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A demographic ménage à trois: interactions between disturbances both amplify and dampen population dynamics of an endemic plant

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Summary

1. Natural and anthropogenic disturbances co-occur in most systems, but knowledge on how they may interact to shape demographic outcomes remains limited. Such interactions may alter dynamics of populations in non-additive ways, making it challenging to predict future demographic status based on experiments without interactions. Thus, understanding the interactive effects of such disturbances is critically important to determine the population viability of most species under a diversity of stressors.
2. We used a hierarchical Integral Projection Model (IPM) parameterized with 13 years of data across 20 populations, encompassing 2,435 individuals of an endangered and narrowly endemic herb, *Liatris ohlingerae* to examine the interactive effects of vertebrate herbivory, fire, and anthropogenic activities on its vital rates (e.g. survival, growth, reproduction, recruitment), and ultimately on its population growth rates. We constructed mega-matrices to determine the coupled dynamics of individuals damaged *vs*. not damaged by herbivores in roadside and Florida scrub habitats and scrub habitats with different time-since-fire.
3. We found noticeable increases in overall population growth rates (λ) in roadside populations compared to scrub populations, and declines in λ with increasing time-since-fire. Herbivory decreased differences in λ due to anthropogenic disturbance and slightly increased differences in λ due to time-since-fire.
4. *Synthesis*. The co-occurrence of various disturbances may both amplify and dampen the effects of other disturbances on population growth rate, thus shaping complex population dynamics that are neither linear nor additive. These realistic non-linearities represent challenges in the examination and projection of population dynamics. Here, we examined

the effects of various sources of disturbance on the population dynamics of a plant, finding complex interactions on the resulting population growth rates. We argue that the proposed approach, the integration of stressors in IPMs in a hierarchical framework, will allow ecologists and managers to more accurately estimate the overall effects of ecological processes on species viability.

Key-words: fire, Florida scrub, herbivory, integral projection models (IPMs), *Liatris ohlingerae,* plant demography, population growth rate λ.

Introduction

Disturbances and their concomitant alterations are critical drivers of many ecological processes, from local to global scales. These disturbances may be biotic (e.g. Rautio *et al.* 2005; Goslee, Peters & Beck 2001), anthropogenic (e.g. Young, Boyle & Brown 1996; Schafer *et al.* 2010) or abiotic (e.g. Bond & Keeley 2005; Smith, Caswell & Mettler-Cherry 2005). In most systems, disturbances do not occur in an isolated manner, but in conjunction with other stressors (Bigler, Kulakowski & Veblen 2005). The interactions of these factors have the potential to alter the ultimate outcome for population dynamics (Platt *et al.* 2002) and the local viability or invasiveness of plants (Kercher & Zedler 2004). Thus, it is of crucial importance to consider interactive effects of disturbances when evaluating population dynamics and informing management decisions for endangered and nuisance species (Dahlgren & Ehrlén 2009; Mandle, Ticktin & Zuidema 2015).

Variation in the effects of common population drivers has been documented previously (Crone *et al.* 2011). For instance, we now know that predation and herbivory significantly affect population dynamics, often by reducing survival and/or fecundity of individuals of the target species (Krupnick & Weis 1999, Creel *et al.* 2007). These effects may vary temporally (Austrheim, Solberg & Mysterud 2011), spatially (Pennings & Silliman 2005), or even due to co-evolved compensation of predation pressure (Rautio *et al.* 2005). Furthermore, evidence exists that the effects of predation and herbivory may also be mediated by other biotic or abiotic factors (Bale *et al.* 2002; Byrnes *et al.* 2006). One of the disturbances that can most drastically affect populations is fire (Bond, Woodward & Midgley 2004), a dominant ecological disturbance in many ecosystems of the world (Bond & Keeley 2005). Furthermore, demographic effects of fire may interact with precipitation (Burgman & Lamont 1992), interspecific competition

(Melgoza, Nowak & Tausch 1990) and herbivory (Hegland, Jongejans & Rydgren 2010).

To further complicate this picture, both biotic and abiotic demographic drivers often occur against a backdrop of anthropogenic disturbance. Human disturbances can produce a wide repertoire of effects depending on the nature of the disturbance and target species, ranging from facilitating invasions (Gibb & Hochuli 2003) to causing local extinctions (Michalski & Peres 2005). For instance, roads are known to alter competitive plant interactions (Gelbard & Belnap 2003) and can cause genetic depression via habitat fragmentation (Keller & Largiader 2003; Jump & Penuelas 2006). Anthropogenic disturbance along sandy roads can increase fecundity, likely due to reduced belowground competition, and population instability in several Florida scrub endemic species (Quintana-Ascencio, Weekley & Menges 2007; Schafer *et al.* 2010; Oakley 2013). Herbivory (Cadenasso & Pickett 2000) and competition (Byers 2002) differ between anthropogenic and native habitats. Roadsides alter the rates and intensity of herbivory (Kettenring, Weekley & Menges 2009). Moreover, herbivory can either increase or reduce the effects of fire or anthropogenic disturbance (Fuhlendorf *et al.* 2009).

Complex life cycles may add an additional layer of challenges to the study of population dynamics. Many species are characterized by life cycles consisting of stages that differ drastically in morphology, physiology, or in sensitivity to environmental variation (e.g. Fox 1981; Parker *et al.* 2003). A/biotic factors may affect differing parts of such complex life cycles at different magnitudes or even in opposing directions (Benton, Plaistow & Coulson 2006). Understanding how differing portions of a life cycle are affected by a/biotic drivers is thus a crucial step in the successful management of many species (Silvertown, Franco & Menges 1996; Caswell 2001).

The flexibility of matrix population models (MPM) makes them ideal to study complex interactions. However, only 40 of 396 recently reviewed plant MPMs assessed the effects of environmental factors, 28% of these examined a single factor, and only 16% assessed biotic interactions (Crone *et al.* 2011). The percentage drops to 8% when examining studies that have quantified interactive effects of two or more factors (Salguero-Gómez *et al.* 2015). The lack of studies assessing the interactive effects of these factors thus represents a significant gap in our understanding of population dynamics.

We studied the importance (magnitude) and direction (negative/positive) of the effects of herbivory, fire, anthropogenic disturbance, and their interactions, on the population dynamics of an endangered endemic Florida scrub species, *Liatris ohlingerae* (Asteraceae). This perennial, fire-resprouting species has a complex life cycle with vegetative dormancy (Weekley & Menges 2003). We built hierarchical integral projection models (IPM) to evaluate the interactive effect of the aforementioned disturbances on its population growth rates (λ) through their effects on the underlying vital rates of survival, growth, dormancy, reproduction and recruitment. *L. ohlingerae* is a long-lived species (>10 years max life expectancy) that resprouts after fire, its population dynamics after fire should be more stable than documented for shorter lived herbaceous species in the same ecosystem that rely on recruitment from the seedbank (Franco & Silvertown 2004; Paula *et al.* 2009). We expect that frequent disturbances and openness in roadside should result in higher fecundity due to reduced competition, and lower overall survival due to the increased mortality (Quintana-Ascencio *et al.* 2007; Oakley 2013), and that more frequent herbivory in roads and recently burned scrub should modulate positive demographic effects of reduced competition on roadsides and after fire, owing to effects of herbivory on survival and fecundity (Kettenring *et al.* 2009). We evaluated the interactive effects between fire and herbivory among scrub populations and, because roads do not burn we assessed the effects of herbivory between roadside and scrub as a whole.

Methods

Study Site and natural history

The study was conducted in Florida scrub, primarily at Archbold Biological Station (27°18’ N, 81° 35’ W, 35-65 m a.s.l.), Venus, FL., USA. Data from additional populations were collected at nearby sites in Gould Road Scrub (27°07’ N, 81° 30’ W) and Lake Wales Ridge State Forest (27 °66’ N, 81° 40’ W, 22.9-30.5 m a.s.l.). All sites occur in the southern portion of the Lake Wales Ridge, a relict sand dune system formed from sediment deposition in the Pleistocene (Abrahamson *et al.* 1984). The climate is sub-tropical and is typically defined by a warmer rainy season and a cooler dry season. Soils are xeric, nutrient poor and sandy. The Florida scrub is characterized by denser patches of Florida rosemary (*Ceratiola ericoides*), xeric oaks (*Quercus* spp.) and palmettos (*Serenoa repens)* interspersed by open gaps including a large number of endemic herbs (Abrahamson *et al.* 1984; Menges *et al.* 1999). The ratio of open patches to shrubby patches is primarily mediated by fire frequency (Hawkes & Menges 1996). Herbivory pressure from vertebrates, particularly white-tailed deer (*Odocoileus virginianus*), is high, with average herbivory rates of reproductive plants being greater than 50% in many cases (Kettenring *et al.* 2009).

Liatris ohlingerae S.F. Blake B.L. Rob. (Asteraceae) is an herbaceous perennial endemic to the Lake Wales Ridge (Evans, Menges & Gordon 2003). Individuals form a corm from which aboveground biomass is produced yearly (Dolan *et al.* 1999). Aboveground biomass dies back during November-December. Flowering scapes are developed in mature individuals during June-

September and its maximum observed lifespan exceeds 10 years (Evans *et al.* 2003). Individuals are self-incompatible (Evans et al. 2003) and genetic differentiation between populations is minimal, although overall genetic diversity is fairly high (Dolan *et al.* 1999). This species exhibits high rates of germination and likely lacks a long term seed bank (Weekley *et al.* 2008; Stephens, Castro-Morales & Quintana-Ascencio 2012). Still, recruitment is often low (Menges *et al.* 2010). The positive effects of fire on its population dynamics are likely related to the maintenance of gaps and reduction of competition (Hawkes & Menges 1996; Menges *et al.* 2008). However, the occurrence of *L. ohlingerae* increases slightly with time-since-fire (Miller *et al.* 2012) and it is not a gap specialist species (Menges *et al.* 2008). Interactions between herbivory (mostly by white-tailed deer), time-since-fire (*TSF* hereafter), and roads affect *L. ohlingerae,* with higher rates of herbivory occurring in recently burned and non-roadside habitats (Kettenring *et al.* 2009).

The life cycle of *Liatris ohlingerae* consists of three distinct life history stages (Fig. 1A): vegetative, reproductive, and vegetative dormant. Vegetative individuals have one or more grassy rosettes. Reproductive individuals develop one or more reproductive stems (scapes). Dormant individuals produce no aboveground biomass in a given year (Shefferson 2009), and instead remain alive exclusively belowground. This species has no clonal reproduction. All possible transitions between these stages may occur between years.

Study design

We collected demographic data of *L. ohlingerae* annually in August from 1998 (in the earliest permanent plot; see Table S1 in supporting information) through 2012 for 20 populations, resulting in a total of 2,345 individuals. At each population, we established permanent plots ranging from 5 m^2 and 600 m^2. We split plots among populations that occurred in the interior of the scrub (*scrub* hereafter) and populations along the edge of unpaved, sandy roads (*roadside*). We further divided populations within the scrub into three time-since-fire (TSF) categories based on unique and known burn histories: <10, 10-20, or >20 years. Roadside populations never experienced fire. Populations were also broadly categorized into two spatially distinct groups (above and below latitude (27 ^{o}0918' N; Table S1 in supporting information) along a north-south axis to test for the possibility of spatial variation. Average annual rainfall and temperature were obtained from Archbold Biological Station (http://www.archbold-station.org/data/weather/ABSweather.cfm).

In order to track individuals of *L. ohlingerae*, within each permanent plot, we individually marked new seedlings with a numbered tag. Seedlings were distinguished from established individuals awakening from vegetative dormancy through anatomic features related to leaf size and number. Data collected for reproductive individuals included total stem length, number of flowering heads, and occurrence of vertebrate herbivory, or "topping". We recorded leaf number and rosette number for vegetative individuals. Damage by vertebrate herbivory was not easy to detect in vegetative individuals and it was not recorded. Tagged individuals not found in the subsequent years aboveground for one year were assumed dormant. "Missing" individuals for two or more years were assumed dead the first year they went missing (*i.e.* in our models mortality does not happen while dormant). Missing individuals in the final year (2012) used in our models were assigned as dormant or dead using data from censuses after 2012 (Menges *et al.*, unpublished data).

