HOW SEASONAL AND ANNUAL VARIATION IN DEMOGRAPHY INFLUENCE POPULATIONS OF A NEOTROPICAL MILKWEED, *ASCLEPIAS CURASSAVICA*

by

KIMBERLY M. KELLETT

(Under the Direction of John M. Drake)

ABSTRACT

Temporal variation is generally examined only at the annual scale in demographic studies. Seasonal variation in demography therefore plays an unclear, but likely important role in the population dynamics and evolution of many species, especially for those with year-round reproduction. To examine the role of seasonal variation to population dynamics and evolution, I use demographic models constructed from data collected every three months for three years from populations of a continuously flowering, long-lived Neotropical milkweed, *Asclepias curassavica*, in Monteverde, Costa Rica. Seasonal variation in demography contributed over twice as much to temporal variation in population growth than annual variation, and seasonal and annual variation in population growth occurred via different demographic pathways. Reproductive costs and payoffs varied over time for these populations, but without a predictable seasonal pattern. Models suggested this variation is integral to the evolution of reproductive delay in this species. The lack of seasonal pattern in the variation of reproductive costs may contribute to the year-round flowering strategy of this species. Response of population growth to precipitation was season-specific during the length of our study. Three seasons responded positively to decreased precipitation, while one responded negatively, and the precipitation measure that best predicted population growth varied among season. Including season-specific responses influenced our predictions for population growth under climate change, and our most realistic model predicted a modest increase in population growth for this species in the future. This dissertation emphasizes the importance of seasonal variation in demography, and encourages further exploration of seasonal variation in the demography of tropical and temperate species.

INDEX WORDS: Demography, tropical plants, seasonality, population growth, climate change

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DEDICATION

This dissertation is dedicated to my loving parents, Bruce and Denise Kellett, who fostered my passion for nature by always encouraging me to “go play outside.”

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Demographic rates respond to temporal heterogeneity in environment, and temporal variation in demographic rates has long been understood as a major driver of population dynamics and life history evolution (Tuljapurkar 1989; Boyce *et al.* 2006). Variation in environment is often greater among seasons than among years, and so seasons often influence demographic rates more than year (Vavrek *et al.* 1997). However, collection of demographic data generally occurs on a once-per-year basis, limiting our understanding of temporal variation in demography to an annual scale for most species. For species without reproductive or growing seasons, which are common in the tropics (Croat 1978), demographic data collected on an annual scale may be inappropriately long and neglect important seasonal patterns in demography. Even for species that do not reproduce year-round, gaining an understanding of seasonal demography could be important, as season-specific responses to climate variables can provide better insight into how changing climates may affect populations in the future (Penuelas *et al.* 2004).

My dissertation seeks to elucidate the role of seasonal variation in the population dynamics, life history evolution, and future persistence of populations of a widespread Neotropical milkweed, *Asclepias curassavica*, in Monteverde, Costa Rica by 1) assessing the relative contributions of seasonal and annual variation to population dynamics 2) exploring the influence of temporal variation in reproductive costs on the evolution of reproductive schedules and 3) incorporating season-specific responses to precipitation into population projection models to predict populations' response to climate change.

First, I test the hypothesis that seasonal variation in demography plays a greater role than annual variation in the population growth of *A. curassavica* using demographic data collected across multiple seasons and years from four populations of *A. curassavica* and life table response experiments (LTREs). I also test whether seasonal and annual variation contribute to temporal variation via distinct demographic pathways. Next, I test for seasonal patterns in reproductive costs and payoffs, and integrate these costs and payoffs into stochastic population projection models to examine how temporal variation in costs of reproduction to growth and survival influence the reproductive schedule of this species. Finally, I ask whether population-level responses to changes in precipitation vary among season, and then use demographic data in conjunction with historical and projected climate data to predict how these populations will response to the future climate of Monteverde.

An additional motivation for my research is to further to our understanding of ecological and evolutionary patterns in a region underrepresented by demographic literature. Demographic studies provide insight into how environmental variables influence components of species' life cycle, which influence population dynamics and evolution (Metcalf & Pavard 2007), and help us make accurate predictions for what to expect for these species in the future (Boyce *et al.* 2006). However, like many fields of ecology, our knowledge of demography is largely biased toward temperate species. The tropics contain an estimated 50 % of the world's plant species, but only 14% of demographic studies have been conducted in the tropics (Salguero-Gómez *et al.* 2015). As tropical plants face different conditions than temperate plants, such as higher competition, a greater diversity of herbivores and pollinators, and different seasonal patterns, what we know about temperate plants may not necessarily extend to tropical species (Kricher 2011).

This dissertation contributes to three major areas of ecology: population ecology, evolutionary ecology, and conservation ecology. The results and conclusions from this work encourage a new focus on seasonal variation in demography within the field, for both tropical and temperate species.

CHAPTER 2

THE INFLUENCE OF SEASONAL AND ANNUAL VARIATION IN DEMOGRAPHY ON POPULATION GROWTH OF A NEOTROPICAL MILKWEED, *ASCLEPIAS CURASSAVICA*[1]

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[1] Kellett, K.M. and R.P. Shefferson. To be submitted to *Journal of Ecology*.

Abstract

Plant demographers typically consider the impacts of temporal environmental variation at the annual scale on their study populations, but this scale may not accurately represent temporal variation in demography for species that reproduce throughout the year. For such species, we know little about how intra-annual variation affects population dynamics relative to inter-annual variation. We studied the population dynamics of *Asclepias curassavica*, a Neotropical milkweed, in Monteverde, Costa Rica, where rainfall varies seasonally. We monitored populations a total of 13 times, one every three months for three years (2011-2013), in 18 field sites, with 1270 total individuals monitored in order to examine how season (early dry, late dry, early wet, late wet) and year influence vital rates and population growth. We constructed function-based matrix models from Generalized Linear Mixed Models (GLMMs) describing vital rates (e.g. survival, growth, reproduction) to estimate temporal variation in population growth rate (λ), and then conducted Life Table Response Experiment (LTRE) analyses to elucidate the demographic processes responsible for seasonal and annual variation in λ. Best-fit GLMMs of vital rates included both seasonal variation and annual variation for all vital rates except survival, which depended only on season. LTRE analyses indicated that seasonal variation influenced λ about twice as much as annual variation and their interaction. The stronger influence of season was due to seasonal variation in λ driven by fecundity, stasis, shrinkage, and growth, while only fecundity and plant shrinkage drove annual variation in λ, with stasis acting as a buffer to variation in λ. We show that for species that lack of obvious seasonal patterns in flowering and fruiting, seasonal variation may be a stronger driver of population dynamics that annual variation, and that seasonal and annual variation in population growth may be governed by different aspects of demography. We emphasize the need to consider multiple time scales in demographic models to understand temporal influences on population dynamics.

Keywords: demography, population growth rate, temporal variation, life table response experiment, tropical seasonality

Introduction

Understanding how populations respond to temporal variation is a central goal of ecological research, especially as the global climate increasingly changes due to human influence (Parmesan 2006). Temporal variability in vital rates such as survival and reproduction and their subsequent contributions to population growth rate must be understood to predict the consequences of these changes on natural populations. Environments vary greatly among years due to stochastic processes, or large-scale climatic cycles such as El Niño. Within years, environmental variables such as temperature, precipitation, and wind speed vary, often in predictable seasonal patterns.

Long-term demographic studies emphasize the importance of inter-annual variation in vital rates to population dynamics of plants (Horvitz and Schemske 1995, Oostermeijer et al. 1996, Pfeifer et al. 2006, Horvitz et al. 2010). However, much remains to be learned about the influence of temporal variation on populations, as even data sets as long as 10 to 15 years may not accurately predict long-term dynamics if demography is driven heavily by weather conditions and variation in weather conditions is high (Bierzychudek 1999, Pfeifer et al. 2006, Jakalaniemi et al. 2013). Although the inclusion of annual variation in demographic models is now standard (Boyce *et al.* 2006), the vast majority of plant demography studies do not consider the effects of within-year variation on plant populations, with only about 10% of plant demographic studies monitoring populations more than once per year (Salguero-Gómez et al. 2015).

Studies of plants that do include two or more seasons generally use periodic matrices (COMPADRE Plant Matrix Database), which estimate annual population growth from seasonal matrices, and so do not directly compare the relative contributions of seasonal versus year to population growth. While periodic-matrices are appropriate for temperate plants, which often have a clear annual pattern in their life histories, many tropical plants do not exhibit annual patterns in their life cycles. For species that reproduce year-round, seasonal variation may be as – if not more – important than annual variation because conditions often vary more among season than among year (Vavrek et al. 1997). To the best of our knowledge, this is the first demographic study of a tropical plant that explicitly examines the relative contributions of among season and among year variation in demographic processes to population growth.

In temperate areas, where the vast majority of long-term demographic studies have taken place (Franco and Silvertown 1990, Salguero-Gómez et al. 2015) most plant species cease reproduction and severely slow above-ground growth during cold, resource-scarce winter months and grow, flower, and fruit during the growing season (Rathcke and Lacey 1985). Monitoring sessions for demographic studies generally occur only once per year during peak flowering because this is when we are best able to estimate reproductive rates, and because temperate plants species tend to produce just one generation per year, annual monitoring periods are assumed to capture all demographic transitions (Elzinga et al. 1998). However, this assumption may not be the case for all plant species.

In the seasonal Neotropics, warm temperatures and consistent day-length eliminate the need for seasonal dormancy, and up to one-third of plant species flower and fruit throughout the year despite drastic seasonal differences in rainfall (Croat 1978). In addition to predictable cycles of wet and dry seasons, these species experience generally unpredictable annual variation in total rainfall and the number of rainy days (Borchert 1998). Tropical plant populations are underrepresented in plant demography studies (Salguero-Gómez et al. 2015), and little is known about environmental drivers of plant population dynamics in Neotropical areas. A few demographic studies of Neotropical plants find substantial variation in vital rates and population growth among years (Horvitz and Schemske 1995, Bruna and Kress 2002), but since average precipitation in the seasonal Neotropics varies more among season than among year (Kricher 1999) variation in vital rates and population growth may depend more on season.

As population growth varies over time, the importance of different aspects of life history to population growth may also vary. For perennial species, fecundity tends contribute strongly to years with high population growth, while survival has greater importance when population growth is low (Oostermeijer et al. 1996, Menges and Dolan 1998, Franco and Silvertown 2004). However, patterns in the contribution of demographic processes to population growth may differ among sources, such as temporal and spatial (Jongejans and De Kroon 2005), and scales. A study on three different plant species showed that the way in which variation in specific demographic processes contributed to population growth differed between variation at the levels of site and region (Jongejans et al. 2010). We suggest differences may also exist at different temporal scales so that the vital rates that determine variation in population growth among years may differ from those that determine variation in population growth among seasons.

We examined how four populations of a common Neotropical milkweed, *Asclepias curassavic*a, respond to two types of temporal variation - seasonal and annual- in San Luis de Monteverde, Costa Rica. We tested the broad hypothesis that seasonal variation is a stronger influence than annual variation on population dynamics. Using demographic data from multiple seasons and years, we constructed generalized linear mixed models to model vital rates, used them to build integral projection models, and then conducted life table response experiments to test the following hypotheses: (1) temporal variation in vital rates will be driven more by season than by year, leading to (2) a larger contribution from season than year to temporal variation in population growth. We also examine how strongly and in what ways seasonal and annual variation in demographic processes (growth, shrinkage, stasis, and fecundity) contribute to temporal variation in population growth.

Methods

Study Species and site

Asclepias curassavica (Asclepiadaceae), hereafter *A.curassavica*, is an evergreen, iteroparous species (estimated 10-15 year lifespan) with a native range extending from Northern Argentina to Southern Mexico. It is the most common *Asclepias* species in the Neotropics and is distributed widely, found in in disturbed areas such as roadsides and pastures ranging from sea level to 2000 m a.s.l. (Zuchowski and Forsyth 2007). It has a limited suite of specialist herbivores due its highly toxic latex (Malcolm 1991).

Asclepias curassavica is an insect-pollinated, primarily outcrossing species, although some self-fertilization can occur (Wyatt and Broyles 1997). Importantly to our research questions, flowers and fruits are produced year round. Pollinators are primarily Nymphalidae butterflies. Fruits contain 70-110 seeds, which are distributed via wind. Seeds germinate within two weeks after dispersal and seed dormancy has not been observed (Kellett unpubl. data). Seedlings reach sexual maturity within six to nine months after germinating (Kellett, personal observations). Adult plants grow as single or multiple stems that increase in height with age. Individual stems typically live for 12 to 18 months. Individual plants may grow or shrink over time as stems grow and die. Individual stems do not shrink in size.

We studied *A.curassavica* populations growing in cow pastures around the University of Georgia Costa Rica campus and research station in San Luis de Monteverde, Costa Rica (N 10° 16.973' W 84°47.882'). San Luis de Monteverde is located in Northwest Costa Rica on the Pacific slope of the Corderilla de Tilarán, and has a seasonal moist forest climate. Monteverde experiences a distinct wet season (May-October) and dry season (November-April). At our field site, analysis of variance for historical daily rainfall data indicates a larger effect of season ($F=39.2$, $p<2\times10^{-16}$) than year ($F=16.79$, $p<4.4\times10^{-5}$) for four seasons over four years (2009-2013). The populations were located 1000-1200 m a.s.l., distributed over an area of about 3 km^2. Each population is in a different pasture and separated by a tract of secondary tropical forest, and all pastures are lightly grazed by 6-8 head of cattle.

Field Methods

In June 2011, we established 18 permanent plots distributed among the four *A.curassavica* populations. Plots contained at least ten plants and were generally 10 m × 10 m. Two corners of each plot were chosen as anchor points for triangulation to relocate individuals (Wells 1967). We monitored populations approximately every three months (July, October, January, and April) to represent a range of seasonal conditions (from very dry in January to very wet in October). Our data thus represent four seasons (early dry, late dry, early wet, and late wet,), and three full years (Aug 2011- to Aug 2014), totaling 1270 monitored individuals over 12 monitoring periods. During each monitoring period, we recorded presence/absence of individuals, each individual's size (total number of nodes); total number of inflorescences and fruits. Nodes are visible notches in stems where each pair of leaves attach, or previously attached, to the stem. As a stem grows, more nodes are added. Plants were added to the study when they appeared as seedlings in plots. We collected 25-40 seedpods per monitoring period from plants outside of demographic plots to estimate average seed production per fruit for each period.

We also established six germination plots, three in pasture habitats and three in edge habitats, outside of demographic plots to determine average germination rates and to test for seed dormancy. We established gardens consisting of 50 seeds in five rows with seeds spaced about three cm apart from one another. For each monitoring period, previous seed gardens were checked for seedlings, and a new garden was established.

Vital rate estimation

We calculated the vital rates from demographic data and compared them among seasons and year to gain a general understanding of seasonal and annual variation in these rates. We parameterized generalized linear mixed models (GLMM) from demographic data to predict individual vital rates – survival (σ) and growth (γ) between t and t+1, flowering probability (β) in time t, fruiting probability (θ) in t, and number of fruits (ω) in t –using the *glmer* function in the *lme4* package (Bates et al. 2014) in *R* 3.1.1 (R Core Team 2014). We used the binomial distribution for models of σ, β, and θ, and the Poisson distribution with an identity link for models of γ and ω, because number of nodes and number of fruits were both count data that did not include zeroes, and exhibited overdispersion. To test whether season and year were important predictors of vital rates, we parameterized a global model separately for each vital rate with fixed effects including size at time t given as the number of nodes (x), season (S), year (Y), and all interactions as fixed effects, and individual identity as a random effect. We used number of nodes as an index of plant size because it differences in vital rate functions better than other measures of size (height, number of stems, leaves). Although nonparametric models may provide better fits for ecological data (Perretti et al. 2013), GLMM-based matrix projection models conventionally use parametric regression models. To maximize fit of GLMMs to our data, we also tested models that included squared and cubic terms for plant size. We then took a backward stepwise regression approach and tested whether removal of factors in our model improved model fit using Akaike's Information Criterion (AIC) values. Following a conservative approach, we considered the best fit model in each case to the model with the lowest AIC, although models with fewer parameters and within two AIC units of the lowest AIC were considered equally parsimonious and used in inference, provided that model made biological sense within our system (Burnham and Anderson 2002).

