size
herb.class <- as.data.frame(table(class.size,BiHerbiv0))
prob.herb <- herb.class[12:22,3]/(herb.class[1:11,3]+herb.class[12:22,3])
points(seq(0.6,5.6,0.5),prob.herb)


p.n <- c(y,rep(phh,26),(1-y),rep(phn,26))


############################################
```

```
################################defining the Herbiv-Herbiv Transition##############
BiHerbiv1 <-d$BiHerbiv[d$LYBiHerbiv==1]
size1     <- size[d$LYBiHerbiv==1]
size12 <- size1^2
covariate1<-covariate[d$LYBiHerbiv==1]
covariate31<-covariate3[d$LYBiHerbiv==1]
covariate41<-covariate4[d$LYBiHerbiv==1]
model1 <- glm(BiHerbiv1 ~ size1,data=d,family=binomial)
summary(model1)
model2 <- glm(BiHerbiv1 ~size1  + size12+ covariate1+covariate31+covariate41
,data=d,family=binomial)
summary(model2)
y <- predict(model2, list(size1=x, size12 =x^2, covariate1=rep(TSF,length(x)),
covariate31=rep(pop,length(x)), covariate41=rep(rain,length(x))),type="response")
plot(x,y,ylim=c(0,1),type="l",col="blue")
x.c <- seq(min(size1[!is.na(size1) & !is.na(BiHerbiv1)]),max(size1[!is.na(size1) &
!is.na(BiHerbiv1)]),0.5)
class.size <- cut(size1,x.c)
class.size <- class.size
herb.class <- as.data.frame(table(class.size,BiHerbiv1))
prob.herb <- herb.class[14:24,3]/(herb.class[2:12,3]+herb.class[14:24,3])
points(seq(0.5,5.5,0.5),prob.herb)


p.h <- c(y,rep(phh,26),(1-y),rep(phn,26))


#########################Constructing overall megamatrix####################

big.matrix_upper <- rbind(overallWH,overallNH)
big.matrix_upper <- p.h*big.matrix_upper
big.matrix_lower <- p.n*rbind(overallNH,overallWH)
big.matrix_lower <-big.matrix_lower
big.matrix <- cbind(big.matrix_upper,big.matrix_lower)
dim(big.matrix)
eigen(big.matrix)$values[1]
image(t(big.matrix^(1/5)))
```

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