Demographic modelling

We constructed three-stage integral projection models (IPMs, Easterling, Ellner & Dixon 2000; Ellner & Rees 2006) to model the life cycle of *L. ohlingerae* using modified code (Ellner

& Rees 2006; Metcalf *et al.* 2013) in *R* (3.0.1, R Development Core Team). In order to model all three stages (dormant [*d*], vegetative [*v*], and reproductive [*r*]), we constructed and merged the following elements to form an overall Goodman matrix (Goodman 1969): (1) four continuous kernel functions: $K_{v,v}$, $K_{v,r}$, $K_{r,v}$, $K_{r,r}$, where $K_{i,j}$ represents transitions from stage *j* (*v* or *r*) in time *t* to stage *i* in *t*+1 (Caswell 2001), (2) four vectors describing transitions involving dormancy as the origin or end stage: $\mathbf{D}_v$, $\mathbf{D}_r$, $\mathbf{V}_d$, $\mathbf{R}_d$, and (3) a scalar quantity D_d indicating the probability of stasis for dormant individuals (Equation 1 and Fig. 1B):

$$\begin{pmatrix} \boldsymbol{V_d} & \boldsymbol{R_d} & D_d \\ P_{r,v} & P_{r,r} & \boldsymbol{D_r} \\ P_{v,v} & P_{v,r} & \boldsymbol{D_v} \end{pmatrix} \qquad \text{Equation 1}$$

The Goodman matrix model describes the population dynamics of three stages, one discrete (dormant), and two continuous (vegetative and reproductive), where individuals are classified by leaf number and log of total stem length, respectively. As in the more established matrix population models (Caswell 2001) and IPMs (Easterling et al. 2000), our hybrid model's eigenstructure has properties that allow us to quantify population growth rates, as well as sensitivities and elasticities with respect to matrix elements or underlying vital rates (Caswell 2001; Tuljapurkar, Horvitz & Pascarella 2003). Furthermore, our model allows us to examine the interactive effects of the parameters linking size, a/biotic factors and their interactions to all vital rates (Merow *et al.* 2014; Zambrano & Salguero-Gómez 2014).

In order to test our hypotheses on the additivity or interactive effect of various disturbances on the population dynamics of *L. ohlingerae*, we carried out model selection to assess the effects of environmental variables (TSF, herbivory, site, precipitation, and roads) and their interactions on each vital rate (vegetative and reproductive survival, transition probabilities between reproductive, vegetative and dormant stages, and growth within vegetative and reproductive stages). We modelled each vital rate using generalized linear models (GLMs). Specifically, we used binomial error distributions for survival (σ) and probability of transitioning between stages (T), normal for changes in size of reproductive plants ($\gamma_{r,r}$, $\gamma_{v,r}$), Quasi-Poisson for changes in number of leaves of vegetative plants ($\gamma_{v,v}$), and negative binomial for flower counts (φ_1) and changes in number of leaves of vegetative plants ($\gamma_{r,v}$). We used Akaike Informantion Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002) to select the most plausible models (Table S2). We checked for overdispersion and when identified (Zuur et al. 2009) we proceed using qAICc scores instead. Upon inspection of the individual models, if there was no evidence of significant interactions we retained only additive effects.

We used a megamatrix approach (e.g. Pascarella & Horvitz 1998) to simulate the coupled dynamics of individuals damaged by herbivores and not-damaged by herbivores in different times-since-fire (< 10, 10-20 or > 20 years), habitats (roadside, scrub), precipitation (high, low) and locations (north, south). High precipitation and low precipitation were defined as those years with above and below the median rainfall (135 cm/year). We first estimated the size-specific probabilities of being damaged by herbivores in time t conditional on herbivory status in time t - 1 for each of the 20 combinations of environmental conditions. Our megamatrix allows for all four possible herbivory transitions between both conditions: damaged *vs*. not-damaged by herbivores. Next, we combined these probabilities with the IPM models with individuals damaged and not-damaged by herbivores to build the megamatrix. Since herbivory was only evaluated in reproductive individuals, non-reproductive individuals were distributed among submatrices using the same probabilities as for reproductive individuals.

Because roads do not burn, we constructed two separate IPMs. The *Habitat Model* was parameterized with data from all populations, while the *Time-Since-Fire (TSF) Model* was parameterized with Florida scrub population data only. In one case where the most plausible models for a vital rate differed radically between the Habitat and TSF models, the overall (Habitat) model was retained because the Habitat model was based on more data and the AIC deltas within the set were < 2. For vegetative plants, we estimated probability of survival, transition probabilities into vegetative, reproductive or dormant stages, and changes in number of leaves. The kernel functions for vegetative individuals that remained vegetative and vegetative individuals that became reproductive are described in equations 2 and 3.

$$P_{v,\,v}(x,y) = \sigma_{\mathrm{v}}(x) \times (1\text{-}T_{v,r}(x,y)) \times \gamma_{v,v}(x,y) \qquad \text{Equation 2}$$

$$P_{\mathrm{r,v}}(x,y) = \sigma_{\mathrm{v}}(x) \times (\ T_{\mathrm{r,v}}(x,y)) \times \gamma_{\mathrm{r,v}}(x,y) \qquad \text{Equation 3}$$

where P, following standard IPM notation (Easterling et al. 2000), indicates the kernel of each sub-matrix, σ indicates survival of an individual of size x in year t to the next year t+1, $T_{i\,j}$ indicates the probability of transitioning from stage j in time t to stage i in time t+1; possible for t + 1 here are v (vegetative), r (reproductive) or d (dormant). Changes in size between year t and t+1 are indicated by $\gamma_{i,j}(x,y)$. Size (x and y) in vegetative individuals was quantified as number of leaves (ranging between 1 and 25) and was modelled using either a quasi-Poisson (vegetative to vegetative) or negative binomial (reproductive to vegetative) error distribution.

We used a similar kernel for reproductive individuals, but the state variable in this case was stem length (cm) and the kernel $K_{i,j}$ contained survival-dependent processes ($P_{i,j}$) as well as reproductive processes ($F_{i,j}$; equation 4). Reproduction was modelled as the number of heads per capita (φ_1, with negative binomial error), and five constants quantified elsewhere for the same species and field sites (Stephens et al. 2012, Weekley 2008, Menges, unpublished data): number of seeds per head ($\varphi_{2,}$), pre- and post-dispersal seed predation collected from estimates of boring insect damage and experimental data on seed removal (φ_3, φ_4), seed viability and germination rates based on growth chamber trials (φ_5, φ_6). This procedure likely represented an overestimation of successful reproduction because we did not have estimates of all possible sources of seed mortality. To compensate, we included a correction factor (φ_7) that adjusts the estimated value to be more consistent with the observed number of germinants in the field (e.g. Quintana-Ascencio, Menges & Weekley 2003; Rose et al. 2005). Successful germinants were assigned a vegetative size based on the observed distribution of first year plants. Thus, we defined the kernel functions for reproductive individuals as:

$$K_{i,j} = P_{i,j} + F_{i,j} \qquad \text{Equation 4}$$

$$P_{r,r}(x,y) = \sigma_r(x) \times T_{r,r}(x,y) \times \gamma_{rr}(x,y) \qquad \text{Equation 5}$$

$$F_{\mathrm{v,r}}(x,y) = (\varphi_1 \times \varphi_2 \times \varphi_3 \times \varphi_4 \times \varphi_5 \times \varphi_6 \times \varphi_7) + (\sigma_{\mathrm{r}}(x) \times (1-T_{r,r}(x,y)) \times \gamma_{v,r}(x,y)) \qquad \text{Equation 6}$$

We estimated size dependent probability of entering dormancy from either reproductive (R_d) or vegetative (V_d) stages. We obtained size distributions of individuals leaving dormancy and entering either reproductive (D_r) or vegetative (D_v) stages. The probability of entering a given continuous stage from dormancy is given by scalar quantities. The probability of individuals remaining dormant ($\mathrm{D_d}$) more than a year was assumed to be zero as it occurred infrequently ($\mathrm{D}_{\mathrm{d}(t=0,t\geq 2)} = 0.016$), and the sensitivity of population growth rate (λ) to $\mathrm{D_d}$ was negligible (not shown). This assumption allowed us to distinguish mortality and dormancy in the final years used in the model. We calculated bootstrapped 95% confidence intervals for the estimated population growth with 200 iterations for each combination of study variables. Additional iterations did not significantly change confidence intervals for a sample of scenarios.

Results

Vital rates and herbivory rates

The most plausible models for each vital rates were summarized in Table 1 (details and plots were shown in Figs. S1 and S2 and Table S2). Survival of vegetative plants was higher in individuals with a small or large number of leaves, and was significantly higher in roadside plots than in scrub and in years with higher precipitation. Survival of reproductive individuals increased significantly with increasing plant total stem length and in the Northern region. Herbivory had a significantly negative effect on the survival of reproductive individuals.

There was a significant higher probability of becoming reproductive from the vegetative stage in roadside habitats as well as a marginal increase in this probability with increased rainfall. In the TSF model, there was a non-significant increase for the probability of a vegetative individual becoming reproductive with increasing time-since-fire (Table 1). The probability of a vegetative transitioning to a dormant individual included only a small decrease in dormancy with increasing number of leaves in both the Habitat and TSF models.

Herbivory showed a negative relationship with the probability of reproductive individuals remaining reproductive in both models. However, in the Habitat Model, there was a significant positive interaction between habitat and herbivory. The probability of reproduction increased with total stem length and in the roadside habitat without herbivory. The rate of dormancy from the reproductive stage significantly decreased in the roadside habitat and increased with herbivory. In the TSF Model, dormancy of reproductive individuals varied with total stem length, time-since-fire, herbivory, region, and precipitation (Table 1). Dormancy decreased with, time-since-fire, and in the northern region. Longer stem length led to significant decreases in dormancy rate in both models and higher precipitation significantly increased dormancy in both models. In addition to the additive effects, there were interactions between total stem length and time-since-fire, habitat and herbivory, and time-since-fire and herbivory.

Number of reproductive heads increased strongly with increasing stem length. In the Habitat model, fecundity increased in the roadside and decreased with higher herbivory. In the TSF model number of reproductive heads decreased with increased TSF and latitude of the region. There was a slightly positive, though non-significant, direct effect of herbivory, however there was also negative interaction between TSF and herbivory.

Herbivory rates were generally high across all environmental conditions (~50 %; Fig. S3). Roadside populations consistently experienced higher herbivory rates as compared to scrub populations, except for long-unburned populations in the southern region. Populations burned long ago generally experienced higher herbivory, but variation was high between environmental conditions. There was no consistent herbivory pattern observed with latitude or precipitation.

Population growth rates

In the Habitat Model, population growth rates (λ) ranged from 1.23 - 1.71 (Fig. 2A). Roadside populations exhibited higher and more variable λ across all sets of environmental conditions. This trend was less pronounced for herbivory scenarios, where differences in λ between road and scrub ranged from 0.31 - 0.35 as compared to 0.40 - 0.43 in scenarios without herbivory. This is due to a marked decline in λ in roadside populations with individuals damaged by herbivores compared to a relatively modest decline in scrub populations with individuals damaged by herbivores. Northern populations produced higher λ than southern populations. High precipitation also produced consistent but modest improvements in λ.

In the Habitat megamatrix, roadside populations once again outperformed scrub populations across all combinations of region and rainfall, despite higher rates of herbivory (Fig. 2B). These differences were relatively uniform, ranging from λ = 0.36 to 0.39. These values are intermediate between the results of the populations with only individuals damaged and not-damaged by herbivores. Populations in northern sites had marginally higher λ than populations in southern sites. Populations in high rainfall years had marginally higher λ than those in low rainfall years.

In the Time-Since-Fire model, λ varied only a small amount, and ranged only between 0.97 - 1.06 (Fig. 2C). In all scenarios λ decreased with increasing time- since-fire. The difference in λ between the highest and lowest time-since-fire classes ranged from 0.02 to 0.05. However, herbivory increased the difference in λ due to time-since-fire. Northern populations had marginally higher λ than southern populations. High precipitation led to a small but consistent improvement in λ both with and without herbivory. In the Time-Since-Fire megamatrix, the negative effect of time-since-fire was consistent (but their 95 % bootstrap CIs always overlapped) in all environmental combinations (Fig. 2D). The differences in λ were once again intermediate between the results of the populations with only individuals damaged and not-damaged by herbivores and from 0.033 to 0.038.

Discussion

Populations of sessile organisms, such as plants, are particularly prone to effects from abiotic and biotic disturbances (Gelbard & Belnap 2003; Bond *et al.* 2004). Such disturbances typically occur in concert, rather than in an isolated manner, thus giving rise to potential amplification and dampening in ecological outcomes (Dahlgren & Ehrlén 2009; Mandle *et al.* 2015). Here we have quantified the complex synergistic effects of herbivory, fire, and habitat on the population dynamics of the endemic plant *Liatris ohlingerae*. Our integral projection models revealed higher and more variable population growth rates in roadsides than in scrub habitats, and slightly higher population growth rates in recently burned than longer-unburned populations. In addition, population growth rates were strongly influenced by interactions of both habitat and time-since-fire with vertebrate herbivory. Spatial and climatic effects (precipitation) played a secondary but significant role.