Population Projection Models

We used the best-fit GLMMs to develop high-dimensional, function-based matrix projection models for each monitoring period, following an approach similar to integral projection models (Easterling et al. 2000) but using a discrete rather than continuous measure of size (number of nodes) (Shefferson et al. 2014). The size distribution of seedlings was described by a Gaussian distribution around mean seedling size Φ (y). Together, these functions describe all possible transitions from size *x* in one monitoring period to another size *y* in the next. Per Easterling et al. (2000), each transition was described by the kernel:

$$k(y,x) = p(x,y) + f(x,y) \qquad (1)$$

where

$$p(x,y) = \sigma(x,U)\gamma(x,y,U) \qquad (2)$$

describes survival and growth from size x in year *t* to size y in year *t*+1, and

$$f(x,y) = \beta(x,U)\theta(x,U)\omega(x,U)\upsilon\delta\xi\Phi(y) \qquad (3)$$

describes fecundity, or the probability of an individual of size *x* having an offspring of size y. We used υ = 85 ± 10 (SE), the mean number of seeds per fruit in our sampled fruits, and δ refers to the germination probability estimated from our germination field plots. We used the following equation to calculate establishment probability (ξ)

$$\xi = \frac{k}{qv\delta} \tag{4}$$

where k is the total number of recruits found in all four populations in $t+1$ and q is the total number of fruits counted in all four populations in t. In the survival, growth, and fecundity functions, U represents season or year.

The full model integrated over all sizes Ω is described by:

$$n(y, t+1) = \int_{\Omega} k(y,x)n(x,t)dx \tag{5}$$

This model was used to populate a 400 × 400 projection matrix separately for each season × year. Since we used a discrete measurement for plant size (nodes), we discretized the bins within our matrix so that each of the 400 bins incorporating a specific plant size from 1 to 400 nodes. Projection matrices were used to estimate the deterministic population growth rate (λ) for each season (early wet, late wet, early dry, late dry), and year (2011, 2012, 2013) as the dominant eigenvalue for each matrix (Caswell 2001). Population growth rates were bootstrapped to obtain confidence intervals. We sampled individuals randomly from our demographic data, with replacement, and then used the re-sampled data to construct new matrices and calculate new λ values 10,000 times. We used these data to calculate mean λ values and standard errors for all λ estimates, and tested for differences in λ among seasons and years by comparing 95% confidence intervals.

Life Table Response Experiments

We tested our hypothesis, that contributions of season to variation in population growth would be greater than those of year, by conducting life table response experiment (LTRE) analysis (Caswell 2001), and summing the total contributions of season and of year to variation in λ. A reference matrix was constructed by averaging all matrices, and then a two-way LTRE with year and season as factors was performed to assess the contribution of variation in matrix elements among seasons and years to overall variation in λ (Caswell 2001).

Our LTRE model was:

$$\lambda^{(sy)} = \lambda^{(\cdot\cdot)} + \alpha^{s} + \beta^{y} + (\alpha\beta)^{(sy)} \tag{5}$$

where $\lambda^{(sy)}$is the population growth rate for any combination of season (s) and year (y), $\lambda^{(\cdot\cdot)}$ is the mean population growth rate across all matrices, α^{s} and $\beta^{y}$are the main contributions of season and year, and $(\alpha\beta)^{(sy)}$is the contribution of the interaction. We performed this analysis using the *LTRE* function in the *popbio* package for *R* 3.1.1 (Stubben and Milligan 2007, R Core Team 2014).

We took the arithmetic mean of the absolute values for each of the main effects to compare the relative contributions of year, season, and their interaction. The effects of each season, year, and interaction were summed to compare individual contributions of specific seasons and years. Individual effects were split up into specific components of life history- growth, stasis, shrinkage, and fecundity – by summing elements within the LTRE matrix that corresponded with these demographic processes. Since survival is composed of growth, stasis, and shrinkage, we did not examine survival explicitly.

To test the hypothesis that seasonal and annual variation in λ were driven by different demographic processes, we tested for correlations in the net contributions of stasis, growth, regression, and fecundity from each year and season against the deviation of each $\lambda^{(sy)}$ from $\lambda^{(\cdot\cdot)}$ using the methods outlined in Jongejans and de Kroon (2005). We expected correlations between contributions and deviations in λ when demographic processes contributed consistently to variation in λ between seasons and years. We followed the same bootstrapping procedure as described for λ estimates, and calculated means and standard errors, and we compared 95% confidence intervals among LTRE statistics to test for statistical difference in mean effects.

Results

Vital rates

Growth (γ) and survival (σ) varied more among seasons than among years. (Figure 1.1). Size was a strong predictor of γ and σ, and best-fit models for growth also included a quadratic function of size. Including season as a factor in generalized linear mixed-models improved model fit for γ and σ. For γ, but not σ, including year as a factor also improved model fit (Table 1.1).

Fecundity varied more among year than among season (Figure 1.1). Size was a strong predictor of all fecundity rates, and best-fit models for all fecundity rates except number of fruits also included a size-squared term. The best fit model for β included all factors and all possible two-way interactions. For θ, the best fit model included all factors and interactions between size and year and season and year, while ω depended on size only (Table 1.1).

Periods with high germination also had high seedling survival, suggesting that factors boosting the former also boosted the latter. Germination rates were highest during early wet season (0.26 ± 0.15), and lowest during late wet season (0.03 ± 0.01). Total recruitment within demographic plots showed significant seasonal variation and was highest during early wet season (55.3 ± 4.6 seedlings) and lowest during late wet season (15 ± 9.7 seedlings). Recruitment varied less among year, but was lower in 2013 (28.8 ± 8.4 seedlings) than in 2011 (41.25 ± 14.1 seedlings) and 2012 (42.25 ± 4.53 seedlings).

Population growth rate

Differences in vital rates among seasons and years caused population growth rate estimates to vary. Deterministic population growth rate (λ) was significantly higher than $\lambda = 1$ during late dry season (1.14 ± 0.06; $t=237$; $p<0.05$) (mean±SE) and early wet season (1.10 ± 0.043; $t=233$; $p<0.05$), indicating periods of population growth, and lower than $\lambda=1$ during early dry season (0.99 ± 0.0; $t=-20.5$; $p<0.05$) and late wet season (0.87 ± 0.07; $t=184$; $p<0.05$), indicating periods of decline. Population growth rate varied much less among year than among season. In 2011 and 2012, mean λ was > 1 (1.06 ± 0.11 and 1.01 ± 0.10; $t=56,10$, $p<0.05$), and <1.0 in 2013 (0.99 ± 0.14; $p<0.05$).

Contributions to variation in λ

The mean effect of season (0.097 ± 0.01) was significantly higher than that of year (0.035 ± 0.01) and of the interaction between season and year (0.034 ± 0.009) ($t=444,450$, $p< 0.05$) (Figure 1.2), indicating that most of the temporal variation in λ comes from seasonal differences in demography. The contributions of year and the interaction of season and year did not differ ($t=6.3$, $p>0.05$). Each season had a relatively strong contribution to temporal variation in λ (Figure 1.3a), while contributions from each year were weaker (Figure 1.3b), and contributions from interactions of season and year were generally weak, with a few strong negative contributions (Figure 1.3c). The largest positive contribution to population growth was from late dry season. Strong negative contributions came from late wet season, and the interaction of late wet season and 2011, early dry season and 2012, and late wet season and 2013 (Figure 1.3). Confidence intervals (95%) indicated all contributions, except those from the interaction of 2012 and early wet and late wet season, were different from one another ($p<0.05$).

Variation in growth was the largest contributor to temporal variation in λ. Shrinkage and fecundity also played roles in influencing λ, and the contribution of stasis was generally low.

Demographic processes differed in their contributions in seasons with higher λ (Figure 1.4a). Demographic processes' contributions to λ varied among year. Negative contributions to population growth rate by demographic processes tended to be buffered, or compensated for, by positive contributions from other components across years (Figure 1.4b).

Seasonal and year-to-year variation in demography impacted population growth in different ways. Fecundity and growth contributed similarly to variation in λ among season and among year (Figure 1.5). However, shrinkage and stasis also contributed to seasonal variations in λ (Figure 1.5a), while a negative association between stasis and annual variation in λ indicates a buffering effect of stasis among years (Figure 1.5b).

Discussion

Demographic studies of plants generally include temporal variation only at an annual scale, but because population dynamics of some species may depend more heavily on *variation* within years, understanding the relative importance of inter versus intra annual variation in demography is critical to understanding the population dynamics of such species. Our study asked whether two aspects of temporal variation – season and year –have important and distinct influences on the population dynamics of a common Neotropical herb. We found that vital rates were better predicted by models that included both scales than by those that included just one, that season contributed substantially more than year to overall temporal variation in population growth rates λ, and that season and year influence λ via separate demographic pathways.

Much work in the Neotropics emphasizes strong seasonality in reproductive phenology (Borchert 1998, Sakai et al. 2005). Indeed, inter-annual variation in rainfall patterns drives flowering and fruiting peaks in some tree species to a great enough extent for climate change to have a devastating impact on animal species that depend on them for food (Corlett and Lafrankie

Jr 1998). However, studies on seasonal variation in reproductive rates of tropical plants are rarely translated into population dynamics. Although we did not observe seasonal peaks in flowering and fruiting, our life table response experiments (LTRE) results indicated that seasonal variation in overall fecundity played an important role in driving variation in population growth, showing that seasonal patterns can be present even when undetectable in raw field data. These "hidden" patterns are the result of variation in overall fecundity (a combination of flowering and fruiting probability, and number of fruit) and sensitivity of population growth to these rates. A lack of observable reproductive peaks indicates that effective pollinators for this species are present year-round (Elzinga et al. 2007), consistent with its generalist pollination strategy (Bierzychudek 1981), and the lack of seasonality in polinia removal (Kellett, unpublished data).

Unlike flowering and fruiting rates, seasonal patterns in survival were obvious in raw data. The striking pattern of high, relatively invariant mortality during the late wet season is likely due to an increase in "catastrophic deaths," or sudden, unpredictable deaths to plants via some environmental factor, rather than an increase in senescence-related deaths during this period. The late wet season experiences extremely heavy rainfall and storms that can knock branches from trees, and temporarily inundate pastures when soil becomes saturated. Individuals, especially small plants, may have a difficult time surviving these conditions. For example, "catastrophic mortality" in Neotropical trees and mortality-driven drops in population growth rate have been documented during hurricanes (Lugo and Scatena 1996, Pascarella and Horvitz 1998). Stress caused by heavy rainfall may impact plants into the early dry season, causing low growth and survival rates we observed during this season as well. "Type" of mortality has been shown to have important demographic consequences for forest trees (Holzwarth et al. 2013), and we suggest that deaths caused by torrential downpours have especially large consequences for population growth, as they can remove healthy, reproductive individuals from the population.

Some demographic studies have considered the impacts of temporal variation in climatic variables for populations of Neotropical plants. For example, dramatic annual variation in vital rates and λ linked to annual rainfall has been noted in a bromeliad population (Mondragón et al. 2004). Our study builds on this previous work by demonstrating the impact on λ of temporal variation in demography at multiple scales. Since the impact of season is large relative to year, the populations varied in demographic performance more similarly among season than among year. This likely occurs because the environmental variation among seasons was generally greater than among year so that variation in vital rates caused directly by seasonal fluctuations in climate overwhelms variation caused by other factors, such as site, and this occurs to a lesser extent among years. Season may also contribute more to temporal variation in λ because the minimum generation time of *A. curassavica* is relatively short (four to six months), linking it strongly to the seasonal timescale.

Work on temperate species has shown that variation in λ over different spatial scales (e.g. region *vs.* site, site *vs.* microsite) occurs via different demographic pathways (Miller et al. 2004, Jongejans et al. 2010). We emphasize the same point for temporal scale. Correlation plots suggest the stasis and shrinkage may respond to different ecological drivers or to the same drivers but over different time scales in our study population, while the ecological factors driving fecundity and growth may operate similarly across temporal scales. Across seasons and years, growing and maintaining size results in higher population growth, likely due to increased survival at larger sizes. Across seasons, shrinkage also appeared to support increased population growth rate, suggesting that it may be an adaptation to predictable temporal patterns in stress (Salguero-Gómez & Casper 2010).

Although season contributed much more to variation in λ, annual impacts of demographic processes on population growth rate were uniquely important. Compensation that occurs between demographic processes may result from trade-offs in resource investment (Jongejans & de Kroon 2005). Our observation that demographic buffering is more apparent in the effects of year than in season may be because the costs of investing in growth or fecundity take longer than one season to manifest within individuals. The annual time scale allowed us to see such buffering patterns that were not apparent when examining seasonal LTREs.

Implications for Neotropical plant populations

Our study populations of *A. curassavica* demonstrated relatively stable population growth. However, climate change may impact this population in the future. In the Neotropics, the strongest effects of climate change are changes to rainfall patterns. Dry seasons are increasing in length, and rainfall events during wet seasons are becoming more extreme and irregular (a few intermittent, but intense periods of rainfall rather than steady, but light rainfall) (Hulme and Viner 1998). The impacts of these changes on population dynamics of Neotropical plants are poorly understood because the importance of seasonal rainfall patterns to population dynamics has not previously been examined. Seasonal patterns in the Neotropics have population-level impacts, even for organisms that exhibit year-round reproduction. Intense rainstorms likely cause "catastrophic deaths" and therefore an increase in extreme rainfall events could result in population decreases. However, because populations showed the highest growth during the end of dry season, an extended dry season may counteract negative impacts of heavy rainfall events.

Organisms have been shown to exhibit different responses in traits such as range size (Rivrud et al. 2010) and abundance (Crumley 2007) to environmental variation occurring at different time scales, and we suggest that population dynamics are driven by demographic response to environmental variation over multiple time scales. We suggest that plant demographers should not only consider the effects of temporal variation set on just an annual scale, but also scales that coincide with generation time of their study species (which may be shorter or longer than one year), and effects that take place over a time scale that includes multiple generations of plants. This may be particularly important for any demographers working with species without distinct seasonal patterns in vital rates.

Table 2.1. Factors included in best fit models for each vital rate and their AIC weights. Weights are calculated based on AIC values from all possible models generated from the global model (all factors and all interactions).

Demographic Function	***Fixed Factors in Best-Fit Model***	***AIC Weight***
Survival (σ)	size ,size^2, season, year, season×year, size×year	0.26
Growth (γ)	size, size^2,season, year, all interactions	0.55
Probability of Flowering (β)	size, size^2, season, year, all 2-way interactions	0.70
Probability of Fruiting(θ)	size, size^2, season, year, season×year	0.45
Number of fruits(ω)	size, season, year, all interactions	0.95

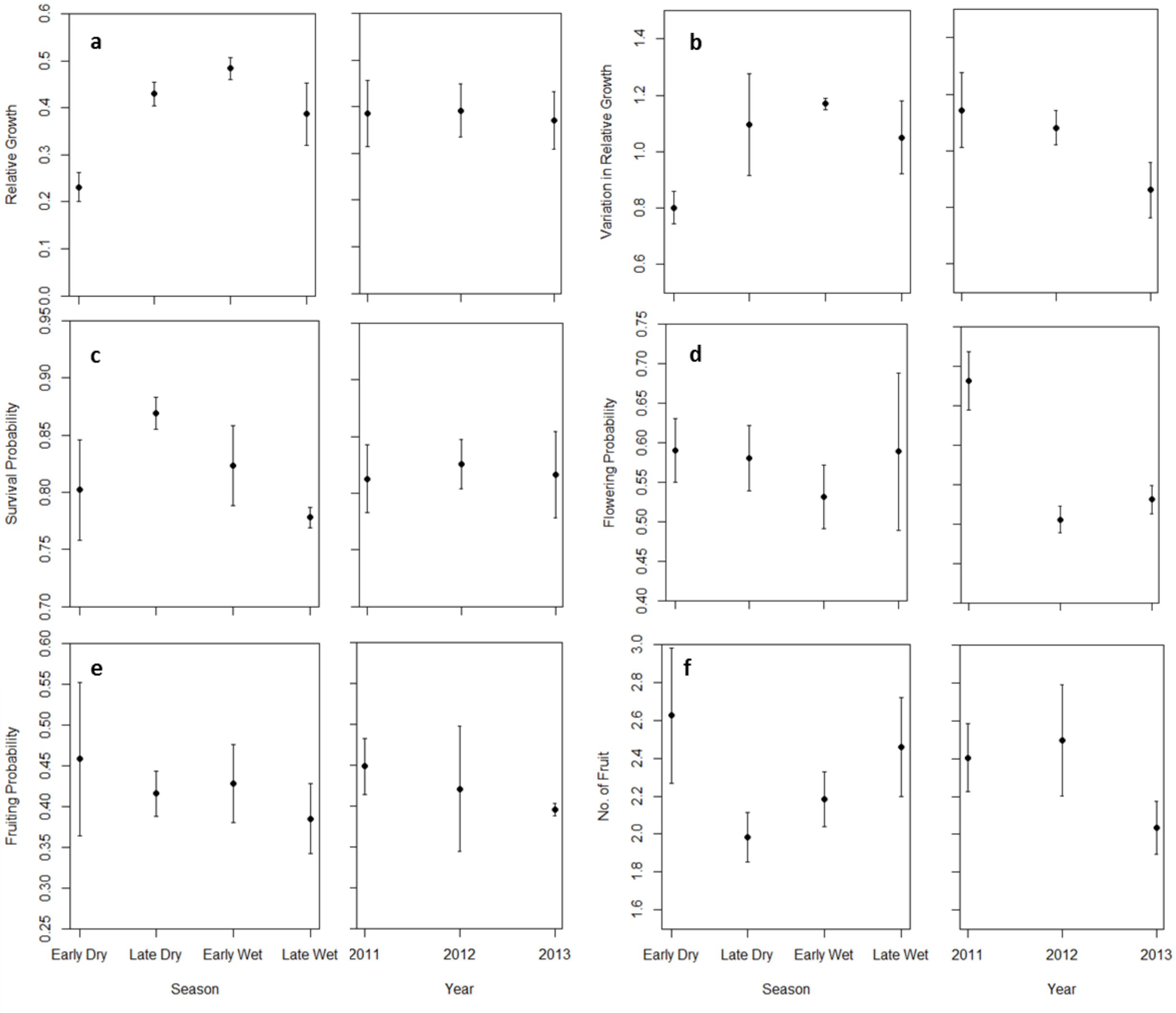

Figure 2.1. Mean vital rates for each season and year in our study. Seasonal patterns in survival (c) and growth (a,b) are present. Error bars show standard error among individuals.

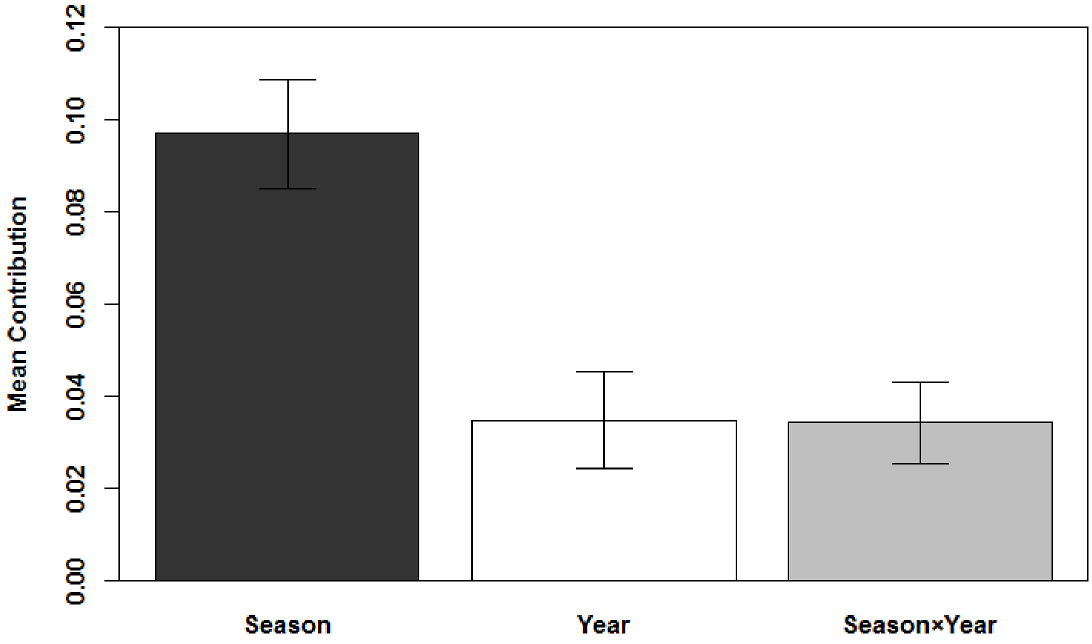

Figure 2.2**.** Contributions (means of absolute values) from season, year, and their interaction in a two-way life table response experiment (LTRE) analysis of temporal variation in population growth rate (λ) between the population projection models for four seasons and three years, showing the largest contributions to temporal variation in λ comes from seasonal variation. Error bars indicate standard errors, calculated from bootstrapped values, for each year, season, and interaction.

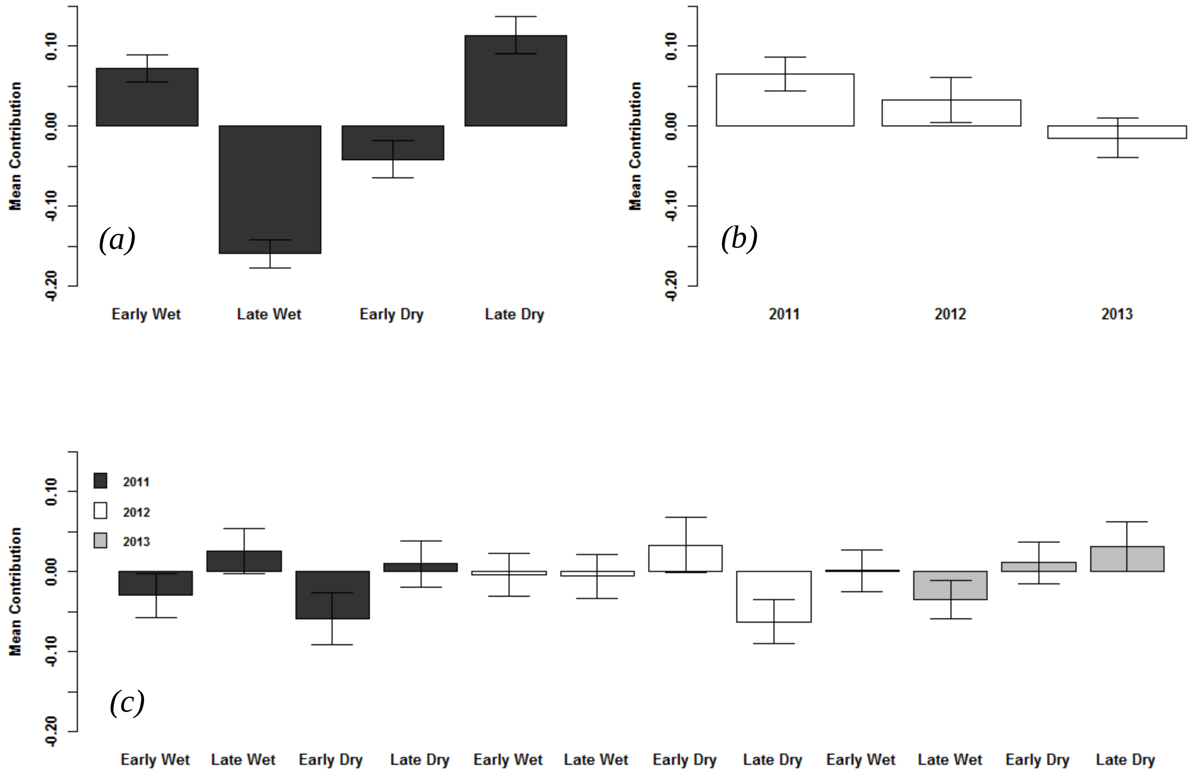

Figure 2.3. Net LTRE contributions of each season (a), year (b), and interaction (c). Bars above zero indicate net positive contributions, while bars below zero indicate net negative contributions. Error bars indicate standard errors, calculated from bootstrapped values.

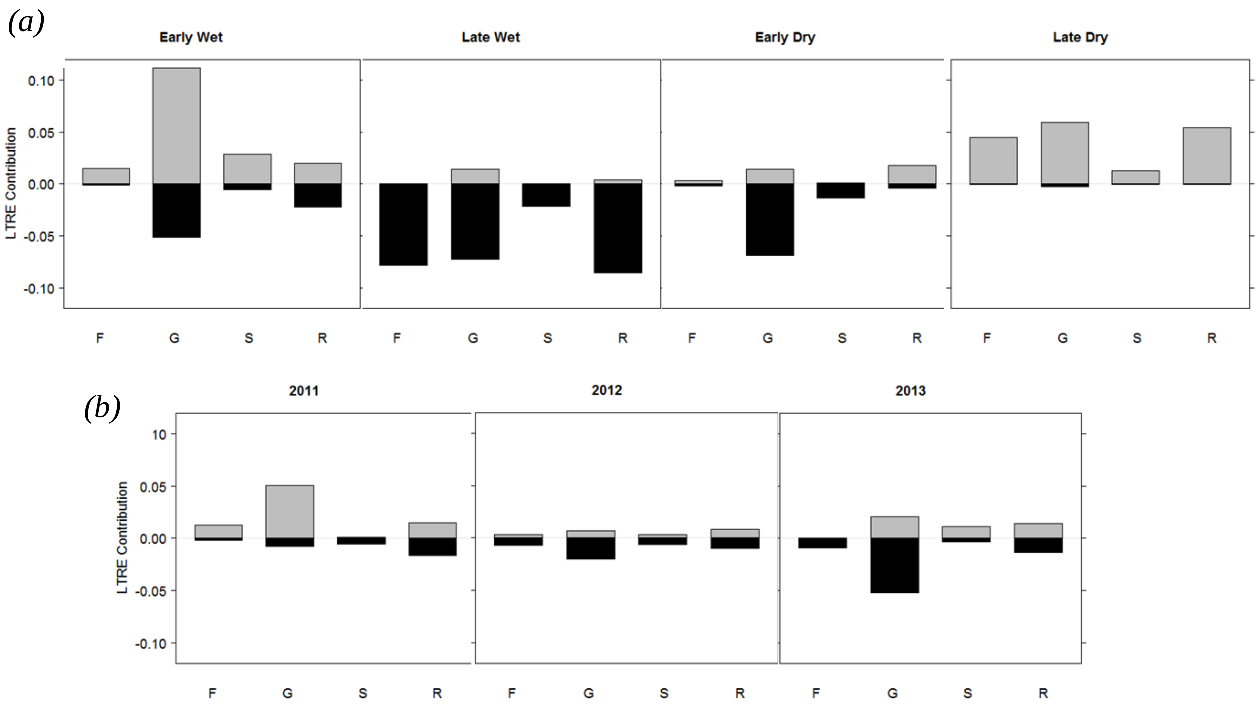

Figure 2.4. LTRE Contributions of demographic processes to variation in population growth. Positive (grey bars) and negative (black bars) contributions of seasons (a) and years (b), grouped by four demographic processes. The demographic processes are fecundity (F), growth (G), stasis (S), and shrinkage (R).

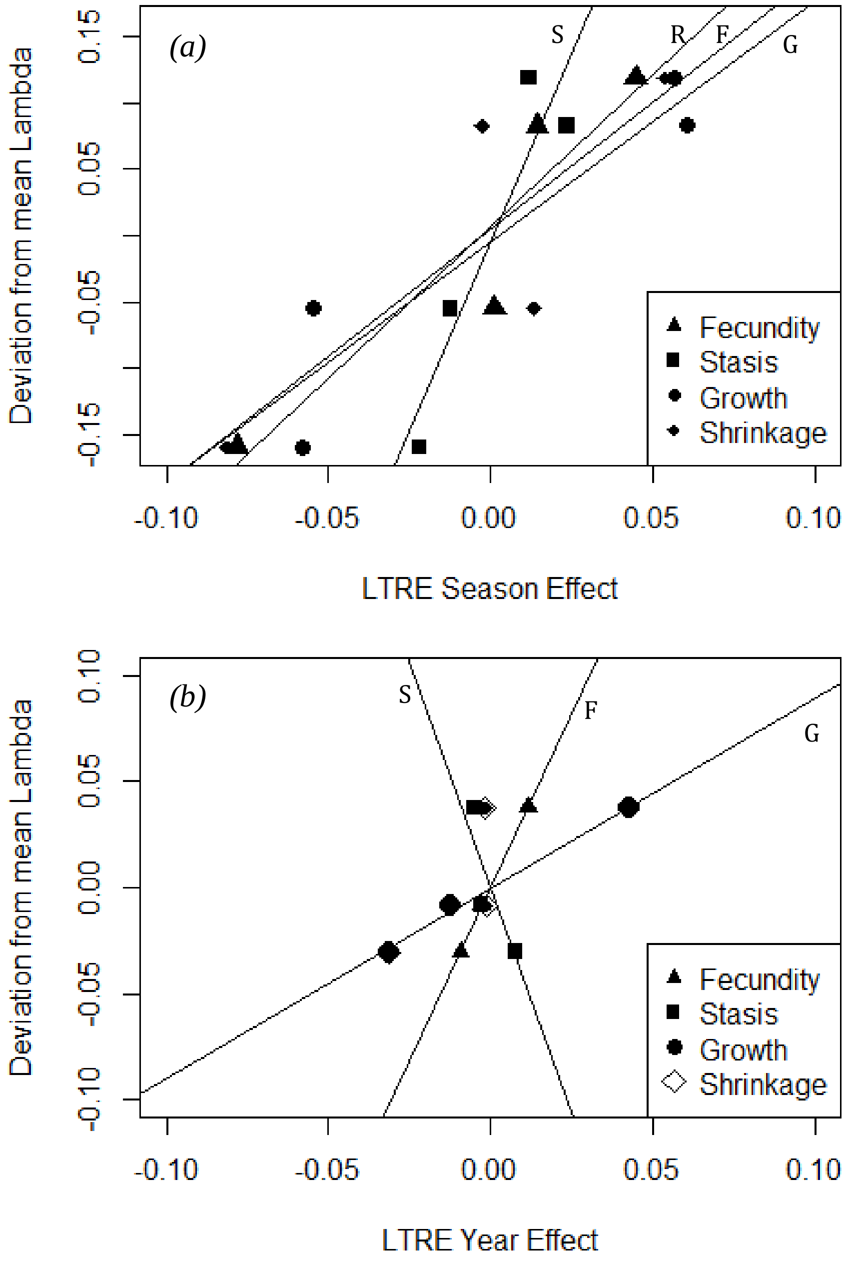

Figure 2.5 Correlation diagrams between variation in population growth rate and variation in four demographic processes (F, G, S, R; See Fig. 3). LTRE contributions, summed and grouped by four vital rates (F, G, S, R) are plotted on the x-axis, and deviation from mean population growth rate is plotted on the y-axis, for main effects of each season (a) and year (b). Filled-in symbols and trend lines indicate strong correlations ($R^2 > 0.75$).