Liatris ohlingerae in sandy roads experienced higher survival in both vegetative and reproductive stages, as well higher fecundity. Shorter-lived scrub endemics of the same region, such as *Hypericum cumulicola* and *Paronychia chartacea* (Quintana-Ascencio *et al.* 2007; Oakley 2013; Schafer *et al*. 2010), experienced higher fecundity but more variable survival in roadsides. Higher survival rates in *L. ohlingerae* and increasing fecundity in general may result from decreased competition in this human disturbed habitat (Petrů & Menges 2003).

Liatris ohlingerae in roadside populations maintained a higher population growth rate under both the condition of full herbivory and in the herbivory megamatrix in comparison with scrub populations. This is despite the fact that individuals in roadside populations generally experienced higher levels of herbivory (Kettenring *et al.* 2009; Fig. S1 in supporting information) and had a larger decrease in population growth rate under herbivory conditions. The differences in population growth rate response to herbivory were most likely mediated through impacts on fecundity and the transitions among stages. These effects may be due to differences in intensity of herbivory and/or a shift in the sizes of plants attacked (Brudvig & Quintana-Ascencio 2003). Differences in herbivore choice and intensity has been previously reported to change with disturbance and vegetative structure in other systems (Jefferies, Klein & Shaver 1994; von Euler, Ågren & Ehrlén 2014). This may indeed affect fecundity both negatively (Kolb 2012) and positively (Shimamoto *et al.* 2011). However, it should be noted that despite the consistently higher population growth rates observed in roadside populations, they may be exposed to an increased potential of total population destruction associated with anthropogenic disturbance, which may negate some of the benefits associated roadsides (Quintana-Ascencio et al. 2007).

Unexpectedly, we found a smaller effect of time-since-fire than habitat on the population growth rates of *L. ohlingerae*. Increasing time-since-fire had a consistent negative effect on population growth rate that amplified in populations with individuals damaged by herbivory. The moderate fire effects on *L. ohlingerae* contrasts with several other co-occurring, well documented species of the Florida scrub such as *Hypericum cumulicola*, *Eriogonum longifolium* var. *gnaphalifolium, Eryngium cuneifolium, or Dicerandra frutescens,* where population growth rates are typically much higher in recently burned than long-unburned populations (Satterthwaite, Menges & Quintana-Ascencio 2002; Quintana-Ascencio, Menges & Weekley 2003; Menges & Quintana-Ascencio 2004; Menges *et al.* 2006).

The demographic resilience to herbivory in roadside habitats, the higher survival in roadsides, and the moderate effect of TSF on the populations of *L. ohlingerae* are consistent with the more stable population dynamics often observed in longer-lived species (García, Picó & Ehrlén 2008; Kuss *et al.* 2008; Dahlgren & Ehrlén 2009) as well as species that resprout post-fire

(Menges and Kohfeldt 1995, Abrahamson and Abrahamson 2009). The moderate effect of time-since-fire on *L. ohlingerae* population growth rates is also consistent with occurrence data for Florida rosemary patches with different times-since-fire (Miller *et al.* 2012), whereby some populations are found in older burned patches. The relatively smaller effect of fire on *L. ohlingerae,* in comparison to other endemic herbs in the same system (e.g. Quintana-Ascencio *et al*. 2003) underscores the importance of fully understanding the life-history strategies of a species as well as its interactions with the environment.

Our study highlights the advantages of combining environmental interactions with a fine-scale approach to modelling (e.g. Dahlgren & Ehrlén 2011; Mandle *et al.* 2015). The viability of incorporating complex life cycles into IPMs has been well studied (Ellner & Rees 2006; Salguero-Gómez *et al.* 2012; Metcalf *et al.* 2013; Merow *et al.* 2014). However, in practice, most studies include one or more discrete stages with a single continuous stage rather than multiple continuous stages (Ramula, Rees & Buckley 2009; but see ; Zambrano & Salguero-Gómez 2014). By incorporating multiple stages, based on continuous, count, and discrete data with environmental interactions, this study allows us to disentangle the effects of interactions between environmental factors and complex life history strategies. For example, we demonstrate how dormant, vegetative and reproductive stages of *L. ohlingerae* respond differently to fire, herbivory and anthropogenic activities that interact to determine the persistence of this species.

There were several assumptions in our model that need consideration. Fecundity was particularly difficult to estimate since involved several phases between seed production and establishment for which we had only point estimates. Consequently, our lambda values should be taken as relative responses more than actual estimates. Our bootstrapping method provided a limited estimate of uncertainty since we did not include variation in several processes nor all correlated effects. Our estimate of herbivory was incomplete since we did not evaluate herbivory on vegetative plants nor herbivory by invertebrates on reproductive individuals. However, topping by deer produces significant biomass changes that were not observed in vegetative plants nor for other consumers.

Observed differences in *Liatris ohlingerae's* response to fire and habitat changes compared to other endemics in the same area demonstrate the folly of one-size-fits-all management strategies. Management interventions such as frequent fire, which is beneficial to certain species (Quintana-Ascencio *et al.* 2003; Menges *et al.* 2006), may have neutral or even negative effects on other species (Schurbon & Fauth 2003). Our study highlights the importance of considering different stages and the interaction of multiple drivers to understand their demographic effects. Further understanding of these interactions may therefore lead to improved management strategies in threatened species.

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Data Accessibility

Data supporting this article will be stored at Dryad (datadryad.org).

Additional supporting information may be found in the online version of this article:

Table S1. Summary of the populations used in this study. ABS = Archbold Biological Station, LWRSF = Lake Wales Ridge State Forest, GRS = Gould Road Scrub.

Table S2. Model selection and model summary tables. This table lists the model selection tables for each vital rate used in the study. In each case it is denoted whether AICc or QAICc was used as well as an estimated overdispersion parameter for each model. The model selected is denoted in bold. In cases where the model selected is not the model with the lowest (Q)AICc score, a short explanation of the reasons follows. In addition a small summary of the selected model is presented after each model selection table.

Fig S1. Vital rates of *Liatris ohlingearae* are strongly affected by the size of its individuals regardless of year and habitat type (black line: scrub; grey line: roadside). (A-E) correspond to vegetative individuals and x axis values represent number of leaves (A) survival, (B) probability of becoming reproductive next year, (C) becoming vegetatively dormant, (D) changes in size conditional on remaining vegetative (E), and changes in size conditional on becoming reproductive. (F-L) correspond to reproductive individuals and x axis values represent log of stem length (F) survival, (G) probability of becoming reproductive next year, (H) becoming vegetatively dormant, and (I) changes in size conditional on becoming vegetative (J) changes in size conditional on remaining reproductive (K) number of flowering heads produced. Solid lines indicate no herbivory, dashed lines indicate herbivory.

Fig S2. Vital rates of *Liatris ohlingearae* are affected by the size of its individuals and time since fire (TSF) (Black ≤10, Dark grey = 10-20, and Light grey ≥ 20 years since last fire). Panels A-E depict the vital rate functions of vegetative individuals, where size in the x axis is number of leaves: (A) survival, (B) probability of becoming reproductive next year, (C) becoming dormant, (D) changes in size conditional on remaining vegetative, and (E) changes in size conditional on becoming reproductive. Panels F-L correspond to reproductive individuals, where size in the x axis is log of stem length (cm): (F) survival, (G) probability of becoming reproductive next year, (H) becoming dormant, and (I) changes in size conditional on becoming vegetative (J) changes in size conditional on remaining reproductive, and (K)

Fig S3. Proportion of reproductive individuals damaged by herbivores in differing environmental conditions (high *vs* low precipitation and North *vs* South site).

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Table 1. Estimates and standard errors of predicting variables of all vital rate models for both the habitat (left) and time since fire (TSF, right) models. Statistically significant estimates at $P < 0.05$ are bolded. See figure 1 for further reference on demographic processes.

		Habitat model	TSF model
Vital rate	**Explanatory variable**	**Estimate (SE)**	**Estimate (SE)**
Vegetative survival (σ_v)	*Intercept*	0.196 (0.279)	0.257 (0.430)
	leaves	-0.067 (0.040)	-0.053 (0.045)
	leaves^2	0.004 (0.002)	0.003 (0.002)
	Habitat	**0.704 (0.139)**	NA
	Time-Since-Fire	NA	0.147 (0.093)
	Region	-	**0.267 (0.151)**
	Precipitation	**0.235 (0.115)**	0.198 (0.131)
Reproductive survival (σ_r)	*Intercept*	0.171 (0.277)	0.122 (0.329)
	length	**0.417 (0.038)**	**0.498 (0.044)**
	Habitat	**0.281 (0.104)**	NA
	Herbivory	-0.107 (0.098)	-0.043(0.119)
	TSF	NA	-0.030(0.080)
	Region	**0.331 (0.096)**	**0.409 (0.111)**
Vegetative- vegetative growth (γ_{vv})	*Intercept*	**0.945 (0.090)**	0.901 (0.111)
	# leaves	**0.149 (0.013)**	0.157 (0.014)
	# leaves^2	**-0.003 (0.001)**	**-0.003 (0.001)**
	Region	**-0.112 (0.048)**	**-0.102 (0.056)**
Vegetative- reproductive growth (γ_{vr})	*Intercept*	**3.717 (0.253)**	**3.450 (0.216)**
	# leaves	-0.034 (0.026)	-0.021 (0.014)
	# leaves^2	-0.001 (0.001)	-
	Region	**-0.280 (0.099)**	**-0263 (0.126)**
	Habitat	**-0.216 (0.103)**	-
Vegetative → reproductive ($T_{r,v}$)	*Intercept*	**-1.781 (0.282)**	-0.281 (0.499)
	# leaves	**0.226 (0.035)**	0.026 (0.103)
	# leaves^2	**-0.006 (0.001)**	-0.007 (0.005)
	Habitat	0.229 (0.124)	NA
	Precipitation	0.202 (0.118)	-
	Region	-	-0.312 (0.171)
	Time-Since-Fire	NA	-0.321 (0.219)
	leaves × TSF	NA	**0.153 (0.072)**
	leaves^2 *× TSF*	NA	**-0.012 (0.004)**
Vegetative → dormancy (V_d)	*Intercept*	**-2.263 (0.145)**	-2.17 (0.172)
	leaves	-0.025 (0.027)	-0.031 (0.032)
Reproductive → reproductive ($T_{r,r}$)	*Intercept*	-0.028 (0.271)	0.386 (0.248)
	length	0.018 (0.154)	-0.069 (0.172)
	length^2	**0.104 (0.027)**	**0.117 (0.030)**
	Habitat	**0.270 (0.134)**	NA
	Herbivory	**-0.657 (0.244)**	-0.146 (0.101)

	Habitat × *Herb*	**0.525 (0.177)**	NA
Reproductive-vegetative growth (γ_{rv})	*Intercept*	**1.020 (0.224)**	**1.362 (0.238)**
	length	-0.118 (0.093)	**-0.227 (0.104)**
	length^2	**0.043 (0.016**	**0.056 (0.017)**
	Habitat	**0.264(0.087)**	NA
	Precipitation	**0.185 (0.050)**	**0.213 (0.060)**
	TSF	NA	-0.008 (0.045)
	Region	**-0.159 (0.052)**	**-0.102 (0.065)**
	Herbivory	**0.555 (0.152)**	**0.249 (0.065)**
	Habitat × *Herb*	**-0.267 (0.110)**	NA
Reproductive-reproductive growth (γ_{rv})	*Intercept*	**3.539 (0.144)**	**3.646 (0.169)**
	length	**-0.401 (0.065)**	**-0.445 (0.078)**
	length^2	**0.136 (0.010)**	**0.140 (0.011)**
	Habitat	**-0.208 (0.049)**	NA
	TSF		-0.044 (0.029)
	Precipitation	**-0.101 (0.031)**	**-0.109 (0.038)**
	Region	**-0.043 (0.031)**	**-0.124 (0.042)**
	Herbivory	**-0.176 (0.091)**	-0.053 (0.038)
	Habitat × *Herb*	**0.127 (0.065)**	**-**
Reproductive → dormant (***R***$_d$)	*Intercept*	**-1.927 (0.341)**	**-1.815 (0.474)**
	Length	**-0.250 (0.053)**	**-0.296 (0.060)**
	Habitat	**-0.380 (0.138)**	NA
	TSF	NA	-0.051(0.104)
	Region	-	**-0.291 (0.153)**
	Herbivory	**-0.274 (0.126)**	-0.207 (0.146)
	Precipitation	**0.345 (0.126)**	**0.450 (0.150)**
Fecundity (φ_1)	*Intercept*	**-5.678 (0.105)**	**-4.788 (0.123)**
	length	**1.534 (0.105)**	**1.491 (0.023)**
	Habitat	**0.497 (0.030)**	NA
	Herbivory	**-0.078 (0.025)**	0.089 (0.067)
	Region	0.045 (0.025)	**-0.065 (0.032)**
	TSF	NA	-0.028 (0.027)
	TSF × *Herb*	NA	**-0.089 (0.043)**
Herbivory rate (X)	*Intercept*	**3.731 (0.389)**	**4.631 (0.551)**
	length	**-2.280 (0.197)**	**-2.620 (0.270)**
	length^2	**0.239 (0.027)**	**0.272 (0.036)**
	Habitat	**0.249 (0.075)**	NA
	Herbivory (Previous Year)	**0.547 (0.065)**	**0.571 (0.082)**
	Region	**0.254 (0.067)**	**0.323 (0.092)**
	Precipitation	**0.231 (0.065)**	**0.201 (0.084)**
	TSF	NA	0.039 (0.063)

Figure legends

Fig. 1. A. The life cycle of *Liatris ohlingearae* consisting of three stages: vegetative (*v*), reproductive (*r*) and vegetative dormant (*d*) individuals. Size in the vegetative stage was measured as number of leaves, and in the reproductive stage as total stem length. Light green, dark green and black arrows indicate transition probabilities of *v*, *r* and *v* individuals, respectively. Rates of dormancy: $\boldsymbol{V}_{\mathrm{d}}$, $\boldsymbol{R}_{\mathrm{d}}$ and D_{d}; Survival-size change kernels within and between vegetative and reproductive individuals: $P_{\mathrm{v,v}}$, $P_{\mathrm{r,v}}$, $P_{\mathrm{r,r}}$, $P_{\mathrm{v,r}}$; Vectors of emergence from vegetative dormancy into vegetative and reproductive stages: $\boldsymbol{D}_{\mathrm{r}}$, $\boldsymbol{D}_{\mathrm{v}}$. The yellow arrow corresponds to the kernel of reproduction, $F_{\mathrm{v,r}}$. Black dotted diagonal line represents no changes in size. **B.** Each demographic process is represented in the Goodman's matrix that accommodates kernels for the integral projection model, and vectors and scalars for the discrete section of the life cycle of the species, dormancy.

Fig. 2. Population growth rates (λ) predicted by (A) the habitat model under varying environmental conditions (B) the herbivory mega-matrix for habitat (C) the time-since-fire model under varying environmental conditions and (D) the herbivory mega-matrix for time-since-fire. Error bars represent bootstrapped 95% confidence intervals (200 iterations). Note differing Y axis scales between upper and lower panels. Horizontal dashed lines represent $\lambda = 1$, where populations are neither increasing nor declining on the long-term.

Figure 1

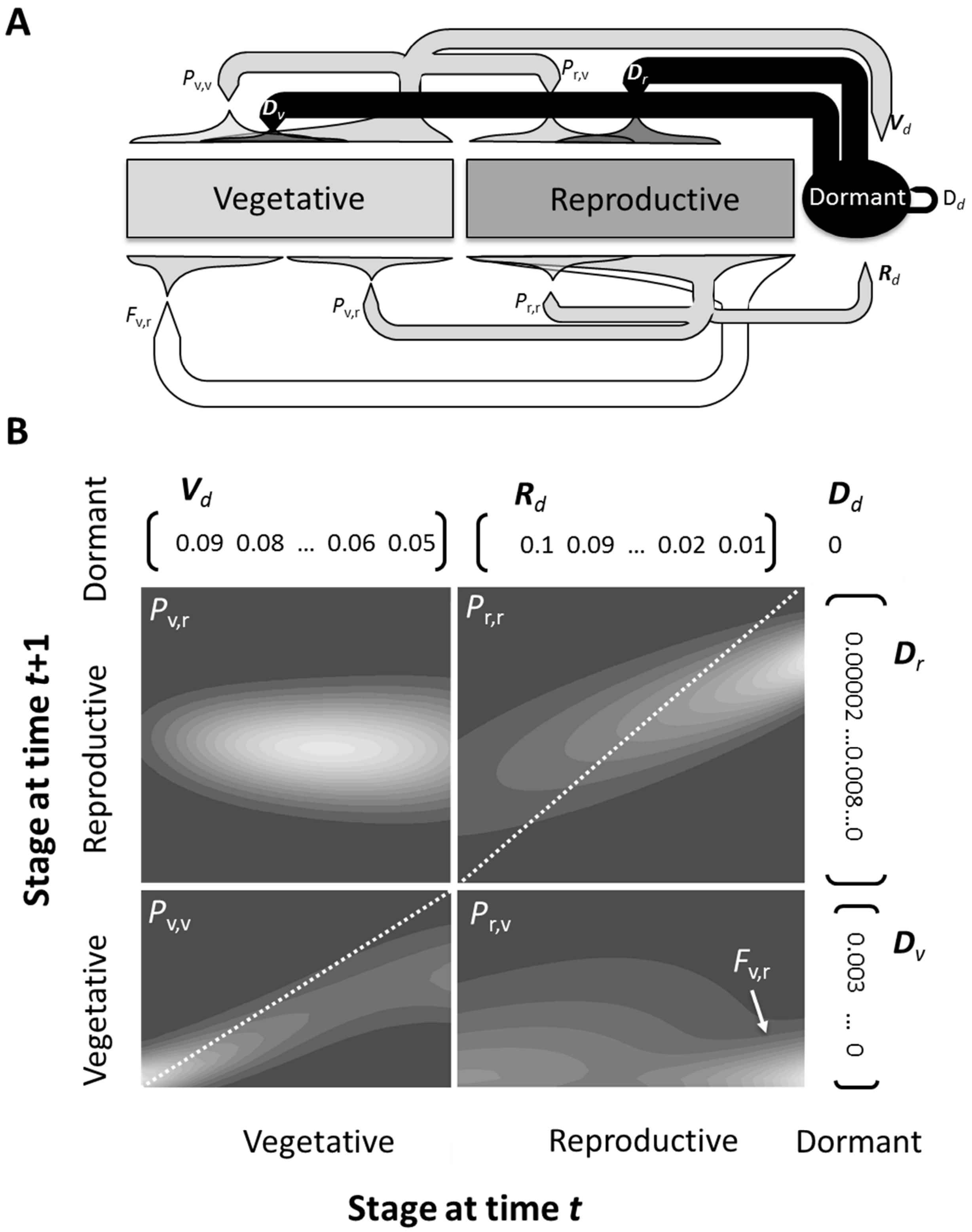
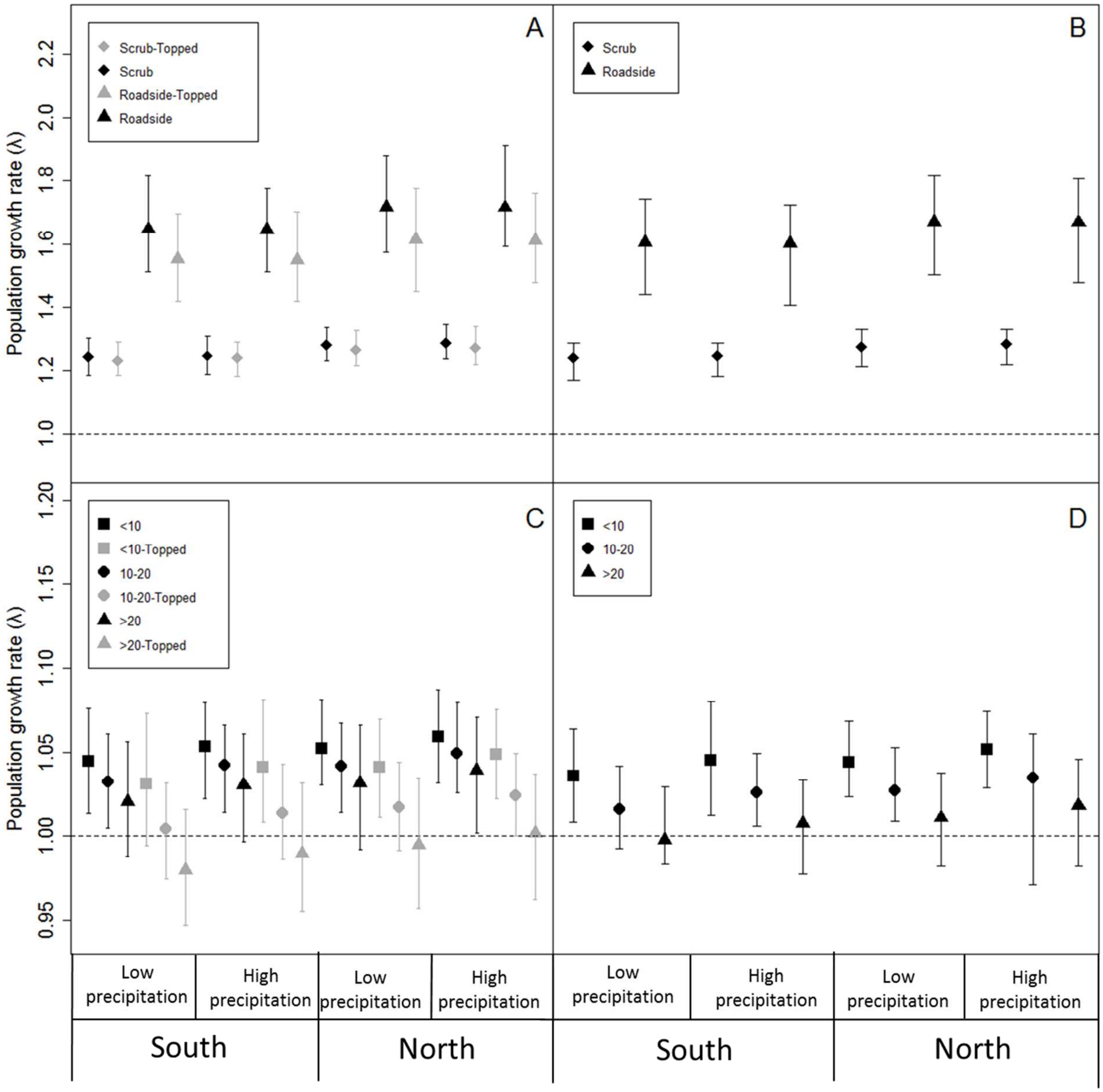

A
$P_{v,v}$
$P_{r,v}$
D_r
D_v
V_d
Vegetative
Reproductive
Dormant
D_d
R_d
$F_{v,r}$
$P_{v,r}$
$P_{r,r}$
B
V_d
R_d
D_d
0.09 0.08 ... 0.06 0.05
0.1 0.09 ... 0.02 0.01
0
Dormant
Reproductive
Vegetative
Stage at time t+1
$P_{v,r}$
$P_{r,r}$
$P_{v,v}$
$P_{r,v}$
$F_{v,r}$
D_r
0.00002...0.008...0
D_v
0.003 ... 0
Vegetative
Reproductive
Dormant
Stage at time t

Figure 2


A
Scrub-Topped
Scrub
Roadside-Topped
Roadside
B
Scrub
Roadside
Population growth rate (λ)
1.0
1.2
1.4
1.6
1.8
2.0
2.2
C
<10
<10-Topped
10-20
10-20-Topped
>20
>20-Topped
D
<10
10-20
>20
Population growth rate (λ)
0.95
1.00
1.05
1.10
1.15
1.20
Low precipitation
High precipitation
Low precipitation
High precipitation
South
North
Low precipitation
High precipitation
Low precipitation
High precipitation
South
North

Lauren Sandhu
Assistant Editor

Subject: Journal of Ecology - JEcol-2015-0316

Dear Lauren,

Please find below our detailed answers to the reviewers comments. We would like to thank you, the editors and the reviewers for your thoughtful suggestions and corrections. These commentaries significantly improved our document. We hope this version will meet the standards of **Journal of Ecology**. These manuscript emphasizes the importance of analyzing the synergistic impacts of multiple disturbances on population dynamics of plant species. In particular, we examined the interactive effects of vertebrate herbivory, fire, and anthropogenic activities on the population growth rates of an endangered and narrowly endemic Florida scrub herb, *Liatris ohlingerae.* We used 13 years of data from 20 populations to develop IMPs with three different stages and megamatrices evaluating the synergistic effects of these disturbances. We are convinced that these results on the importance of evaluating multiple disturbances contribute to our understanding of population ecology and had significant conservation and management implications.

Our answers are in italics and detailed after the reviewer's comments.