CHAPTER 3

TEMPORAL VARIATION IN REPRODUCTIVE COSTS AND PAYOFFS SHAPE THE FLOWERING STRATEGY OF A NEOTROPICAL MILKWEED, *ASCLEPIAS CURASSAVICA*[1]

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[1] Kellett, K.M. and R.P. Shefferson. To be submitted to *Evolutionary Ecology*.

Abstract

A central goal of evolutionary ecology is to understand the factors that select for life history strategies, such as delaying reproduction. Environmental variation and reproductive costs to survival and growth have been shown to select for reproductive delays in semelparous and iteroparous species, respectively. In this study, we examine how variation in reproductive cost, which we define as a reduction to growth, survival, or future reproduction, may select for reproductive delay in an iteroparous Neotropical milkweed. We analyzed demographic data collected every three months for three years from populations of *Asclepias curassavica* in Monteverde, Costa Rica. We detected costs of flowering to survival and growth that varied in magnitude among our twelve monitoring periods without a seasonal pattern. The populations also exhibited temporal variation in reproductive payoffs measured as seedling establishment. We incorporated these reproductive costs into demographic projection models, which predicted a delayed flowering strategy only when we included temporal variation in costs and payoffs. This study highlights the importance of variation in reproductive costs and payoffs as a selective force in the evolution of delayed flowering in iteroparous species, and suggests that a lack of predictable seasonal pattern to reproductive costs and payoffs, may contribute the evolution of the year-round reproductive strategy of our study species and other Neotropical species with year-round reproduction.

Keywords: Reproductive costs, stochastic population models, optimality models, life history evolution, demography

Introduction

Understanding the selective factors that shape life history schedules has been a long-standing goal of evolutionary ecology, and has increased in importance and relevance as human activities and climate change alter these selection pressures (Mangel 1994, Crozier et al. 2008). Investment in reproduction results in offspring production, a payoff, but carries a necessary cost to investment in traits related to survival, or growth (Cody 1966). If costs to reproduction did not exist, organisms would reproduce as soon as they possibly could, as many times as they could (Roff 2002), leading to a Darwinian Demon (Law 1979). Understanding why species reproduce when they do requires assessing the costs and payoffs of reproducing and, importantly, how they vary with the environment (Boyce 2006). When variability in reproductive costs and payoffs are unaccounted for or misrepresented, evolutionary models may be inaccurate and contradict our understanding of theoretical life history trade-offs (Reznick et al. 2000). Various studies have shown how temporal variability influences life history evolution of semelparous plants (species that reproduce one time) (Childs et al. 2010), and including reproductive costs in demographic models has accurately explained flowering size in an iteroparous (reproduces multiple times) orchid (Miller et al. 2012). However, how temporal variability in reproductive costs may influence the life history schedule of some iteroparous plants remains unresolved.

Costs and payoffs of reproduction vary depending on the age or size of the individual, and demography-based models can account for this variation to examine how it shapes life histories (Metcalf and Pavard 2007). For semelparous plants, the ‘decision’ to reproduce removes the chance for future reproduction. This lethal cost of reproduction is easily incorporated into demographic models, and optimal size for reproduction can be predicted by such models (Wesselingh et al. 1997, Metcalf et al. 2003). Although iteroparous plants have multiple chances to reproduce, they also delay flowering, likely because reproducing carries costs to growth and/or survival so that reproducing too early decreases lifetime fitness (Proaktor et al. 2008). Because the number of offspring produced increases with parent size in many plant species, delaying reproduction until reaching an optimal size may maximize fitness despite the costs in terms of increased chance of death before reproduction that are incurred by this delay (Bell 1980, Stearns and Crandall 1984). Understanding the relationship between size and vital rates allows us to assess the costs and payoffs to delaying reproduction (Kozłowski and Wiegert 1986, Stearns 1992). Although they can be difficult to detect, and are more complicated to measure than the lethal reproductive cost in semelparous species, the costs of reproduction to survival and/or growth in iteroparous species are well supported in the empirical and theoretical literature (Obeso 2002) and can be modeled to help predict an optimal size at reproduction for iteroparous plant species (Miller et al. 2012).

Reproductive costs and payoffs, however, are not dependent only on an individual's state, but also vary with environment. This variation may change the magnitude and direction of selection on strategies throughout time and space (Orzack 1993, Childs et al. 2010). While incorporating temporal variation has improved IPM-based predictions of optimal flowering size in several semelparous plants (Childs et al. 2004, Rees et al. 2006, Rees and Ellner 2009), similar models for iteroparous plants would require additional estimates of temporal variation in reproductive costs, which though represented in the literature (Primack and Hall 1990, Sletvold and Ågren 2011, 2015), have not yet been incorporated into models predicting life history schedules. Thus understanding of the life histories of iteroparous plants lags behind that of semelparous plants (Miller *et al.* 2012) . In general, reproductive costs should be low or unapparent in resource rich environments because resources do not constrain allocation to opposing life history components, and more apparent in poorer environments (Horvitz and Schemske 1988). For example, in the terrestrial orchid *Orchis purpurea*, reproductive costs are lower in light environments than shady environments, possibly resulting in threshold flowering sizes in shady environments three times as large as those in light environments (Jacquemyn et al. 2010).

The seasonal Neotropics represent a particularly useful environment in which to examine variation in reproductive costs and payoffs, and its resulting effects on life history schedules, because up to 30% of Neotropical plant species exhibit year-round flowering and fruiting (Croat 1978). Yet little work has been done to investigate how intra-annual variation may influence the reproductive schedule of these species.

In previous work, we found significant variation in flowering and fruiting across seasons and years with no obvious seasonal patterns, but did find seasonal patterns in germination and seedling recruitment (Kellett and Shefferson 2015). As theory predicts that strong seasonal patterns in costs and payoffs in reproduction should result in discrete reproductive seasons (Roff 2002), species with year-round reproduction, such as *A. curassavica*, may experience lower reproductive costs during seasons when the payoff for investing in reproduction is also low.

In this study, we used demographic data from twelve, three-month-long, monitoring periods to examine how temporal variation in costs and payoffs in reproduction shape the life history schedule of a long-lived plant that reproduces year-round. We addressed the following questions: 1) In which vital rates (survival, growth, future reproduction) are costs of reproduction apparent? 2) How do reproductive costs and payoffs vary temporally? And 3) How does temporal variation in reproductive costs and payoffs influence flowering size? We hypothesized that if there are seasonal patterns in reproductive costs and payoffs, costs of reproduction will be lower when reproductive payoffs are also low, to favor a year-round reproductive strategy. We expected that accurate predictions of optimal flowering size require accounting for temporal variation in reproductive costs and payoffs.

Methods

Study species and data collection

Asclepias curassavica (Asclepiadaceae), hereafter *A. curassavica,* is an evergreen perennial species with a native range extending from Northern Argentina to Southern Mexico. It is the most common *Asclepias* species in the Neotropics and is distributed widely, found in in disturbed areas such as roadsides and pastures ranging from sea level to elevations of 2000m above sea level. *A.curassavica* grows as single or multiple stems, and individual stems typically live for 12 to 18 months, while we estimate that individual plants may live up to ten or fifteen years. Individual plants may grow or shrink over time as stems grow and die (Kellett, unpublished data). It has a limited suite of specialist herbivores due its highly toxic latex (Malcolm 1991). *A.curassavica* is an insect-pollinated, primarily outcrossing species, although some self-fertilization can occur (Wyatt and Broyles 1997). Flowers and fruits are produced throughout the year. Fruits contain 70-110 seeds, which are wind-dispersed. Seeds germinate within two weeks after dispersal, and we did not observe evidence of seed dormancy. Seedlings usually reach sexual maturity within six to nine months after germinating (Kellett, personal observations).

We studied *A.curassavica* populations growing in four cow pastures around the UGA Costa Rica campus and research station in San Luis de Monteverde, Costa Rica (N10° 16.973’ W84° 47.882’) (http://www.dar.uga.edu/costa_rica/). San Luis de Monteverde is located in Northwest Costa Rica on the Pacific slope of the Corderilla de Tilarán, and has a seasonal moist forest climate. The populations were located between 1000m and 1200 m.a.s.l., distributed over an area of about 3 square kilometers.

Field Methods

In June 2011, we established 18 demographic plots within four *A.curassavica* populations. Plots were chosen to equally represent pasture and edge habitat types, and were generally 10m x 10m. Two corners of each plot were chosen as anchor points for triangulation, which was our method to identify individuals across time (Wells 1967). We monitored populations approximately every three months (July, October, January, and April). We recorded each individual's reproductive status. Reproductive (*R*) plants had flowers, fruits, or both, while vegetative (*V*) plants had neither. We also recorded total number of nodes, total number of inflorescences, and total number of fruits. Nodes are visible notches in stems where each pair of leaves attach, or previously attached, to the stem. As a stem grows, more nodes are added. We collected 25-40 seed pods per monitoring period from plants outside of demographic plots to estimate average seed production per fruit for each monitoring period. In total we monitored populations in four seasons (early dry, late dry, early wet, and late wet), for three full years (2011-12, 2012-13, and 2013-14) hereafter referred to as 2011, 2012, and 2013. We collected data from a total of 1270 individuals over 12 monitoring periods (denoted A-L, with alphabetical representing chronological order).

Detection of Reproductive costs

We defined reproductive costs as reductions in vital rates (survival from year t to t+1, growth from year t to year t+1, and flowering & fruiting probabilities in year t+1) for reproductive individuals, as compared to vegetative individuals of the same size. We tested for costs of reproduction to vital rates via generalized linear mixed-models (GLMMs), with size (number of nodes) as a fixed factor and site as the sole random factor, by assessing whether adding reproductive status (*R* or *V*) as a predictor improved each model's fit, and if so, whether a status of *R* had a negative influence on vital rates. We constructed twelve separate models using data from each of the twelve monitoring periods. We limited our data set to plants smaller than 125 nodes to eliminate influence of the largest reproductive plants on the models because all plants over 125 nodes in size tend to be reproductive. In GLMMs predicting probability of survival, fruiting, and flowering, we assumed a binomial distribution, and we assumed a Poisson distribution for the growth model, since plant size was estimated by count data (number of nodes), and mean size was about equal to variance.

We compared AIC values among candidate models for vital rates in each of the twelve monitoring periods. Candidate models included a null model, which did not include reproductive status as a factor, a model that included the main effect of reproductive status, and a model that included the main effect of reproductive status and its interaction with size. For survival and growth, we constructed models that included reproductive status in monitoring period $t-1$, t, and $t+1$ as factors, as well as each combination of these time periods, in case costs of reproduction were time-lagged. For flowering and fruiting probabilities, we only included reproductive status in year t and $t-1$. For growth models, a squared term for plant size was also included as a factor, because our previous work had shown this term to improve model fits. Due to limited data, we were unable to soundly test for additional costs of fruiting for reproductive plants in individual monitoring periods. Instead, we pooled data from all monitoring periods and tested for costs of fruiting for reproductive plants within the entire data set. We tested for costs of fruiting in a similar manner as described above, except using fruiting status (fruiting or just flowering) as a factor instead of reproductive status. For each demographic rate and each monitoring period, we selected the model with the lowest AIC value as the best-fit model, unless a model with fewer parameters was within two AIC units (Burnham and Anderson 2002). We considered reproductive costs present if the best fit models 1) included a reproductive status factor and 2) reproduction resulted in reduced predicted values via negative impacts on the intercept and/or slope of a model.

We pooled size data from all monitoring periods together and followed a bootstrapping procedure, and resampled these data 10,000 times. To test whether flowering sizes in periods with costs of reproduction were larger than those without costs, we then compared mean size of reproductive plants and their 95% confidence intervals between monitoring periods with and without reproductive costs.

Construction of Population Projection Models

We used best fit models for vital rates to develop life history function-based matrix projection models for each monitoring period. Each model included demographic functions that predicted probabilities of survival ($\sigma(x)$), growth ($\gamma(y,x)$), flowering ($\beta(x)$), and fruiting ($\theta(x)$), as well as the number of fruits ($\omega(x)$), as functions of plant size (x), and reproductive status (R), if reproductive costs were apparent, per each respective best-fit model. The size distribution of seedlings was described by a Gaussian distribution around mean seedling size Φ (y). Together, these functions describe all possible transitions from size (x) in one monitoring period to another size (y) in the next. Per Easterling et al. (2000), each transition was described by the kernel:

$$k(y,x) = p(x,y) + f(x,y) \qquad (1)$$

where

$$p(x,y) = s(x,R)g(x,y,R) \qquad (2)$$

describes survival and growth from size x in year t to size y in year t+1, and

$$f(x,y) = \beta(x,R)\theta(x,R)\omega(x,R)\upsilon\delta\xi\Phi(y) \quad (3)$$

describes fecundity, or the probability of an individual of size x having an offspring of size y. We used υ = 85 ± 10 (SE), the mean number of seeds per fruit in our sampled fruits, and δ refers to the germination probability estimated from our germination field plots. We used the following equation to calculate establishment probability (ξ)

$$\xi = \frac{k}{q\upsilon\delta} \quad (4)$$

where k is the total number of recruits found in all four populations in $t+1$ and q is the total number of fruits counted in all four populations in t. We used ξ as a measure of reproductive pay-offs. Probability of fruit production is another possibility for measuring reproductive payoffs, but since we did not find costs to investing in fruit, and fruit production was not correlated with number of seedlings produced, we considered probability of seedling establishment as the best proxy for reproductive payoff . For functions ($g(x)$) describing vital rates that included R, functions were weighted by probability of flowering (β) such that:

$$g(x) = g_V(x)\big(1-\beta(x)\big) + g_R(x)(\beta(x))$$

where g_V describes the function for vegetative plants, and g_R describes the model for reproductive plants.

The full model integrated over all sizes Ω is described by:

$$n(y,t+1) = \int_\Omega k(y,x)n(x,t)dx \quad (4)$$

This integral projection was used to populate a 400 x 400 projection matrix separately for each monitoring period. Since we used a discrete measurement for plant size (nodes), we discretized the bins within our matrix so that each of the 400 bins incorporating a specific plant size from 1 to 400 nodes.

Stochastic and time invariant simulations

We then performed seasonal-stochastic population simulations by randomly selecting a matrix from among the three possible matrices for each season, but following a seasonal order, for 10,000 time steps. We took this seasonal approach because our previous work indicated strong seasonal patterns in survival and growth. The last 7,000 time steps were used to calculate stochastic population growth (λs). We calculated λs for four different scenarios to evaluate the role of temporal variation in reproductive costs and payoffs on fitness. First, we conducted simulations exhibiting no costs to reproduction (i.e. vegetative and reproductive plants exhibited the same vital rates) and all parameters were allowed to vary. Next, we conducted a fully stochastic simulation, in which reproductive costs and seedling establishment (payoffs) were allowed to vary with each monitoring period. Third, we conducted a time invariant reproductive costs simulation in which reproductive costs were held constant at the value estimated by GLMMs for survival and growth constructed from data across all monitoring periods for each monitoring period, but all other parameters were allowed to vary. Our final simulation had time invariant payoffs - we held seedling establishment rate constant at the mean establishment rate for all monitoring periods, and allowed all other parameters to vary.

Life history optimization

To calculate optimal size at reproduction for each of the four scenarios described above and to test whether including temporal variation in costs and payoffs improves predictions of optimal flowering size, we estimated an adaptive landscape over a range of values for intercept of the probability of flowering function. As a proxy for fitness, we used λs. We optimized λs over the intercept of the flowering function $\beta(x)$ while holding all other parameters constant, per Miller et. al. (2012). For each model, we ranged the intercept between values that resulted in flowering probabilities under 1% for all sizes and over 99% for all sizes. Lower intercept values result in larger mean flowering sizes, and values for the intercept that result in the highest values for λs represent the optimal flowering strategy. We optimized intercept values for each monitoring period, individually. We then determined at which seedling establishment values fitness was at an optimal value for the observed intercept value.