Reviewer's comments

The manuscript is quite interesting, but suffers from some major flaws. The authors should re-work major sections of the manuscript to address these issues. Most notably, both reviewers and I agree that the manuscript is rather difficult to read, and might deter ecologists who are not experts on matrix modeling. This is in part due to the density of technical jargon throughout the MS , but also due to a lack of general conclusions that can be used to guide other studies (really, the discussion currently offers only that studies would do well to incorporate stressors into their studies, rather than offering points about how stressors can generally impact ecological dynamics, nor about how the average ecologist, working with only 3-5 years of data, might manage to incorporate such trends/data meaningfully) . In addition, reviewer 1 raises a very strong point about methodology - that we really have no information provided here to infer whether the interaction terms used to make the major inferences are really worth making inferences with in the first place. I would strongly urge the authors to consider that criticism, and address it properly.

We have worked to reduce jargon throughout the manuscript. We decreased the modelling description by 250 words, the results by 300 words and simplified language throughout these sections.

Our discussion now details about how interactive disturbances can generally impact ecological dynamics. We described how population dynamics can differ between human and native habitats and among native habitats with different history of disturbance (first paragraph). We compared the population dynamics of our focal species with coexisting short lived species (second paragraph). We discussed potential explanations of the contrasting effect of herbivory between habitats and possible causes of the smaller effect of time-since-fire to the dynamics of our focal species compared with other endemic species (third and fourth paragraphs). We emphasized the advantages of combining environmental interactions with a fine-scale approach to modelling (sixth paragraph). We discussed some limitations of our approach and how they may affected our conclusions (seventh paragraph). We cautioned on the need to consider several stages and multiple disturbances to assess population dynamics *of other species (final paragraph). We would argue that these goals can also be reached with short term studies and this is not the main contribution of our study.*

In addition, I think that the authors could include a bit more data on the populations, particularly how many individual plants were observed in each population (right now, all that is presented is the study total and the number of individual observations per plot), and how the authors decided to delineate populations (the "sites" listed in the supplement look like plots to me, rather than actual populations).

We added number of individuals to Table S1 in the supplementary material and corrected number of observation to show the sum of the total number of times that each individuals was visited. Population is a concept that it is defined by the circumstances of a study. We argue that because Liatris ohlingerae inhabits rosemary scrub that occur as habitat islands within a matrix of more mesic vegetation and wetlands we can consider our sites represent different populations (Quintana-Ascencio et al 1996). However, we emphasize that we do not use this scale for analysis and group populations by region.

Finally, I found the figures to be confusing. The life cycle presented in fig 1a is not a standard model, and the use of thick overlapping arrows is rather difficult to look a t. Fig. 1b doesn't seem particularly important. Fig 2 and 3 seem to have too much information, most of which is probably not that important and can be moved to the supplements.

Figure 1a has been redesigned to eliminate the thick arrows and simplify its interpretation. We feel as though figure 1b provides a visual representation of the actual model structure and is thus informative and important to retain, as representation of the IPM kernel has become standard in IPM literature (e.g. Coulson 2012, Zambrano & Salguero-Gómez 2014).

Figures 2 and 3 were moved to supplementary material.

Referees' comments:

Reviewer: 1

COMMENTS FOR THE AUTHOR

Tye et al. use an arresting title to introduce analyses that assess the synergistic impacts of environmental change on the population dynamics of the herbaceous perennial *Liatris ohlingerae*, endemic to the Florida scrub. The data is enviable and the analysis has generated an abundance of results and figures.

Unfortunately, I have a series of issues with the analytical presentation and approach that, in my opinion, need addressing before the manuscript is acceptable for publication in the Journal of Ecology.

The synergistic "menage a trois" pivots on some very weak interactions (Table 1). The 3-way fecundity interaction is not statistically significant at the 5% level; the reproductive -> dormant interaction is marginally statistically significant at the 5% level (I assert this based on the coefficient and its standard error; t-values and/or p-values are not given in the table and should be included in any revision). Given the non-significant two-way interactions, reliance on a very weak three-way interaction does not make for a robust defence. If you are going to stick with the three-way interaction, it should be discussed and its effect over and above the two-way interactions declared. In the present version, this discussion would fit around lines 330-333.

We now have in Table S2 in supplemental material complete standard statistical summaries for the most plausible model of each vita rate including the values, standard errors and the significance of all the coefficients.

Based on the suggestion on the reviewer regarding to over parameterization, we only kept significant interactions. However, synergistic effects of disturbances arise not only from these interactions within vital rates, but also from non-overlapping (among various rates) or opposing effects between vital rates, making things a true ménage-a-trois. We have made edits throughout the text to make this clearer.

The major problem with this interpretation is that the authors have failed to incorporate overdispersion in their analysis. Overdispersion is an inflation (or deflation) of the standard error estimates, which impact statistical significance, based on the observed error distribution being different to the assumed by the model. For example, a Poisson glm assumes that the variance increases linearly with the mean. Overdispersion can change the gradient of the line. Overdispersion (when the variance increases linearly but with gradient >1) would increase the standard errors and therefore decrease statistical significance, pushing the marginal reproductive -> dormant interaction back into not significant territory. The opposite is also true: the if the gradient is <1, then the standard errors would decrease and statistical significance increase.

Following this advice, we assessed overdispersion in all vital rate models. We did find evidence for overdispersion in the vegetative to vegetative growth function as well as in flower production. To control for overdispersion we have modified the vegetative growth model to a quasi-Poisson distribution and flower production model to a negative binomial distribution. The new model for fecundity combined the probability of producing a head and heads per capita into a single function as includes producing zero fruits. These resulting changes lead to a better estimation of the vital rates in question and reduced concerns about overdispersion. The response of these new models changed some of the modelling results. We still document a different behaviour among populations in scrub and roadsides and interactive effect with herbivory but now we identified a larger response to time-since-fire with increasing effects in populations with damaged plants.

Since the analysis does not appear to be on an individual basis (there is no overdispersion for binary data), the overdispersion needs to be tested and reported in any revision. Model selection can then proceed using qAIC scores, which are controversial among pure statisticians but good enough for Ben Bolker: see an R implementation at http://cran.r-project.org/web/packages/bbmle/vignettes/quasi.pdf

We have assessed qAIC scores for all overdispersed vital rate models and proceed accordingly (lines 217-219 and Table S2 in supplemental materials).

The results feature phrases like "The most plausible model..." (284), "...was best predicted by a ..." (305) and "The most informative variables..." (310), but nowhere do we see a comparison table of model AIC scores with and without given parameters so I am required to assume this is the case. The model selection (line 210) is not present in the Results. Please include such a table in any revision that makes clear the evidence behind the support for given parameters and parameter interactions. This is crucial to address the focal question in the title - how much better are the models with three way interactions than simpler ones? Given the possibility of overfitting in Table 1 (weak three-way interaction, non-significant two-way interactions, small effect sizes [lines 357-360]), this new table should embrace Whittingham et al.'s (J Anim Ecol. 2006 Sep;75(5):1182-9.) call to abandon stepwise selection and compare the global model set.

Following this suggestion, we have included full model selection tables for each vital rate as well as whether or not AICc or QAICc was used based on the calculated over dispersion parameters in Table S2 of supplementary material. We agree with the reviewer about the shortcomings of stepwise selection, thus all model selection is based on comparisons of the full set of considered models.

More generally, why did the authors choose *not* to fit an LTRE to the problem? The title evokes an LTRE approach: impacts of climate on population dynamic parameters, even if not strictly an experiment but one that, nonetheless can be, and has been, explored in a statistical regression framework. Please justify this decision in the Discussion.

We agree with the reviewer that an LTRE could be a possible extension from the work presented. However, we are convinced that an LTRE is not an indispensable step to addressing the questions posed in this manuscript. Thera are several demography papers that have not used LTREs when assessing the impact of one or more environmental factors (Mandle et al 2015, Dahlgren and Ehrlén 2011). Additionally as we are lacking true control plots we would be forced to use controls based on midpoint matrices (Caswell 2001) which would be difficult to interpret in this case.

Other edits and queries

63: Delete etc. ***Done***

73: Delete Yet. ***Done***

*88 ... and *can* cause...* ***Done***

132: Where there significant differences among sites?

We did not evaluate differences among populations because large variation of sample sizes, instead we grouped the populations by region.

140: What does relatively mean? *We deleted the word relatively*

148: What does fairly mean? *We deleted the word fairly*

217: Akaike *Information* Criterion. *We corrected this sentence*

218: How are defining most parsimonious? Different readings of AIC scores evoke different definitions.

We used the model with lowest AIC weight except when indicated.

234: Define TSF before its first use here. ***Done***

252: ... variable *in* this case. ***Done***

280: Is 199 iterations enough? Where does the variability come from? I can't see it discussed elsewhere in the text.

During bootstrapping individuals (randomly selected with replacement) participating in the evaluation of the vital rates change among iterations producing variation in estimates (Manly B.F.J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, Chapter 1. Chapman & Hall). *We performed 499 iterations for two scenarios and found these commensurate with 199 and we decided reducing the number of iterations for subsequent simulations.*

387: Why is *Hypericum* a stressor?

This sentence was confusing as written. We changed the text to clarify the meaning.

393: Delete redundant words in this sentence (are able to), and elsewhere. . ***Done***

400: Define "strong". Where is this strong? See above. . ***Done***

441: Correct reference formatting. . ***Done***

Table 1: Why not the same explanatory variables for all models? A table summarising the mechanisms/hypotheses being tested in each would be useful.

We used the most plausible model per vital rate. See section on AIC above.

Fecundity models in Table 1: how is S2xH significant at a 5% level? The standard error is larger than the coefficient. If it is through the retention of a non-significant three-way interaction, then my concerns about overfitting and overinterpretation of results given the title are larger.

We reviewed all our models and removed all non-significant interactions. See also above argument on overdispersion.

It is clear that a lot of work has gone into the study, and I hope these comments help the authors revise their manuscript so that it realises its potential.

Reviewer: 2

COMMENTS FOR THE AUTHOR

This study uses sophisticated demographic modelling to examine the individual and interactive effects of herbivory, fire, roads and precipitation on the demography of a focal plant species. They find that each of these factors can affect demography, and most interestingly that there are interactions between factors. In particular, the effects of fire (expected to be strong in this system) are altered by herbivory, and roads turn out to be better for these plants than even burned natural habitat.

This study provides a nice integration of the effects of multiple factors on plant demography, and in doing so finds some surprising results. Data collection, analyses and conclusions all seem correct to me. The demographic modelling used here is a nice and unusual combination of different approaches. This paper is a valuable contribution to our understanding of plant demography and how to study it.

The writing in the introduction and discussion could, however, use some work to increase clarity (specific suggestions below). The paper reads as though the methods and results were carefully written and then the introduction and discussion were done with a bit less thought and care. It would be particularly helpful for the authors to lay out hypotheses or general questions that they then directly address or answer in the results and discussion. There is a lot of information in this paper and it is easy to get lost in the details. The authors could use that last paragraph of the introduction to better focus the reader on what the authors see as the main points of the study. I also suggest that the authors include a sentence or two in the introduction introducing the reader to the relatively unusual combination of IPMs and matrix modelling that is used in this paper. I suggest this both to highlight what I think is a strength of the paper (the modelling approach) and to prepare less quantitative readers for the general structure of what you are doing before the reader is lost in the details of the methods section. Just explain generally that this will be a combination of different approaches, each of which might be more familiar to general readers on its own. You already highlight the approach in the summary - do something similar in the introduction.

We modified the introduction and discussion to address these concerns.

Line 28: maybe replace "examine" with "determine"? . ***Done***

Line 35: why "cascading"? . ***Word removed***

Line 38: "herbivorized" is not a word. Rephrase. Same comment for all uses of "herbivorized" through the whole paper. Instead you could use "damaged by herbivores" or "eaten". ***Changed across the text***

Line 47: "this" should be "these" (to agree with "non-linearities"). Also, you just said in the previous sentence that the dynamics are not linear or nonlinear, but this sentence is now focused on non-linear dynamics. Why talk about non-linear when you said they aren't?

Line 49: "various sources of stress onto a plant population dynamic" is hard to follow. Maybe replace with "the effects of various sources of stress on the population dynamics of a plant, "? ***Changed***

Line 50: delete "through". ***Done***

Line 52: "on" should be "of" ***Changed***

Line 61: I wouldn't have included herbivory or especially allelopathy as disturbances. And what is "transformation"? I didn't read the cited paper, but I did ask a few ecologists I found nearby and none of them recognized this as a type of disturbance. Do you mean land-transformation due to development or agriculture? If so that seems like it would fit under "anthropogenic". ***Words changed or deleted***

Line 66: "outcome on" doesn't make sense. Replace "on" with "for". Also what does "their" refer to? As written it seems to refer to "dynamics" but it must refer to plants, so instead you could say "and the the local viability or invasiveness of plants". ***Done***

Line 68: "on" should be "for". ***Done***

Line 72: you are missing an "of". ***Done***

Line 118: this first question seems focused on comparing responses of two different plants to fire, which doesn't follow from the set-up earlier in the paragraph which focuses on factors affecting the demography of this one species. In general, this list of hypotheses didn't help me follow the rest of the paper. If you are going to list specific hypotheses like this, then I expect you to return to them explicitly in the discussion (e.g. "we hypothesized that. and in fact our data showed ..") but you don't do that. Either return to these hypotheses directly, or (and this would be my preference) use this paragraph to lay out the specific main effects and interactions you are testing for and why you expect them to be important. This is more how your discussion and results are structured, and would allow you to warn the reader that not all interactions between your three main factors can be tested. ***Changed***

Line 199: Seems like all the letters after the first ones in each element should be should be sub-scripts, to match the text and the later equations? ***Done***

Line 209: here you mention hypotheses about additivity, but you didn't state hypotheses specifically about additivity. Maybe restate your hypotheses to match.

We changed the text

Line 217: This should be "the Akaike Information Criterion", not Index, and usually without apostrophe. Why not cite Akaike instead of B&A?

Wording changed. We used AICc and the reference B&A describe this procedure.

Line 227: here you reference four possible transitions and then list two. I think you mean four transitions between damage states between years (damaged to damaged, damaged to undamaged, undamaged to damaged, undamaged to undamaged). If that is the case then you should call this transitions between stages or statuses, not transitions between stages (which are your three parts of the life cycle). ***Changed***

Line 231: It would help to state this as an assumption: that risk of attack is the same for reproductive and non-reproductive individuals. This is a pretty big assumption, and should be made really obvious to the reader. I would also consider addressing this assumption in your discussion.

Since we did not include herbivory to evaluate the fates of any vital rate of vegetative plants the allocation of vegetation plants in the megamatrix does not affect model output. We also argue in the text that vertebrate herbivory of reproductive individuals of L. ohlingerae resulted in large losses of biomass that we did not find in vegetative plants.

Line 232: This is the first time in the paper that I figure out you can look for interactions between fire and herbivory, or roads and herbivory, but not between fire and roads. It would help to lay this out when you state your hypotheses at the end of the introduction. ***Done***

Line 242: Should these two equations also be indexed for "herbivorized" or "not herbivorized"? It isn't clear to me how herbivory state enters into the model.

The GLMs used to build the IPMs include coefficients allowing the calculation of the effects of the different factors including herbivory. Including indices for each variable will made the equations awkward.

Line 362: This sentence is confusing - are you talking about growth rates in damaged and undamaged populations, or damaged and undamaged plants? Here is how it reads to me: Burned population growth rate is higher than undamaged population growth rate and unburned population growth is higher in plants that are damaged. Please clarify. Also, "was" should be "were" ***Changed***

Discussion in general: I would like to see some discussion of potential limitations to your study. All models make assumptions. Are there any key assumptions in this work that might influence the outcome? Limitations to the way you took data? One thing that stands out in particular is the assumption that herbivory is the same for different life stages. This is often not true in other systems. How might that assumption have affected your conclusions?

We have included a paragraph describing some potential limitations of our study.

Line 385: "for its performance" doesn't make sense here. ***Deleted.***

Line 397: "mitigate" should be replaced with "negate". This is an incorrect use of "mitigate" ***Changed.***

Line 400: the construction "interaction..on" doesn't make sense. Could re-write as "the strong effect on fecundity of the interaction between habitat, plant size and herbivory." ***Changed.***

Sentence starting line 402: This sentence doesn't make sense as written. Try "Herbivore preference for different plant sizes and the intensity of damage have been reported to.." (if I understand what you are saying correctly). ***Changed.***

Line 419: The sentence starting here isn't clear. When incorporating herbivory into what? As written it sounds like "the results of a model including herbivory had a similarly small effect of fire as a model including herbivory". ***Changed.***

Line 421: this sentence isn't clear to me either. The effects of fire in the non-herbivory model were reduced when herbivory was considered? But herbivory isn't in that model. Do you mean that the effects of fire are smaller in the model with herbivory than in the model without it? ***Changed.***

Line 430: "its" should be replaced with the species name. ***Changed.***

Line 431: should "in" be "for" or "from"? ***Changed.***

Line 436: It is good to have this paragraph about the strength and novelty of your approach. You could make it more convincing to non-quantitative readers by providing a specific example. Here you just generally say that by including this detail you could disentangle many things. How about a "for example, if we had used a simple matrix model alone we could not have done X, or an IPM alone would not have allowed us to do Y". ***Done***

Best regards,

Matthew Tye and co-authors

A demographic ménage à trois: interactions between disturbances both amplify and dampen population dynamics of an endemic plant

Matthew R. Tye, Eric S. Menges, Carl Weekley,
Pedro F. Quintana-Ascencio, and Roberto Salguero-Gómez

Supporting Information

Table S1. Summary of the populations used in this study. ABS = Archbold Biological Station, LWRSF = Lake Wales Ridge State Forest, GRS = Gould Road Scrub.

Region	Site	Individual Observations	Number of individuals	Years Measured	Habitat	Mean Herbivory Rate	2010 Time-since-fire
2	ABS	149	34	2003-2012	Scrub	0.41	25
2	ABS	293	63	2003-2012	Scrub	0.62	9
2	ABS	527	105	2002-2012	Scrub	0.61	9
2	ABS	539	89	2003-2012	Scrub	0.64	8
2	GRS	40	28	2005-2006	Scrub	0.43	NA
1	ABS	227	53	2000-2012	Scrub	0.54	0
1	ABS	494	124	2000-2012	Scrub	0.56	42
1	ABS	148	75	2000-2012	Scrub	0.44	74
1	ABS	564	116	2000-2012	Scrub	0.46	12
1	ABS	131	58	2000-2012	Scrub	0.67	2
1	ABS	449	147	2000-2012	Scrub	0.54	38
1	ABS	344	63	2000-2012	Scrub	0.66	0
1	ABS	473	109	2003-2009	Scrub	0.65	7
1	LWRSF	2559	710	1997-2012	Scrub	0.47	12
2	ABS	384	85	2003-2012	Roadside	0.49	Unburned
2	ABS	277	71	2003-2012	Roadside	0.45	Unburned
1	ABS	281	79	2003-2012	Roadside	0.49	Unburned
1	ABS	839	199	2003-2012	Roadside	0.52	Unburned
1	ABS	241	52	2003-2012	Roadside	0.35	Unburned
1	ABS	997	175	2000-2012	Roadside	0.34	Unburned

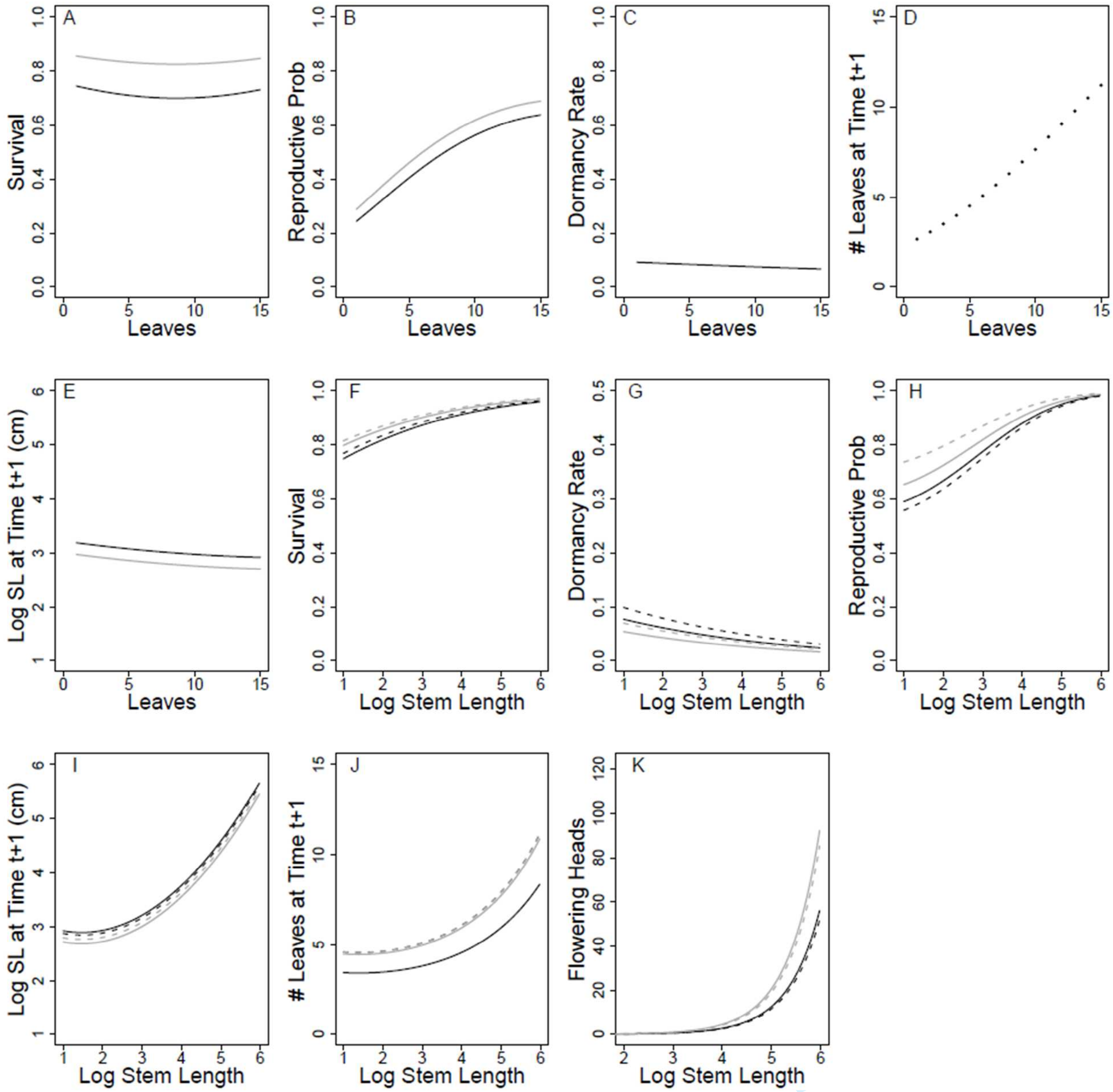


Fig. S1. Vital rates of *Liatris ohlingearae* are strongly affected by the size of its individuals regardless of year and habitat type (black line: scrub; grey line: roadside). (A-E) correspond to vegetative individuals and x axis values represent number of leaves (A) survival, (B) probability of becoming reproductive next year, (C) becoming vegetatively dormant, (D) changes in size conditional on remaining vegetative (E), and changes in size conditional on becoming reproductive. (F-L) correspond to reproductive individuals and x axis values represent log of stem length (F) survival, (G) probability of becoming reproductive next year, (H) becoming vegetatively dormant, and (I) changes in size conditional on becoming vegetative (J) changes in size conditional on remaining reproductive (K) number of flowering heads produced. Solid lines indicate no herbivory, dashed lines indicate herbivory.