Results

Temporal variation in reproductive costs

We detected costs of reproduction to growth and survival in some monitoring periods, but costs did not vary seasonally. We did not detect any costs of reproduction to future probability of flowering or fruiting. For monitoring periods in which we detected reproductive costs, including reproductive status in time t as a factor improved model fit, while status at time $t-1$ and $t+1$ did not, indicating no time lag in costs. Among monitoring periods, including fruiting status as a factor did not improve model fit for any vital rates (Table 1.1).

We found costs of reproduction to survival in two of the twelve monitoring periods, D and G. Costs were not detected for all sizes within these time periods, however. In D, the main and interaction effects of reproductive status resulted in higher survival for small, reproductive plants but lower survival for large, reproductive plants in comparison with vegetative plants. Contrastingly, in G, small, vegetative plants showed a survival advantage over reproductive plants, but had lower survival after reaching larger sizes (Figure 3.1).

We detected costs of reproduction to growth in seven of the twelve monitoring periods. Monitoring periods in which we detected costs included A, B, E, F, G, H and L. Four of these periods (E-H) were all during the second year of our study. Among monitoring periods with reproductive costs, the magnitude of these costs varied, and generally appeared as a reduced slope of growth for reproductive plants, so that vegetative plants of the same size grew faster.

Intercept values for vegetative plants were usually lower than those of reproductive plants, resulting in lack of reproductive costs for very small plants. In most monitoring periods, smaller plants tended to grow, while larger plants shrank in size. However, in A and G large vegetative plants also grew, while large reproductive plants shrunk. In H, both vegetative and reproductive plants grew at large sizes. For monitoring periods with reproductive costs, reproductive plants tended to grow less, and shrink more than vegetative plants, except for very small plants (Figure 3.2).

Temporal variation in reproductive pay-offs and observed flowering sizes

Probability of seedling establishment (ξ) varied greatly among monitoring period, and ranged from 0.0021 to 0.051. Mean probability of seedling establishment was lowest during late wet season, but was not significantly different from other seasons ($t=-1.9, p>0.1$) due to high variation in ξ among years. The other three seasons had similar values for ξ (Figure 3.3), and ξ did not differ between periods with costs (0.023±0.0062) (mean±SE) and without costs(0.029±0.0056) ($t=-0.70, p=0.5$). We found that average size of flowering plants tended to vary from one monitoring period to the next, with no clear seasonal pattern. Mean flowering size during monitoring periods with reproductive costs (51.5±0.53) was higher than mean flowering sizes during periods without reproductive costs (47.4±0.48) ($t=5.4$, $p<0.05$) (Figure 3.4).

Optimization of flowering size

Fitness plots varied greatly among the four different simulations we examined. Fitness values produced by the models ranged from 0.98 to 1.07. When reproductive costs were excluded, fitness was highest when the flowering function intercept was highest (i.e. optimal flowering size was very small), as expected. In the fully stochastic simulation (reproductive costs and payoffs varied), fitness was highest when the flowering intercept was 3.5 under the observed value, and lowest between 0.25 and 1 over the observed value. However, the range of fitness values produced was relatively small compared to that produced by other simulations. In the time invariant reproductive *costs* model, fitness was highest when flowering intercept values were highest, and a similar pattern was observed in our time invariant reproductive payoffs model, indicating that plants should flower at the smallest possible size when costs and payoffs do not vary throughout time (Figure 3.5).

Discussion

Temporal variation in costs and payoffs in reproduction has helped shape the life history schedule of a long-lived tropical plant with year-round reproduction. Environmental variation alone can cause the evolution of delayed reproduction in some species (Tuljapurkar 1990), but when adults have higher survival than juveniles, as is the case for most iteroparous plants, the evolution of delayed reproduction can only be driven by environmental variation when it is much higher than in most natural environments (Koons et al. 2008). It therefore may be more likely for reproductive delays in iteroparous plants to be driven by the presence of reproductive costs to growth and survival (Miller *et. al.* 2012). In our study however, the presence of cost alone did not select for delayed flowering, as it favored flowering at very small sizes. Only when variation in costs and payoffs were included did our model favor a delayed flowering strategy. This suggests that the life history schedule of this species evolved as a response to selection determined by both the potential for costs to reproduction and the variation in them.

In nature, environments vary over time, driving vital rates and population growth. Assuming constant, mean conditions for demographic analysis sometimes results in inaccurate predictions (Boyce et al. 2006). Although *Miller et al.* (2012) were able to accurately predict flowering size without including temporal variation for an orchid using mean costs from across years, for other species, such as *Asclepias curassavica*, demographic costs to reproduction may only exhibit selective pressure on flowering size when allowed to vary throughout time. In our study, costs of reproduction varied greatly, and were not always present. In species with such high variation in costs, including this variation in demographic models may be particularly important, as periods with high costs may disproportionately impact fitness.

Our study may help explain why many Neotropical species, such as *A.curassavica*, do not exhibit discrete reproductive seasons, despite drastic seasonal variation in precipitation. Theory predicts that when environmental variation affects reproductive payoffs and costs in a predictable manner, such as in a seasonal pattern, reproductive schedules should evolve to favor periods in which payoffs for investing in reproduction are high and reproductive costs are low (Roff 2002). A lack of predictable seasonal pattern to reproductive costs and payoffs, such as found in our study, may contribute the evolution of the year-round reproductive strategy of *A.curassavica* and other Neotropical species that reproduce all year.

Although analysis shows selection for reproductive delay in *A. curassavica*, our models were based on data from plants that may or may not have previously flowered and therefore we cannot determine whether *A. curassavica* necessarily delays *first* reproduction . In addition to delaying first reproduction, it may be optimal for plants to undergo periods of not flowering. In a terrestrial orchid and a long-lived perennial herb, it has been found that costs of sprouting to survival may select for periods of vegetative dormancy (i.e. failing to sprout) (Shefferson et al. 2014). Reproductive costs may similarly select for periods of reproductive dormancy (not flowering) in iteroparous species, and future studies should investigate these reproductive decisions more thoroughly.

Although the full stochastic model was the only one that indicated selection for reproductive delays, and thus the most realistic, the predicted flowering size was higher than what we observed. Our model may have overestimated optimal flowering size due to inaccuracies in our estimation of reproductive costs and payoffs. We estimated seedling establishment by counting seedlings within our demographic plots. However, the wind-dispersed seeds of this species may establish outside of demographic plots, resulting in underestimated reproductive payoffs. Additionally, due to a somewhat limited number of individuals in each monitoring period, and a large variation in observed demographic patterns among individuals, our generalized linear models may overestimate reproductive costs for some monitoring periods. One caveat for our study is that what we refer to as fitness "costs" – a reduction in growth for reproductive plants – may not necessarily translate to reduced λ*s*. Faster growth is viewed as generally beneficial for fitness for individuals, because larger sizes increase both survival rate and reproduction. However, growth can be costly as well (Shefferson et al. 2014). When growth rate exceeds a certain value, it may actually decrease λ due to impacts on size distribution within the population, and too many large individuals may negatively impact the population. In our projection models, there was a slight negative quadratic effect of size on fruit production, resulting in a negative impact of very large individuals on fitness.

Numerous models supporting selection for reproductive delay in semelparous plants have been developed, but very few have examined the same phenomenon in iteroparous plants, which represent the majority of plant species (Hart 1977). We expand on the finding that reproductive costs help shape flowering size of iteroparous species (Miller et al. 2012) by highlighting the role that temporal variation in these costs plays in selection on flowering size for some species. Assessing temporal variation in life history costs can help us predict species' evolutionary response to climate change (Sletvold and Ågren 2015), and we encourage demographic modelers to account for temporal variation in reproductive costs and payoffs, especially when costs and payoffs are not seasonably predictable. We also encourage exploration of other aspects of variation in reproductive costs, such as spatial, which may also contribute to the evolution of life-history strategies.

Table 3.1. Model summaries for monitoring periods that demonstrated reproductive costs to survival and/or growth. Size is number of nodes and status is reproductive status (*R* or *V*). ΔAIC gives the AIC difference between the best-fit model and the best-fit model that did not include reproductive status as a predictor variable (only size or size^2). AIC weight gives the proportional weight of the AIC value. "All periods" models show the intercept and slope values used for the population projection model with time invariant reproductive costs.

Demographic Function	**Monitoring Period**	**Factors included in Best-Fit Model**	**ΔAIC**	**AIC weight**	***Effect of flowering on*:**	
					intercept	**slope**
Growth	A	size, size^2,status, size×status	18	0.0053	6.81	-0.41
	B	size, size^2,status, size×status	27.3	0.0071	6.45	-0.31
	E	size, size^2,status, size×status	55.7	0.012	1.44	-0.15
	F	size, status	10	0.0019	-2.59	
	G	size, size^2,status, size×status	56.8	0.013	7.57	-0.35
	H	size, size^2,status, size×status	20.4	0.0051	5.97	-0.11
	L	size, size^2,status, size×status	3.6	0.00079	1.34	-0.09
	All periods	size, size^2,status, size×status			-0.09	2.03
Survival	D	size, status, size×status		6.86	0.020	2.03
	G	size, status, size×status	2.4	0.0075	-1.24	-0.08
	All periods	size, status, size×status			-0.013	0.04

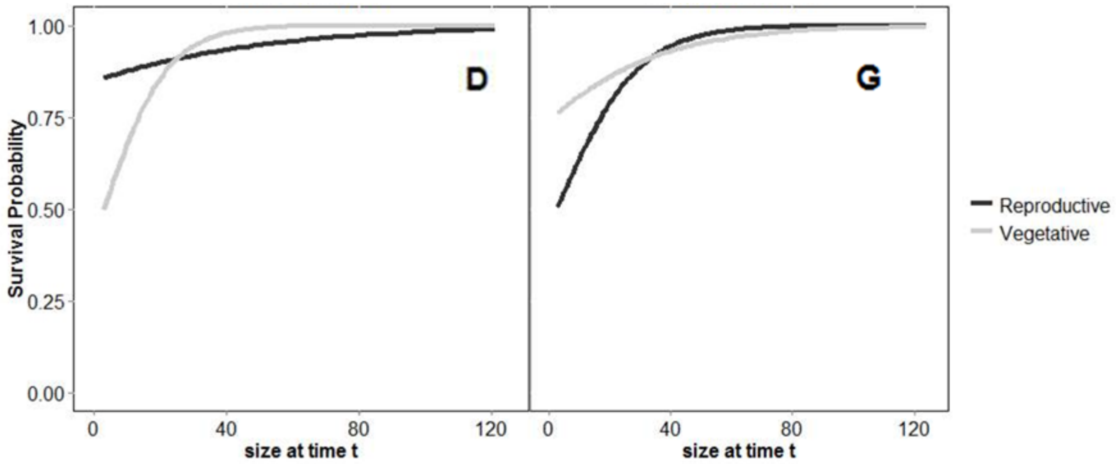

Figure 3.1. Survival functions for reproductive (black lines) and vegetative (grey lines) plants in the two monitoring periods that demonstrated reproductive costs to survival for larger plants in D and smaller plants in G from monitoring period *t* to monitoring period *t+1*.

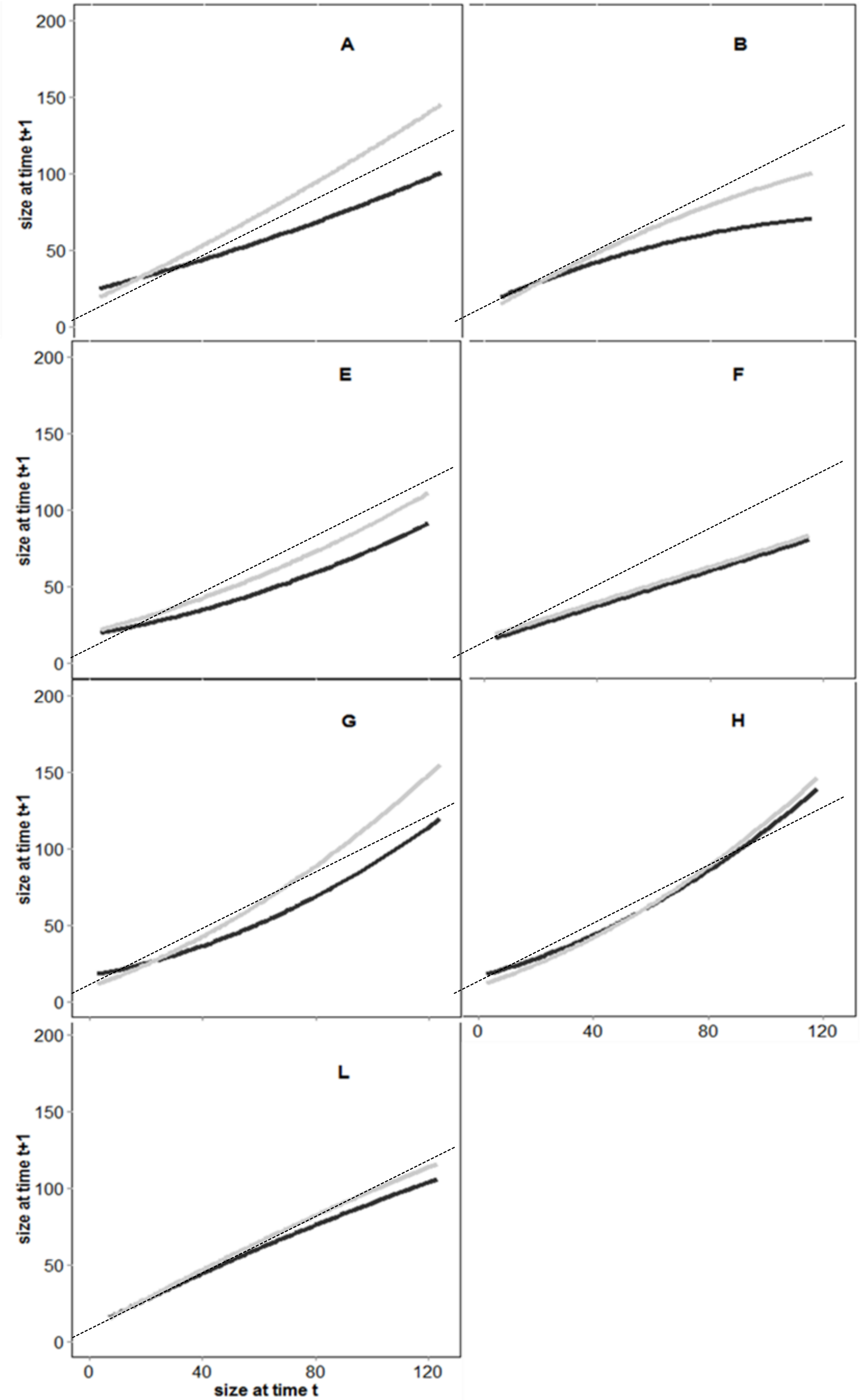
A
B
E
F
G
H
L
size at time t+1
size at time t
0
50
100
150
200
0
40
80
120

Figure 3.2. Growth functions for reproductive (black lines) and vegetative (grey lines) plants in the seven seasons that demonstrated reproductive costs to growth from monitoring period *t* to monitoring period *t+1*. The black dotted line is a 1:1 line representing size stasis (no growth or shrinkage).

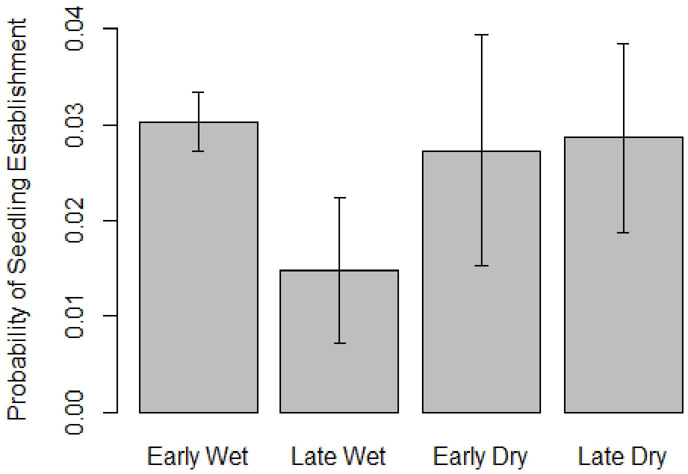

Figure 3.3. Seasonal means for probability of seedling establishment (ξ). Error bars show standard errors among ξ values from three years of data. Probability of seedling establishment did not vary significantly among seasons.