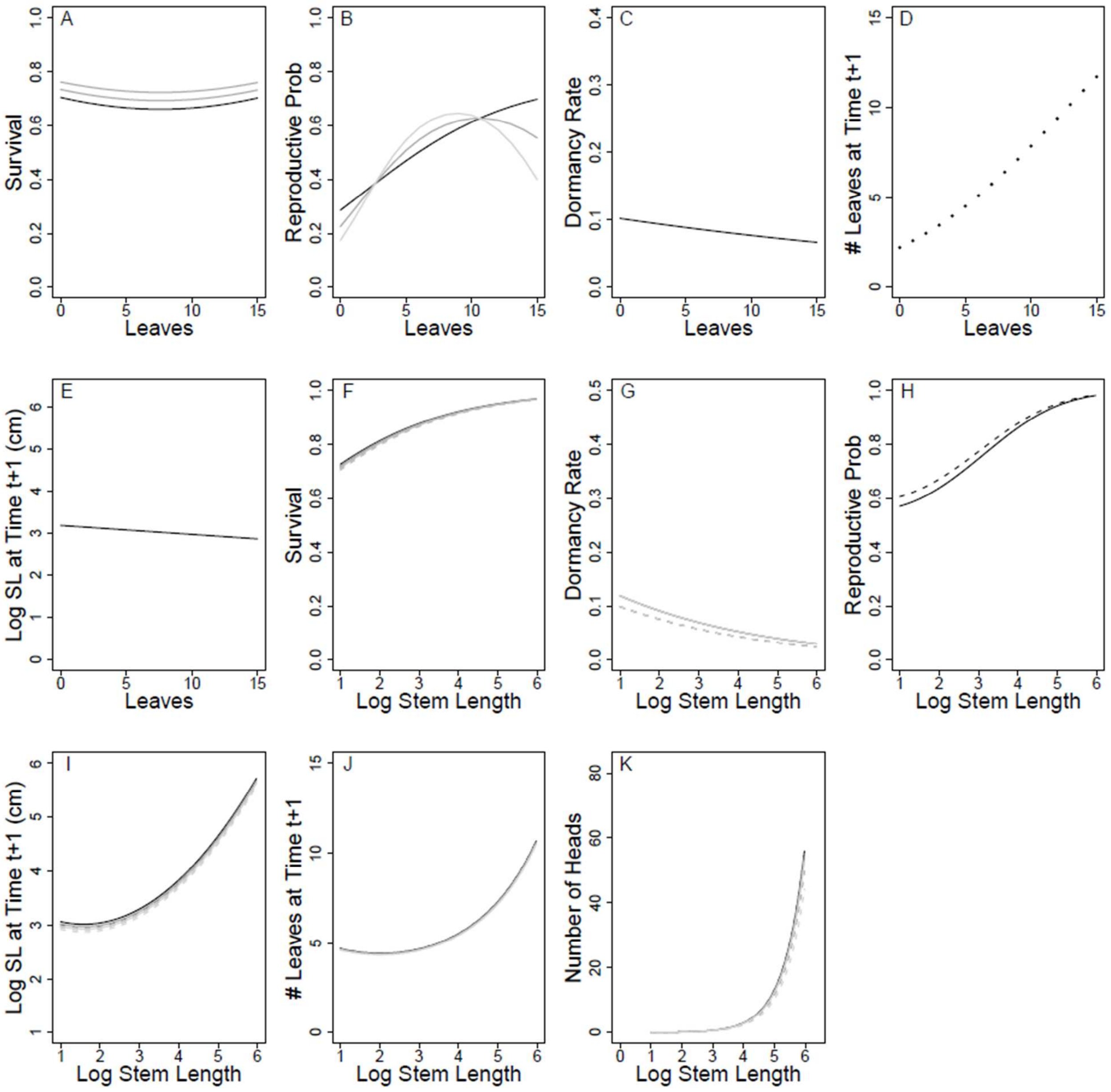


Fig. S2. Vital rates of Liatris ohlingearae are affected by the size of its individuals and time since fire (TSF) (Black ≤10, Dark grey = 10-20, and Light grey ≥ 20 years since last fire). Panels A-E depict the vital rate functions of vegetative individuals, where size in the x axis is number of leaves: (A) survival, (B) probability of becoming reproductive next year, (C) becoming vegetatively dormant, (D) changes in size conditional on remaining vegetative, and (E) changes in size conditional on becoming reproductive. Panels F-L correspond to reproductive individuals, where size in the x axis is log of stem length (cm): (F) survival, (G) probability of becoming reproductive next year, (H) becoming vegetatively dormant, and (I) changes in size conditional on becoming vegetative (J) changes in size conditional on remaining reproductive, and (K) number of flowering heads produced. Solid lines indicate no herbivory, dashed lines indicate herbivory.

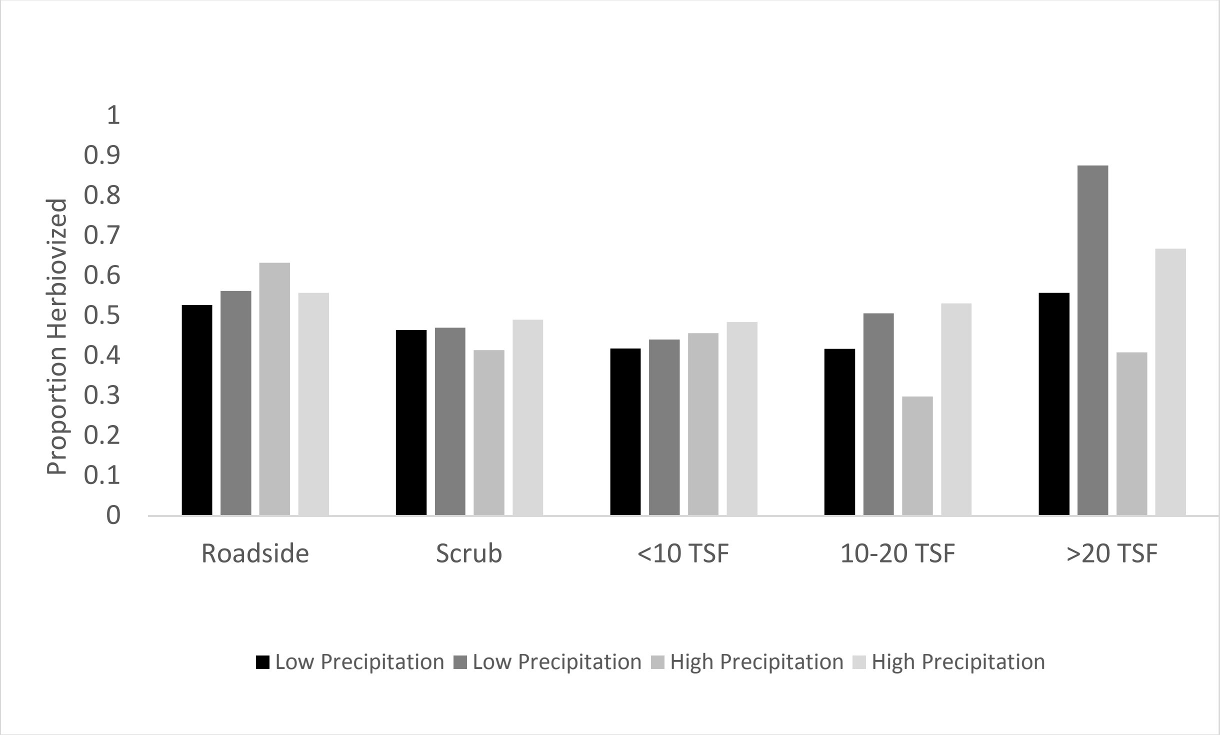


Figure S3. Proportion of reproductive individuals herbivorized in differing environmental conditions (high *vs.* low precipitation, and North *vs.* South site).

Table S2. Model selection and model summary tables for each vital rate used in the study. In each case it is denoted whether AICc or QAICc was used as well as an estimated overdispersion parameter for each model. The model selected was denoted in bold. In cases where the model selected was not the model with the lowest (Q)AICc score, a short explanation of the reasons follows. In addition a small summary of the selected model was presented after each model selection table.

Vegetative to Vegetative Growth (Habitat)

Model selection based on QAICc : (c-hat estimate = 1.717849)

	K	QAICc	Delta_QAICc	Quasi.LL
Leaves(t+1) ~ Leaves+Leaves^2+ Region	5	1995.33	0	-992.63
Leaves(t+1) ~ Leaves+Leaves^2 + Habitat + Region	6	1997.25	1.92	-992.57
Leaves(t+1) ~ Leaves +Leaves^2	4	1998.68	3.36	-995.32
Leaves(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain	7	1998.86	3.54	-992.36
Leaves(t+1) ~ Leaves +Leaves^2 + Habitat + Region +Leaves:Habitat+Leaves^2 :Habitat	8	1998.93	3.61	-991.37
Leaves(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain +Leaves:Habitat+Leaves^2 :Habitat	9	2000.25	4.92	-991.01
Leaves(t+1) ~ Leaves+Leaves^2 + Habitat	5	2000.29	4.97	-995.11
Leaves(t+1) ~ Leaves +Leaves^2 + Rain	5	2000.49	5.16	-995.21
Leaves(t+1) ~ Leaves +Leaves^2 + Habitat + Rain	6	2002.03	6.7	-994.96
Leaves(t+1) ~ Leaves+Leaves^2 + Habitat+ Leaves:Habitat+Leaves^2 :Habitat	7	2002.09	6.77	-993.97
Leaves(t+1) ~ Leaves +Leaves^2 + Habitat + Rain +Leaves:Habitat+Leaves^2 :Habitat	8	2003.59	8.27	-993.7
Leaves(t+1) ~ Leaves + Region	4	2032.11	36.79	-1012.03
Leaves(t+1) ~ Leaves + Habitat + Region	5	2033.99	38.67	-1011.96
Leaves(t+1) ~ Leaves + Habitat + Region + Rain	6	2035.33	40	-1011.61
Leaves(t+1) ~ Leaves × Habitat + Region	6	2035.99	40.66	-1011.94
Leaves(t+1) ~ Leaves × Habitat + Region + Rain	7	2037.36	42.03	-1011.61
Leaves(t+1) ~ Leaves	3	2038.85	43.52	-1016.41
Leaves(t+1) ~ Leaves + Habitat	4	2040.16	44.83	-1016.05
Leaves(t+1) ~ Leaves + Rain	4	2040.47	45.14	-1016.21
Leaves(t+1) ~ Leaves + Habitat + Rain	5	2041.66	46.33	-1015.79
Leaves(t+1) ~ Leaves × Habitat	5	2042.05	46.73	-1015.99
Leaves(t+1) ~ Leaves × Habitat + Rain	6	2043.62	48.29	-1015.75
Leaves(t+1) ~ 1	2	6978.56	4983.23	-3487.27

Vegetative to Vegetative Growth (Habitat)				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.944954	0.090035	10.495	< 2e-16
leaves	0.14914	0.012721	11.724	< 2e-16
Leaves^2	-0.0029	0.000494	-5.873	6.33E-09
Region	-0.1119	0.048444	-2.31	0.0212

Vegetative Survival (Habitat)

Model selection based on AICc : (c-hat estimate = 1.00032)

	K	AICc	Delta_AICc	LL
Survival ~ Leaves +Leaves^2+ Habitat + Region + Rain	6	1912.17	0	-950.06
Survival ~ Leaves +Leaves^2 + Habitat + Rain*	5	1912.71	0.54	-951.34
Survival ~ Leaves+Leaves^2 + Habitat + Region	5	1913.97	1.8	-951.97
Survival ~ Leaves + Habitat + Region + Rain	5	1914.03	1.86	-952
Survival ~ Leaves + Habitat + Rain	4	1914.77	2.6	-953.38
Survival ~ Leaves+Leaves^2 + Habitat	4	1914.85	2.68	-953.41
Survival ~ Leaves + Habitat + Region	4	1915.32	3.15	-953.65
Survival ~ Leaves × Habitat + Region + Rain	6	1915.67	3.5	-951.81
Survival ~ Leaves +Leaves^2 + Habitat + Region + Rain +Leaves:Habitat+Leaves^2 :Habitat	8	1915.79	3.62	-949.85
Survival ~ Leaves +Leaves^2 + Habitat + Rain +Leaves:Habitat+Leaves^2 :Habitat	7	1916.21	4.04	-951.08
Survival ~ Leaves × Habitat + Rain	5	1916.3	4.14	-953.14
Survival ~ Leaves + Habitat	3	1916.37	4.2	-955.18
Survival ~ Leaves × Habitat + Region	5	1917.05	4.88	-953.51
Survival ~ Leaves +Leaves^2 + Habitat + Region +Leaves:Habitat+Leaves^2 :Habitat	7	1917.63	5.47	-951.79
Survival ~ Leaves × Habitat	4	1918.01	5.84	-954.99
Survival ~ Leaves+Leaves^2 + Habitat+ Leaves:Habitat+Leaves^2 :Habitat	6	1918.41	6.24	-953.18
Survival ~ Leaves +Leaves^2	3	1938.48	26.32	-966.24
Survival ~ Leaves +Leaves^2 + Rain	4	1938.51	26.34	-965.24
Survival ~ Leaves	2	1939.71	27.54	-967.85
Survival ~ Leaves + Rain	3	1940.04	27.87	-967.01
Survival ~ Leaves+Leaves^2 + Region	4	1940.49	28.32	-966.24
Survival ~ Leaves + Region	3	1941.71	29.54	-967.85
Survival ~ 1	1	6447.41	4535.24	-3222.71

*The region variable was not significant and had a very low effect size, this combined with the small difference in AICc lead us to select the second model.