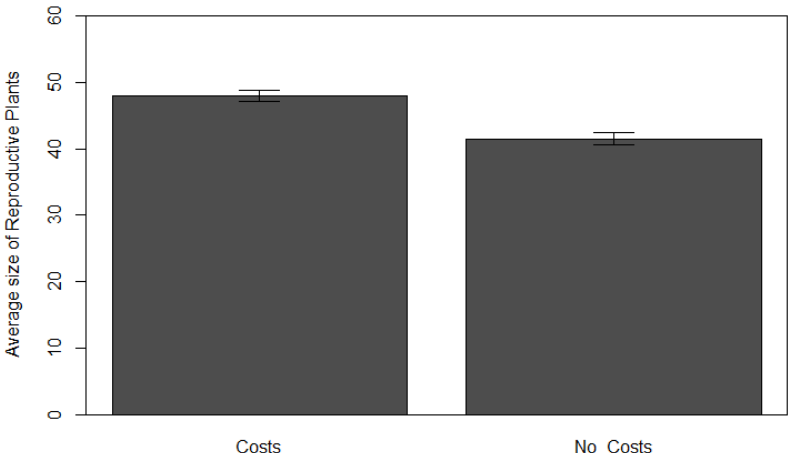

Figure 3.4. Mean sizes of flowering plants in monitoring periods with reproductive costs versus monitoring periods without reproductive costs showing larger flowering sizes in periods with reproductive costs. Error bars represent standard errors calculated from bootstrapped values.

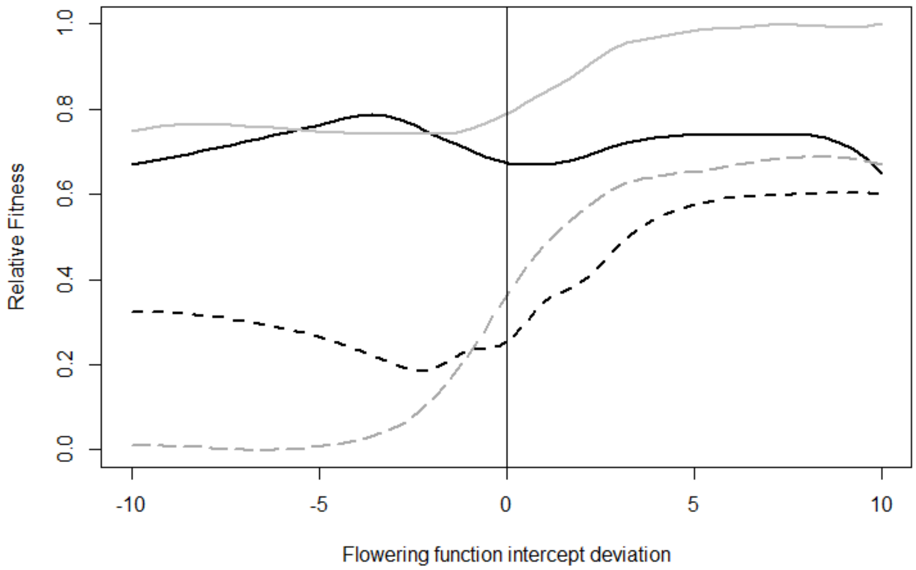

Figure 3.5. Plots showing relative fitness for a range of flowering intercept values. The vertical black line shows fitness values unaltered flowering intercept values. Fitness values produced by a fully stochastic model (solid black line), a model with time invariant reproductive costs (dashed black line), and a model with time invariant reproductive payoffs (solid grey line), and a model with no reproductive costs (dotted grey line) Relative fitness was calculated with estimates of population growth rate with the highest λ value in the set of models receiving a value of 1, and the lowest a value of 0.

CHAPTER 4

HIGH AND DRIER: SEASON-SPECIFIC RESPONSES OF A NEOTROPICAL MILKWEED, *ASCLEPIAS CURASSAVICA*, TO REDUCED PRECIPITATION IN A MONTANE CLOUD FOREST[1]

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[1] Kellett, K.M. Shefferson, R.P., and R. Mizuta. To be submitted to *Global Change Biology*.

Abstract

Central America is among the regions of the world most vulnerable to climate change, and rainfall patterns, especially those in mountainous regions are undergoing large changes. Rainfall is predicted to decrease dramatically in these areas, and we currently lack an understanding of how such climatic shifts will influence plant populations. For plants that reproduce throughout the year, changes in rainfall patterns may have season-specific impacts on population growth (λ). We used demographic data collected every three months from 2011 to 2014, in conjunction with historic weather data, to show that the impacts of two measures of rainfall - mean daily rainfall and proportion of rainy days - on the λ of *A. curassavica* vary depending on season. We then used future climate predictions and climate-based population projection models to determine and how future changes to climate may impact long-term λ. As a result of season-specific responses to rainfall, our predictions for λ under future climate conditions varied depending on whether we allowed for seasonal patterns in our simulations, and which factor (mean daily rainfall or proportion of rainy days) we included in our simulations. Our most realistic model predicts an increase in population growth for these populations under future climate conditions, due to an increase in survival and fruit production. We emphasize that for species with year-round reproduction, demographic response to changes in climate may vary among seasons, and season-specific response should be considered when constructing predictive models. We also offer support that generalist species may be well-buffered to future changes in climate.

Keywords: Climate change, population growth, tropical plant populations, seasonal demography

Introduction

Direct and indirect effects of changes in climate on species' demography are influencing species distributions, population sizes, and evolutionary trajectories throughout the world (Parmesan 2006). Rising global temperatures are causing changes to patterns in weather that define a region's climate, and vital rates (survival, growth, fecundity) are often closely linked to weather variables such as temperature and precipitation (Huey and Berrigan 2001). Recently developed models can provide reliable predictions of past and future weather data for any area, down to 20-km^2 in size (Mizuta et al. 2012). Demographic studies, coupled with these weather data, can provide valuable insight into how climate change may impact populations in the future, but are generally underutilized (Boyce et al. 2006). Importantly, such studies also provide a mechanistic explanation of why populations will change over a time, information that commonly used climate envelope-based approaches lack (Moritz and Agudo 2013).

It is well-established that vital rates (survival, growth, fecundity) often correlate with weather (Pierson and Turner 1998, Nicole et al. 2011, Salguero-Gómez et al. 2012, Sletvold et al. 2013), but the direction and strength of these correlations may vary over time or space (Stenseth and Mysterud 2002). Accurately predicting how changes to a region's climate will influence population dynamics requires understanding which variables are the primary drivers of population growth, the direction and magnitude of the relationship, and how these relationships may vary over time. For some species, demographic response to weather may vary among different seasons (e.g. Penuelas *et. al.* 2004). Therefore, response to climate change will depend on how weather patterns change within each season, as well as season-specific relationships between weather variables and vital rates.

Latin America, especially the Central American isthmus, is predicted to be especially vulnerable to the impacts of climate change. Alterations in the hydrological cycle caused by climate change are expected to have large impacts on ecosystems, especially those in mountains (Parry 2007). In fact, the hydrological conditions that currently characterize tropical montane cloud forests may no longer exist anywhere on earth within a century due to rising cloud cover (Williams et al. 2007). Changes to rainfall patterns in cloud forest ecosystems have been associated with declines in amphibian (Lips 1998), birds, and reptile populations (Pounds et al. 1999), and there is also evidence that these changes could devastate epiphyte populations (Nadkarni and Solano 2002). However, existing demographic data sets underrepresent tropical and arctic regions, and over represent northern temperate ecosystems (Salguero-Gómez et al. 2012). Thus, our knowledge of how climate change will impact Neotropical species is strikingly limited.

Monteverde, a paramount example of a tropical montane cloud forest region in Costa Rica, is characterized by a rainy season typically lasting from the beginning of May to mid-November, and light periods of rain or mist throughout dry season due to the year-round persistence of clouds. Recently developed high resolution climate models (Mizuta et al. 2012) predict a reduction in mean daily rainfall throughout most of the year for Monteverde, an increase in the variation of mean daily rainfall and, an increase in the number of days without rain (Mizuta, *personal communication*) (Figure 4.1). The few studies that have examined impacts of climate change on species in this region focus on species with limited distributions that are specially adapted to cloud forest conditions. Generalist species in this area are more widely distributed, and may tolerate, or even benefit from changes to rainfall patterns (Clavel et al. 2010).

Asclepias curassavica, hereafter *Asclepias,* is a Neotropical milkweed species commonly distributed in disturbed areas throughout Central and South America in a variety of ecoregions.

This generalist species is the only widely-distributed milkweed species in Costa Rica, and serves as the primary host plant for several butterfly species including Monarch butterflies (Bierzychudek 1981). Monteverde supports local populations of Monarch butterflies that peak in numbers during late dry season (Haber 1993). However, *Asclepias* also is an agricultural pest throughout its distribution because its toxic chemical defenses cause severe illness and abortion in cattle that accidentally ingest it. Thus, understanding the impact of future climate scenarios for this species is important for conservation of native butterflies and local agriculture.

In previous work, we showed that the influence of seasonal variation on population growth rate is more than twice that of annual variation, and we detected clear seasonal trends in vital rates (Kellett and Shefferson 2015). In general, population growth tended to be highest during late dry season (the driest period), and lowest during late wet season (the wettest period). However, the role that rainfall plays in driving population growth remains unclear. Since we have found distinct seasonal patterns in demography, we suggest that demographic response to rainfall may vary among season (e.g. plants may respond differently to rainfall during wet versus dry season). Additionally, the aspect of rainfall that drives demography (mean daily rainfall, variation in daily rainfall, etc.) may vary among season. We take a season-specific approach to modeling response of *Asclepias* populations to climate change.

In this manuscript we first examine how several precipitation variables drive population dynamics of *Asclepias*, and test whether response of population growth to rainfall variables is season-specific. Second, we examine how populations of Asclepias in Monteverde may respond to future climate scenarios, and test whether ignoring season-specific patterns in demographic response to precipitation may influence model predictions. Finally, we examine the demographic mechanisms responsible for changes to population growth under a realistic projection for these populations. We predict that population growth within seasons will respond differently to variation in rainfall measures, and that a drier climate in this region will result in increased population growth for this species.

Methods

Study species and data collection

Asclepias curassavica (Asclepiadaceae) is an evergreen perennial species with a native range extending from northern Argentina to southern Mexico. It is the most common *Asclepias* species in the Neotropics and is found in disturbed areas such as roadsides and pastures ranging from sea level to 2000m elevation (Zuchowski and Forsyth 2007). It has a limited suite of specialist herbivores due its toxic latex (Malcolm 1991). We estimate the lifespan of *A.curassavica* to be ten to fifteen years (Kellett, unpublished data). It flowers and fruits throughout the year with no seasonal patterns in reproduction. However, it demonstrates seasonal variation in growth and survival (Kellett and Shefferson 2015).

We studied *A.curassavica* populations growing in four cow pastures around the UGA Costa Rica campus and research station in San Luis de Monteverde, Costa Rica (N10° 16.973’ W84° 47.882’) (https://dar.uga.edu/costa_rica/index.php). San Luis de Monteverde is located in Northwest Costa Rica on the Pacific slope of the Corderilla de Tilarán, and has a seasonal moist forest climate. The populations were located between 1000m and 1200m elevation, distributed over 3 km^2.

In June 2011, we established 18 demographic 10m × 10m plots within four *A.curassavica* populations all located within 5.0 km of the UGA Costa Rica campus. Plot sites all contained at least ten plants, and were chosen to represent the typical range of conditions at each site. We monitored all plants within sites sites approximately every three months (July, October, January, and April). We recorded each individual's reproductive status. Reproductive (R) plants had flowers, fruits, or both, while vegetative (V) plants had neither. We also recorded total number of nodes, total number of inflorescences, and total number of fruits. Nodes are visible notches in stems where each pair of leaves attach, or previously attached, to the stem. As a stem grows, more nodes are added. We collected 25-40 seed pods per monitoring period from plants outside of demographic plots to estimate average seed production per fruit for each monitoring period. In total we repeated this procedure in four seasons (early dry, late dry, early wet, and late wet), for three full years (2011-12, 2012-13, and 2013-14) hereafter referred to as 2011, 2012, and 2013. We collected data from a total of 1270 individuals over 12 monitoring periods.

Population Modeling

We constructed generalized linear mixed models (GLMMs) predicting probability of survival ($\sigma(x)$), growth ($\gamma(y,x)$), probability of flowering ($\beta(x)$), probability of fruiting ($\theta(x)$), and number of fruits ($\omega(x)$) for each of the 12 monitoring periods. We considered plant size (x), a squared-term for plant size, and reproductive status (R) as fixed factors, and used plot as the only random factor. We constructed a global model using all of these terms and their interactions, and then took a backward stepwise regression approach and tested whether removal of factors in our model improved model fit using Akaike's Information Criterion (AIC) values. Following a conservative approach, we considered the best fit model in each case to the model with the lowest AIC, although models with fewer parameters and within two AIC units of the lowest AIC were considered equally parsimonious and used in inference , provided that model made biological sense within our system (Burnham and Anderson 2002).

We used best fit models for vital rates to develop life history function-based matrix projection models for each monitoring period. Each model included demographic functions that predicted probabilities of survival ($\sigma(x)$), growth ($\gamma(y,x)$), flowering ($\beta(x)$), and fruiting ($\theta(x)$), as well as the number of fruits ($\omega(x)$), as functions of plant size (x), and reproductive status (R), if reproductive costs were apparent, per each respective best-fit model. The size distribution of seedlings was described by a Gaussian distribution around mean seedling size Φ (y). Together, these functions describe all possible transitions from size (x) in one monitoring period to another size (y) in the next. Per Easterling et al. (2000), each transition was described by the kernel:

$$k(y,x) = p(x,y) + f(x,y) \tag{1}$$

where

$$p(x,y) = s(x,R)g(x,y,R) \tag{2}$$

describes survival and growth from size x in year *t* to size y in year *t*+1, and

$$f(x,y) = \beta(x,R)\theta(x,R)\omega(x,R)\upsilon\delta\xi\Phi(y) \tag{3}$$

describes fecundity, or the probability of an individual of size *x* having an offspring of size *y*. We used $\upsilon = 85 \pm 10$ (SE), the mean number of seeds per fruit in our sampled fruits, and δ refers to the germination probability estimated from our germination field plots. We used the following equation to calculate establishment probability (ξ)

$$\xi = \frac{k}{q\upsilon\delta} \tag{4}$$

where *k* is the total number of recruits found in all four populations in *t+1* and *q* is the total number of fruits counted in all four populations in *t*. For functions ($g(x)$) describing vital rates which included R, functions were weighted by probability of flowering (β) such that:

$$g(x) = g_V(x)\big(1 - \beta(x)\big) + g_R(x)(\beta(x))$$

where g_V describes the function for vegetative plants, and g_R describes the model for reproductive plants.

The full model integrated over all sizes Ω is described by:

$$n(y, t+1) = \int_{\Omega} k(y, x) n(x, t) dx \qquad (4)$$

This integral projection was used to populate a 400 x 400 projection matrix separately for each monitoring period. Since we used a discrete measurement for plant size (nodes), we discretized the bins within our matrix so that each of the 400 bins incorporating a specific plant size from 1 to 400 nodes.

Population growth and precipitation

We used matrices to calculate deterministic population growth (λ) for each monitoring period. To determine which aspects of climate exerted the largest influence of population dynamics, we tested for correlations between estimated λ and climate data. We obtained daily precipitation data from the UGA weather monitoring station on the UGA Costa Rica Campus (collected January 2005-April 2015), and estimates of historical precipitation data from the MRI-AGCM3 super-high-resolution climate model (Mizuta et al. 2012) . The models were run for the 20 km^2 grid centered on the GPS coordinates of the UGA Costa Rica Campus, and back-projected using the AMIP (Atmospheric Model Intercomparison Project) scenario. Model output contained daily precipitation values (1979–2003) (R. Mizuta, 2015, personal communication). We combined data from the model (1979-2003) with data from the weather monitoring station (2005-2015) to estimate four rainfall measures for each season: mean daily rainfall, variation in daily rainfall (CV of mean daily rainfall), percentage of rainy days (days with >0 cm of precipitation), and days with extreme rainfall (days with > 1.2 cm of rain, the 90th percentile value for all days in our data set) during each season. Seasons were defined as early wet (May-July), late wet (August-October), early dry (November-January), and late dry (February-April), in January 2005-April 2015.

Variation in daily rainfall was highly correlated with percentage of rainy days, so both measures correlated similarly with predicted λ values. We chose to use proportion of rainy days, and not variation in daily rainfall, for the rest of our analyses, as an increase in days without rain is expected to have important biological consequences (Nadkarni and Solano 2002). To later build our predictive future population projections, we first had to decide which climate variable best predicted λ values for each season. For each of the four seasons, we compared fits of four generalized linear models using the *glm* function in R version 3.1.1 (R Core Team 2014). We compared models using mean daily rainfall, proportion of rainy days, extreme rainfall as predictor variables against one another and against a null model with no predictor variables. Since we only had three data points for each season, we could only include one predictor variable per model. For each season, we chose the model with the lowest AIC value as the best predictor for that season. We also calculated Spearman's rank coefficient using the *cor* function in R version 3.1.1 (R Core Team 2014) between climate variables and λ within season, across all seasons, and across both wet and both dry seasons to gain a better understanding of how strongly rainfall variables relates to λ within and across seasons.

Future population projections

We developed a stochastic population projection model to assess the influence of climate on these populations. After testing for normality in these data using Shapiro-Wilk normality tests, we modeled the probability distributions for mean daily rainfall, proportion of rainy days (the two rainfall measures that best predicted λ). We used these distributions to estimate the probability of each monitoring period within our study occurring under current precipitation conditions, and used these probabilities to determine the appropriate matrix for use in a 10,000 timestep simulation. The final 7,000 timesteps were used to estimate the stochastic population growth rate (λs). We then bootstrapped this simulation 10,000 times to produce a standard error associated with λs.

To examine the importance of season-specific responses to climate variation, we repeated the 10,000 timestep simulation using matrix probabilities using the following three different assumptions for our models: (1) Responses to rainfall are not season-specific. We calculated probabilities of each of the twelve monitoring periods based on a single normal distribution of proportion of rainy days (the strongest predictor of λ across monitoring periods) across all seasons and years and matrices were chosen for the simulation with these probabilities, with no regard to season. (2) Populations respond to the same rainfall variables among seasons: We constructed (a) a “Daily Rainfall” model that chose matrices based on probabilities calculated from seasonal distributions of daily rainfall, and followed a seasonal order and (b) a “Rainy days” model that chose matrices based on probabilities calculated from seasonal distributions of proportion of rainy days, and followed a seasonal order. (3) Populations respond to different rainfall variables in different seasons. We used a “Best Factor” model, which chose matrices based on probabilities calculated from seasonal distributions of the factor that best predicted λ in each season, and followed a seasonal order.

We repeated the above analysis, but adjusting matrix occurrence probabilities to account for future changes to climate. We calculated new probability distributions based on future predicted rainfall values from the climate model, and then repeated each of the four scenarios described above with these probabilities. We note that our approach is similar to that of (Salguero-Gómez et al. 2012).

To understand which aspects of demography were responsible for differences in λs between current and future scenarios we calculated the response of stochastic population growth rate to changes in vital rates. We followed the procedure of Salguero-Gomez *et. al (*2012) and performed our analysis by perturbing the intercept of each vital rate function that contributes to our matrix models (survival, growth, probability of flowering, probability of fruiting, and number of fruits produced) by a small amount (0.01) and calculating the proportional change in λs. This analysis informs us which vital rates are most important to current population growth rate, and whether the importance of each vital rate will change under future conditions.

Results

Rainfall

Over the 34 years of historical rainfall data, late dry season had the lowest mean daily rainfall, proportion of rainy days, and proportion of days with extreme rain, while late wet season had the highest values for these measures (Table 4.1) Early wet season and early dry season were very similar in their rainfall values and the distributions of all rainfall measures overlapped greatly. Future climate had lower mean rainfall in all seasons except early wet, and greatly reduced percentage of rainy days during both dry, but not wet, seasons (Figure 4.2). Under future climate projections, late dry season remained driest and late wet season wettest, but early wet season and early dry season became more different in their rainfall measures. Early wet season became wetter and early dry season drier (Table 4.1). The occurrence probability of our sampling periods in 2011-2014 shifted from current to future climate, especially during dry seasons. In general, higher rainfall values from our sampling periods became rarer as dry seasons become drier (Figure 4.2).

Population growth

During our sampling period (2011-2014, population growth rate (λ) was consistently higher in the late dry (1.13±0.032 cm/day) (mean±SE) and early wet seasons (1.11±0.029).

Population growth was lowest in the late wet season (0.85±0.034). Although the early wet and early dry seasons experienced similar rainfall levels, the early wet season exhibited much lower population growth (0.99±0.020), perhaps due to the lagged effects of the late dry season (high λ) and the late wet season (low λ).

Deterministic λ was strongly affected by precipitation variables in all seasons. Within individual seasons, estimated λ for late dry season was driven most strongly by percent of rainy days, while the other three seasons were more strongly driven by mean daily rainfall (Table 4.2). Higher rainfall resulted in lower population growth for all seasons, except late wet season, which showed a very strong positive relationship between λ and rainfall measures (Figure 4.3). Across all seasons, population growth showed a negative relationship with all rainfall measures, but these relationships were driven primarily by dry seasons.

Population growth under future conditions

Future conditions had different consequences for stochastic population growth (λs) depending on which model we used. When we did not include season-specific responses to rainfall in our stochastic simulations, λs did not differ between current (1.043±0.0025) (mean±SE) and future (1.0474±0.0025) climate conditions ($t=-1.6$, $p>0.1$). It decreased between current (1.047±0.0035) and future (1.032±0.0031) climate when we used mean daily rainfall to determine probabilities of our sampled monitoring periods in our simulation ($t=-7.6$, $p<0.005$). However, when we assigned probabilities to matrices based on proportion of rainy days, we observed a large increase in λs from current (1.045±0.0033) to future (1.067±0.0045) conditions ($t=-29.2$, $p<0.1\text{x}10^{-5}$). This discrepancy between the two models occurred due to the inconsistent responses of λ to these two rainfall variables among different seasons (e.g. late dry season λ increases consistently under reduced rainy days, but not under reduced daily rainfall). When we used the factor that best predicted determinisitic λ for each of our monitoring periods, which best represents reality, we observed a small, but significant, increase in λs from current (1.044±0.0029) to future (1.052±0.0035) conditions ($t=-15.1, p<0.005$) (Figure 4.4). We observed a decrease in λs in our "daily rainfall" model and an increase in λs in our "rainy days" model. Overall, the differences we observed between current and future λs were modest, partially because the positive effects of reduced precipitation on λ during both dry and early wet season is buffered by its negative effect in late wet season.

The responses to perturbations to vital rates did not differ significantly between current and future conditions, suggesting the demographic strategy of *A.curassavica* will not be heavily influenced by climate change (Figure 4.5).

Discussion

We found that *A.curassavica* populations in Monteverde, Costa Rica, an ecological zone very sensitive to changes in rainfall patterns, are expected to increase under predictions of future climate change. Our prediction that populations would benefit from drier conditions was supported with predictions from our most realistic model. However, due to season-specific responses to different measures of rainfall, models that did not consider these season-specific responses resulted in different predictions. We therefore emphasize the importance of considering season-specific responses of populations to a changing climate. Rainfall measures vary in seasonal patterns, and populations respond differently to higher rainfall levels depending on the present season, responding positively to high rainfall during the wettest season and negatively to high rainfall during dry seasons. This pattern may suggest adaptive plasticity at the seasonal scale in response to climate. Our seasonal matrix approach more accurately conveys the effects of rainfall patterns within a year onto overall population dynamics. This is in contrast to most demographic studies, which use weather variables at the annual level (e.g., Shefferson et al. 2001) and so may miss the impacts of seasonal events. For a species such as *A.curassavica*, which reproduces throughout the year, using an annual timescale would overlook season-specific responses to weather, resulting in inaccurate predictions for responses to future changes to climate. Additionally, though many studies tend to focus on mean rainfall values as a measure for precipitation (Huxman et al. 2004, Salguero-Gómez et al. 2012), we highlight that different measures of rainfall may be stronger drivers of population dynamics and may influence populations in different ways than mean rainfall values.

Our study highlights the importance of season-specific responses in a tropical species that reproduces and grows throughout all seasons. Considering responses to weather variables on a seasonal or monthly timescale could improve our understanding of response to climate change for species throughout the globe. Effects of climate change themselves, such as increased extreme precipitation events or a decrease in annual rainfall, are often season-specific (Scanlon et al. 2002, Schmidli and Frei 2005, Nakagawa et al. 2006). For example, in our study annual reduction in rainfall was due to reduced rainfall in only three out of the four seasons (and the reduction varied in magnitude among those). Further, there are differences in how individuals respond to seasonal variation that may not be apparent on an annual scale (Vavrek et al. 1997). For example, plant species in the Netherlands showed a strong growth response to increased temperatures during winter, but not during spring and summer (Penuelas et al. 2004). These differences in season-specific responses may be vital in predicting species response to changing climate, but could be overlooked if only an annual scale is considered.

To our knowledge, this is the first time a demographic approach has been used to predict the response of Neotropical plants to future climate change. Although other approaches predict changes to rainfall regimes in cloud forest regions like Monteverde will be devastating to their endemic plants and animals (Pounds et al. 1999, Foster 2001), we show the opposite for a widespread, generalist species. This supports a growing body of literature suggesting such species will thrive under climate change (Jiguet et al. 2007, Davey et al. 2012, Mair et al. 2012, Stroud and Feeley 2015).

Our study joins many other demographic studies which support that long-lived species may be particularly well-buffered to the effects of climate change (Morris et al. 2008). Changes to stochastic population growth rate of *A. curassavica* occurred with no discernable change in the relative impact of each vital rates, indicating that all aspects of *A. curassavica's* life cycle will respond similarly to future climate change.

Collecting demographic data over many years increases accuracy of predictions, but the reality is that most demographic studies are temporally-limited, with an average length of 3.1 annual matrices (Crone et al. 2011). Although our study is limited to three years, we were able to calculate relative probabilities of the monitoring periods within our study based on historical climate data, and we suggest this approach to other temporally-limited demographic studies. Although our data do not represent the full range of possible climate conditions, representing relatively probabilities of each monitoring periods ensures that our prediction is as realistic as possible. Extending our study to include as many years as possible would strengthen the accuracy of our prediction even further. Although we show climate change will not threaten *A.curassavica* populations in Monteverde, our data are limited to predictions for populations in this area. If all *A.curassavica* populations respond similarly to rainfall, those in Southern Costa Rica may be threatened, as mean annual rainfall and rainfall during dry season is expected to increase for this region (Diaz and Sanchez 2012).

In conclusion, we encourage our approach to be used for other Neotropical, as well as temperate, species. The Neotropics, especially specialized ecosystems like that of Monteverde, have already begun to experience the impacts of climate change, and the need to understand future implications of climate change on species in this region is great in order to plan for conservation of this biodiverse area. Unfortunately, the availability of demographic data sets on tropical species limits the application of our approach to species for which these data exist. However, due to the availability of historic and future climate data predicted by increasingly accurate Global Climate Models (GCM's) our approach is feasible for any species for which demographic data have been collected, even if site-specific climate data have not been collected (Salguero-Gómez et al. 2012). This approach may be particularly beneficial for species which are perceived to be under the greatest threat from climate change. As climate change represents just one of the primary threats to tropical species (Laurance 2007) predictions could be extended to include fragmentation or other environmental threats to species in this reach.

Table 4.1. Mean and standard error of rainfall measures for each of the four seasons calculated for current (1979-2015) conditions and future conditions (2079-2099). Future conditions are, in general, drier for all seasons, except for early wet season.

	Mean Daily Rainfall (cm)		**Proportion of Rainy Days**		**Proportion of days with Extreme Rain**	
Season	***Current***	***Future***	***Current***	***Future***	***Current***	***Future***
Early Wet	0.78±0.040	0.86±0.035	0.78±0.089	0.84±0.010	0.10±0.041	0.071±0.048
Late Wet	1.3±0.048	1.0±0.063	0.88±.012	0.89±.0094	0.15±0.099	0.071±0.096
Early Dry	0.72±0.034	0.37±0.032	0.72±0.022	0.52±0.018	0.10±0.0041	0.016±0.0034
Late Dry	0.24±0.010	0.16±0.013	0.51±0.021	0.37±0.020	0.023±0.0013	0.0014±0.0048

Table 4.2. Model selection data for the four models we tested among four seasons, showing mean daily rainfall to be the best predictor of λ in all seasons except late dry. Best fit model values are shown in bold. AIC weights were calculated based on AIC values from all four models.

Model	**Daily Rainfall**		**Proportion of Rainy Days**		**Proportion of Extreme Rain days**		**Null**	
Season	***ΔAIC***	***AIC weight***	***ΔAIC***	***AIC weight***	***ΔAIC***	***AIC weight***	***ΔAIC***	***AIC weight***
Early Wet	**0**	**0.86**	5.4	0.058	6.9	0.027	5.6	0.052
Late Wet	**0**	**0.79**	8.8	0.0097	2.7	0.2	14.61	0.00053
Early Dry	16.8	0.00028	**0**	**0.99**	16	0.00034	16.4	0.00027
Late Dry	2.8	0.38	**0**	**0.13**	2.4	0.16	2	0.19

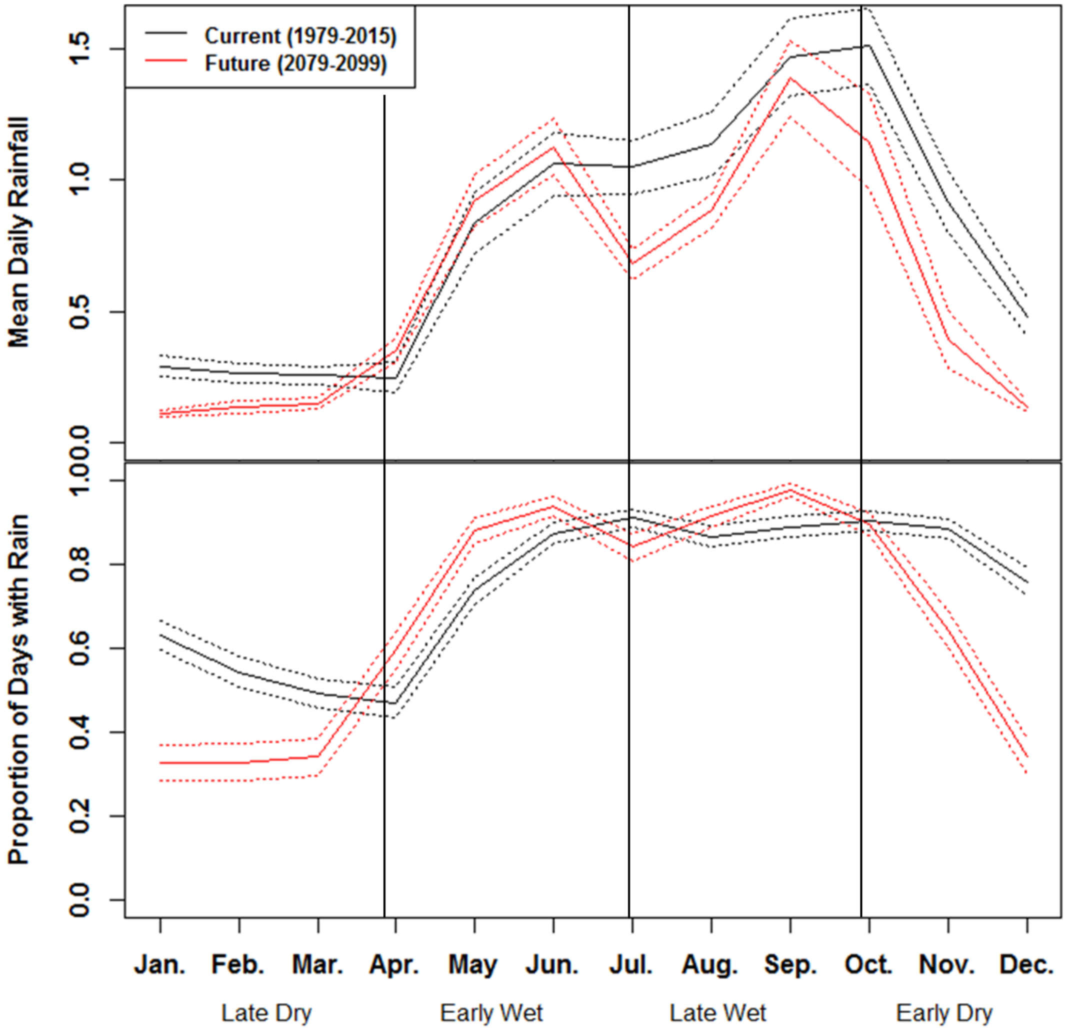


Figure 4.1. Mean daily rainfall values and proportion of days with rain by month and by the four seasons we used as monitoring periods based on historical projected and observed data (black) and future projected data (red) showing a drier future climate, but different patterns in mean daily rainfall and proportion of rainy days. Dotted lines show standard errors around the means.

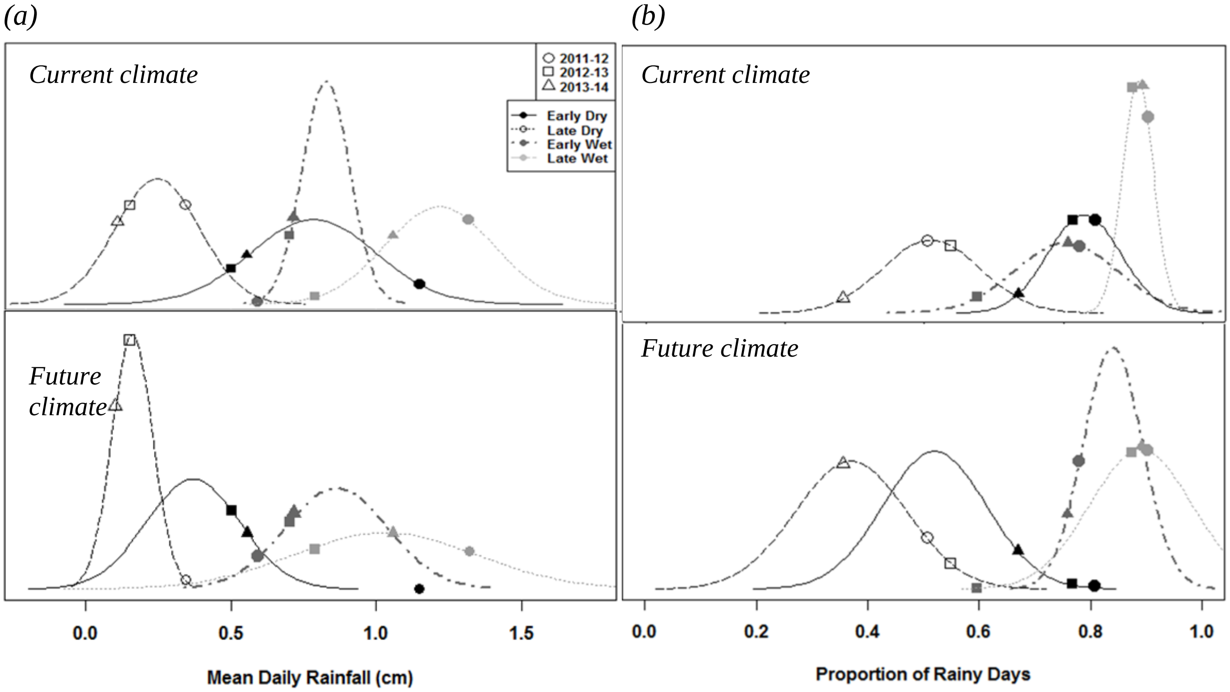
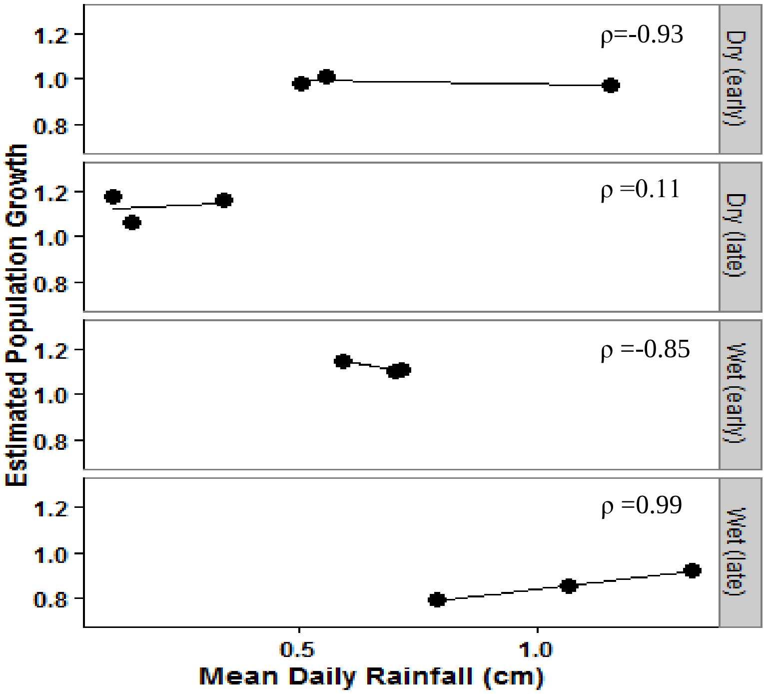


Figure 4.2. Normal distributions of mean daily rainfall (*a*), proportion of days with rain (*b*) for each of four seasons based on current climate patterns (1979-2015) and future climate patterns (2079-2099). Points on the distributions show values from monitoring periods during our three years of demographic sampling and where they fall on current and future climate distributions.

(a)


Estimated Population Growth
1.2
1.0
0.8
ρ=-0.93
Dry (early)
ρ =0.11
Dry (late)
ρ =-0.85
Wet (early)
ρ =0.99
Wet (late)
0.5
1.0
Mean Daily Rainfall (cm)

(b)

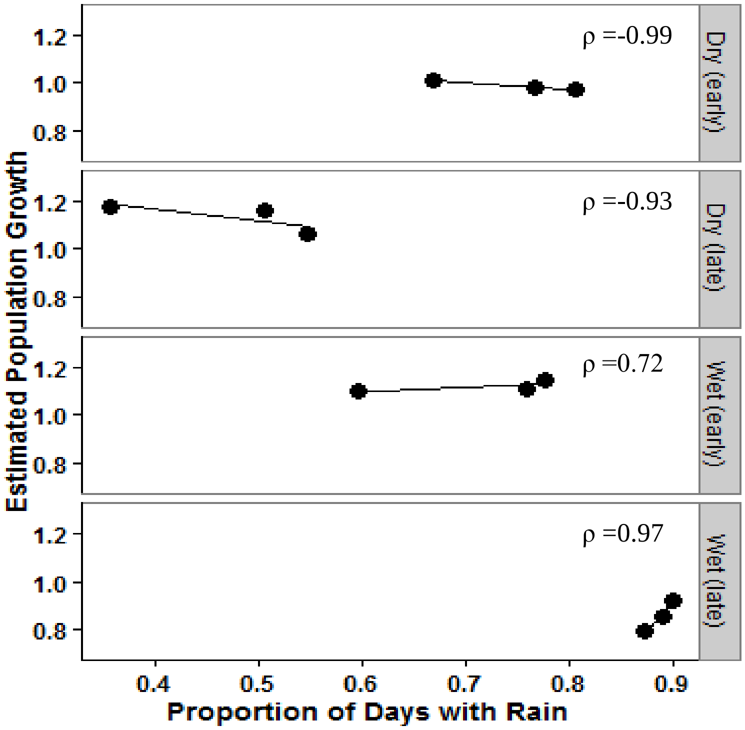

Estimated Population Growth
1.2
1.0
0.8
ρ =-0.99
Dry (early)
ρ =-0.93
Dry (late)
ρ =0.72
Wet (early)
ρ =0.97
Wet (late)
0.4
0.5
0.6
0.7
0.8
0.9
Proportion of Days with Rain

Figure 4.3. Relationship between deterministic population growth (λ) estimated from monitoring data in each of twelve sampling periods and mean daily rainfall (*a*) and proportion of days with rain (*b*) across three years for each of four seasons (early dry, late dry, early wet, late wet) showing λ in dry seasons driven by proportion of rainy days and λ in wet seasons driven by mean daily rainfall.

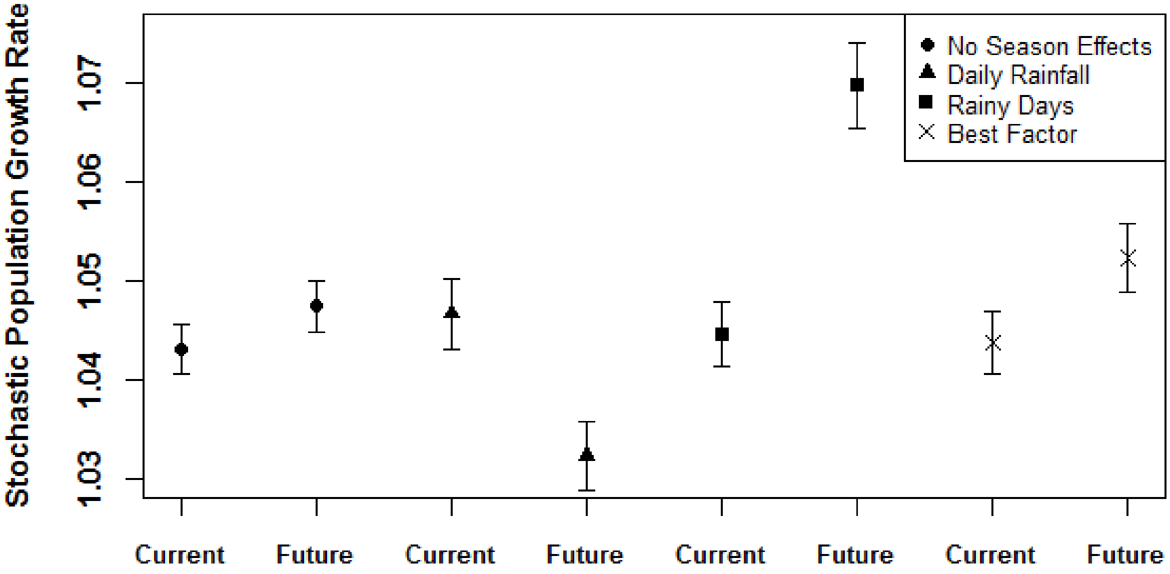


Figure 4.4. Stochastic population growth (λs) estimates for current and future climate based on four different scenarios: no seasonal effects, estimates based on mean daily rainfall, estimates based on proportion of rainy days, and estimates based on the most predictive factor for each season. Error bars show standard errors from bootstrapped estimates.

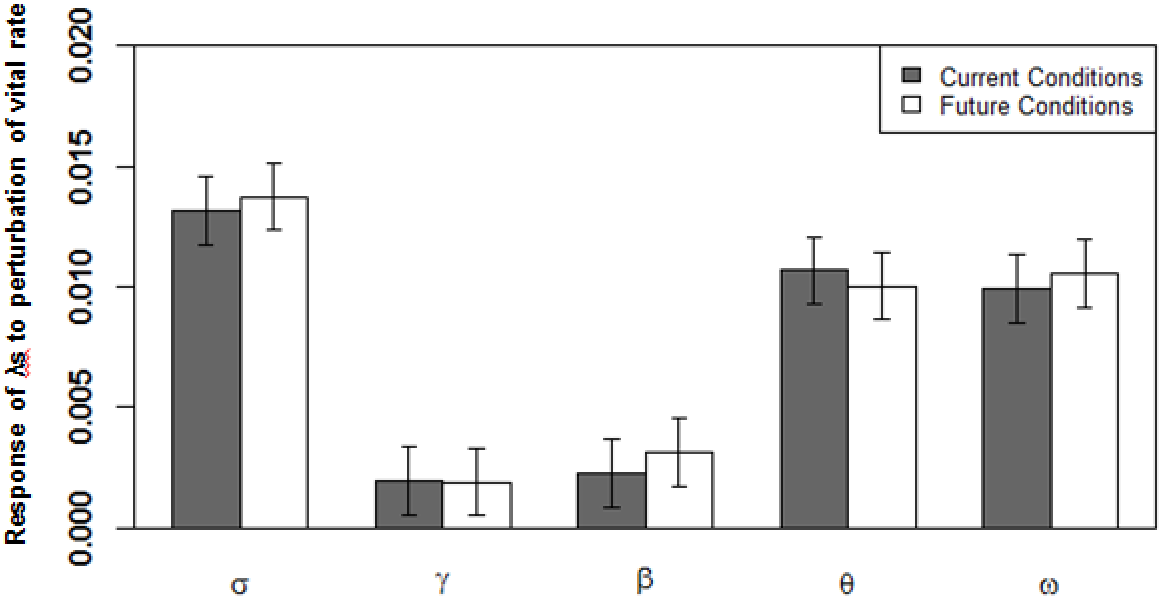


Figure 4.5. Change in *λs* to perturbations (a 0.001 increase in intercept) in functions describing survival (σ), growth (γ), probability of flowering (β), probability of fruiting (θ) and number of fruits produced (ω) under current conditions and predicted climate scenarios. Error bars show standard errors from bootstrapped estimates.

CHAPTER 5

CONCLUSIONS

This dissertation elucidates the role that seasonal patterns play in the population dynamics and life history evolution of populations of a Neotropical milkweed, *Asclepias curassavica,* in Monteverde, Costa Rica. In chapter 2, I first show that there is a distinct seasonal pattern in population growth rate (λ), despite the lack of obvious seasonal patterns in fruiting and flowering. I then determine that season contributes twice as much as year to overall temporal variation in λ, and that seasonal variation in λ occurs via a different demographic pathway than annual variation in λ. Chapter 3 explores how the temporal patterns in demography discussed in chapter 2 may apply to costs of reproduction in *A. curassavica*, and ultimately shape the reproductive schedule of this species. I found that while temporal variation in costs of reproduction plays an integral role in selecting for delays in flowering, there were no clear seasonal patterns in reproductive costs. The lack of seasonal patterns in reproductive costs may however, select for the year-round flowering schedule of this species. In the final chapter of this dissertation, I continue to highlight the importance of seasonal patterns for these populations by showing that responses of λ to rainfall are season-specific. I emphasize that not recognizing these season-specific responses can result in inaccurate predictions of populations' response to changes in rainfall patterns induced by climate change.

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