Vegetative Survival (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.195894	0.279333	0.701	0.4831
leaves	-0.06652	0.04033	-1.649	0.0991
Leaves^2	0.003846	0.002169	1.773	0.0762
Rain	0.234982	0.115302	2.038	0.0416
Habitat	0.70432	0.139443	5.051	4.40E-07

Vegetative to Reproductive Probability (Habitat)

Model selection based on AICc : (c-hat estimate = 1.007766)

	K	AICc	Delta_AICc	LL
Reproduction(t+1) ~ Leaves +Leaves^2 + Habitat + Rain	5	1717.05	0	-853.5
Reproduction(t+1) ~ Leaves+Leaves^2 + Habitat	4	1717.99	0.94	-854.98
Reproduction(t+1) ~ Leaves +Leaves^2 + Habitat + Rain +Leaves:Habitat+Leaves^2 :Habitat	7	1718.44	1.39	-852.18
Reproduction(t+1) ~ Leaves +Leaves^2 + Rain	4	1718.45	1.4	-855.21
Reproduction(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain	6	1718.74	1.68	-853.34
Reproduction(t+1) ~ Leaves +Leaves^2	3	1718.76	1.71	-856.37
Reproduction(t+1) ~ Leaves+Leaves^2 + Habitat+ Leaves:Habitat+Leaves^2 :Habitat	6	1719.34	2.29	-853.64
Reproduction(t+1) ~ Leaves+Leaves^2 + Region	4	1719.54	2.48	-855.75
Reproduction(t+1) ~ Leaves+Leaves^2 + Habitat + Region	5	1719.7	2.64	-854.83
Reproduction(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain +Leaves:Habitat+Leaves^2 :Habitat	8	1720.19	3.14	-852.04
Reproduction(t+1) ~ Leaves +Leaves^2 + Habitat + Region +Leaves:Habitat+Leaves^2 :Habitat	7	1721.11	4.06	-853.51
Reproduction(t+1) ~ Leaves × Habitat + Rain	5	1735.4	18.35	-862.68
Reproduction(t+1) ~ Leaves + Habitat + Rain	4	1736.25	19.19	-864.11
Reproduction(t+1) ~ Leaves × Habitat + Region + Rain	6	1736.95	19.9	-862.44
Reproduction(t+1) ~ Leaves × Habitat	4	1737.28	20.23	-864.63
Reproduction(t+1) ~ Leaves + Habitat + Region + Rain	5	1737.68	20.63	-863.82
Reproduction(t+1) ~ Leaves + Rain	3	1738.11	21.06	-866.05
Reproduction(t+1) ~ Leaves + Habitat	3	1738.37	21.32	-866.18
Reproduction(t+1) ~ Leaves × Habitat + Region	5	1738.85	21.8	-864.4
Reproduction(t+1) ~ Leaves	2	1739.44	22.39	-867.72
Reproduction(t+1) ~ Leaves + Region	3	1739.71	22.66	-866.85
Reproduction(t+1) ~ Leaves + Habitat + Region	4	1739.83	22.77	-865.9
Reproduction(t+1) ~ 1	1	9984.5	8267.45	-4991.25

Vegetative to Reproductive Probability (Habitat)					
	Estimate	Std. Error	z value		Pr(>|z|)
(Intercept)	-1.7814	0.282601	-6.304		2.91E-10
leaves	0.22584	0.035009	6.451		1.11E-10
Habitat	0.228592	0.123543	1.85		0.0643
Leaves^2	-0.00652	0.001487	-4.388		1.14E-05
Rain	0.201934	0.117538	1.718		0.0858

Vegetative to Dormant Probability (Habitat)

Model selection based on AICc : (c-hat estimate = 1.004602)

	K	AICc	Delta_AICc	LL
Dormancy ~ Leaves	2	842.77	0	-419.38
Dormancy ~ Leaves + Habitat	3	843.71	0.94	-418.85
Dormancy ~ Leaves +Leaves^2	3	844.56	1.79	-419.27
Dormancy ~ Leaves + Rain	3	844.78	2	-419.38
Dormancy ~ Leaves + Region	3	844.78	2	-419.38
Dormancy ~ Leaves+Leaves^2 + Habitat	4	845.52	2.75	-418.75
Dormancy ~ Leaves + Habitat + Region	4	845.54	2.76	-418.75
Dormancy ~ Leaves × Habitat	4	845.58	2.8	-418.78
Dormancy ~ Leaves + Habitat + Rain	4	845.72	2.95	-418.85
Dormancy ~ Leaves +Leaves^2 + Rain	4	846.56	3.79	-419.27
Dormancy ~ Leaves+Leaves^2 + Region	4	846.57	3.79	-419.27
Dormancy ~ Leaves+Leaves^2 + Habitat + Region	5	847.33	4.56	-418.65
Dormancy ~ Leaves × Habitat + Region	5	847.42	4.65	-418.69
Dormancy ~ Leaves +Leaves^2 + Habitat + Rain	5	847.54	4.76	-418.75
Dormancy ~ Leaves + Habitat + Region + Rain	5	847.55	4.77	-418.75
Dormancy ~ Leaves × Habitat + Rain	5	847.59	4.82	-418.77
Dormancy ~ Leaves+Leaves^2 + Habitat+ Leaves:Habitat+Leaves^2 :Habitat	6	849.01	6.24	-418.48
Dormancy ~ Leaves +Leaves^2 + Habitat + Region + Rain	6	849.35	6.58	-418.65
Dormancy ~ Leaves × Habitat + Region + Rain	6	849.43	6.66	-418.69
Dormancy ~ Leaves +Leaves^2 + Habitat + Region +Leaves:Habitat+Leaves^2 :Habitat	7	850.84	8.07	-418.38
Dormancy ~ Leaves +Leaves^2 + Habitat + Rain +Leaves:Habitat+Leaves^2 :Habitat	7	851.03	8.25	-418.47
Dormancy ~ Leaves +Leaves^2 + Habitat + Region + Rain +Leaves:Habitat+Leaves^2 :Habitat	8	852.86	10.09	-418.38
Dormancy ~ 1	1	4270.41	3427.64	-2134.21

Vegetative to Dormant Probability (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.26308	0.14551	-15.552	<2e-16
leaves	-0.02484	0.02716	-0.915	0.36

Vegetative to Reproductive Growth (Habitat)
Model selection based on AICc

	K	AICc	Delta_AICc	LL
Size(t+1) ~ Leaves + Habitat + Region	5	1598.11	0	-794
Size(t+1) ~ Leaves × Habitat + Region	6	1598.78	0.67	-793.31
Size(t+1) ~ Leaves + Habitat + Region + Rain	6	1599.31	1.2	-793.57
Size(t+1) ~ Leaves+Leaves^2 + Habitat + Region*	6	1599.32	1.21	-793.58
Size(t+1) ~ Leaves × Habitat + Region + Rain	7	1599.95	1.85	-792.87
Size(t+1) ~ Leaves + Region	4	1600.54	2.44	-796.23
Size(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain	7	1600.66	2.56	-793.22
Size(t+1) ~ Leaves+Leaves^2 + Region	5	1601.67	3.57	-795.78
Size(t+1) ~ Leaves +Leaves^2 + Habitat + Region +Leaves:Habitat+Leaves^2 :Habitat	8	1602.11	4	-792.92
Size(t+1) ~ Leaves +Leaves^2 + Habitat + Region + Rain +Leaves:Habitat+Leaves^2 :Habitat	9	1603.43	5.32	-792.54
Size(t+1) ~ Leaves	3	1603.59	5.48	-798.77
Size(t+1) ~ Leaves × Habitat	5	1603.71	5.6	-796.8
Size(t+1) ~ Leaves + Habitat	4	1603.73	5.62	-797.83
Size(t+1) ~ Leaves × Habitat + Rain	6	1604.71	6.6	-796.28
Size(t+1) ~ Leaves + Habitat + Rain	5	1604.76	6.66	-797.32
Size(t+1) ~ Leaves + Rain	4	1604.82	6.72	-798.37
Size(t+1) ~ Leaves +Leaves^2	4	1605.07	6.96	-798.5
Size(t+1) ~ Leaves+Leaves^2 + Habitat	5	1605.31	7.2	-797.6
Size(t+1) ~ Leaves +Leaves^2 + Rain	5	1606.42	8.31	-798.15
Size(t+1) ~ Leaves +Leaves^2 + Habitat + Rain	6	1606.46	8.35	-797.15
Size(t+1) ~ Leaves+Leaves^2 + Habitat+ Leaves:Habitat+Leaves^2 :Habitat	7	1607.38	9.27	-796.58
Size(t+1) ~ Leaves +Leaves^2 + Habitat + Rain +Leaves:Habitat+Leaves^2 :Habitat	8	1608.5	10.39	-796.11
Size(t+1) ~ 1	2	20964.26	19366.15	-10480.1

* We deliberately retain the quadratic for the growth following Morris & Doak (2003; page 194) since we want our growth model to be the best model to predict survival as well as commensurate with other growth vital rates.

Morris, W.F. & D. F. Doak. 2003 Quantitative Conservation Biology. Sinauer. Sunderland, Massachusets.

Vegetative to Reproductive Growth (Habitat)				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.717421	0.253453	14.667	<2e-16
leaves	-0.0336	0.025795	-1.303	0.1932
Leaves^2	0.000891	0.000978	0.911	0.3626
Habitat	-0.2156	0.103006	-2.093	0.0368
Region	-0.28019	0.098929	-2.832	0.0048

Reproductive to Reproductive Probability (Habitat)

Model selection based on AICc :(c-hat estimate = 1.089186)

	K	AICc	Delta_AICc	LL
Reproduction(t+1) ~ Size + Habitat × Herbivory+ Size^{2}	6	4164	0	-2075.99
Reproduction(t+1) ~ Size + Habitat × Herbivory + Rain+ Size^{2}	7	4164.38	0.38	-2075.18
Reproduction(t+1) ~ Size + Habitat × Herbivory + Region+ Size^{2}	7	4165.93	1.93	-2075.95
Reproduction(t+1) ~ Size + Habitat × Herbivory + Region + Rain+ Size^{2}	8	4166.31	2.3	-2075.14
Reproduction(t+1) ~ Size + Habitat + Herbivory+ Size^{2}	5	4170.77	6.77	-2080.38
Reproduction(t+1) ~ Size + Habitat + Herbivory + Rain+ Size^{2}	6	4171.43	7.42	-2079.71
Reproduction(t+1) ~ Size + Habitat + Herbivory + Region+ Size^{2}	6	4172.64	8.64	-2080.31
Reproduction(t+1) ~ Size + Habitat + Herbivory + Region + Rain+ Size^{2}	7	4173.29	9.29	-2079.63
Reproduction(t+1) ~ Size + Habitat × Herbivory + Rain	6	4177.59	13.58	-2082.78
Reproduction(t+1) ~ Size + Habitat × Herbivory	5	4177.66	13.66	-2083.83
Reproduction(t+1) ~ Size + Habitat × Herbivory + Region + Rain	7	4179.59	15.59	-2082.78
Reproduction(t+1) ~ Size + Habitat × Herbivory + Region	6	4179.67	15.66	-2083.83
Reproduction(t+1) ~ Size + Habitat + Herbivory	4	4185.86	21.86	-2088.93
Reproduction(t+1) ~ Size + Habitat + Herbivory + Rain	5	4186.13	22.13	-2088.06
Reproduction(t+1) ~ Size + Habitat + Herbivory + Region	5	4187.86	23.86	-2088.93
Reproduction(t+1) ~ Size + Habitat + Herbivory + Region + Rain	6	4188.13	24.12	-2088.06
Reproduction(t+1) ~ Size + Habitat+ Size^{2}	4	4193.76	29.75	-2092.88
Reproduction(t+1) ~ Size + Herbivory+ Size^{2}	4	4210.84	46.84	-2101.42
Reproduction(t+1) ~ Size + Habitat	3	4214.9	50.9	-2104.45
Reproduction(t+1) ~ Size + Herbivory	3	4216.58	52.58	-2105.29
Reproduction(t+1) ~ Size + Region+ Size^{2}	4	4231.03	67.03	-2111.51
Reproduction(t+1) ~ Size + Size^{2}	3	4233.94	69.94	-2113.97
Reproduction(t+1) ~ Size + Rain+ Size^{2}	4	4234.35	70.34	-2113.17
Reproduction(t+1) ~ Size + Region	3	4242.59	78.58	-2118.29
Reproduction(t+1) ~ Size	2	4243.35	79.34	-2119.67
Reproduction(t+1) ~ Size + Rain	3	4243.76	79.75	-2118.88
Reproduction(t+1) ~ 1	1	9984.5	5820.5	-4991.25

Reproductive to Reproductive Probability (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.02726	0.27077	-0.101	0.919795
Size	0.0184	0.15408	0.119	0.904921
Size^2	0.10463	0.02694	3.884	0.000103
Habitat	0.26968	0.13428	2.008	0.044609
Herbivory	-0.65734	0.24463	-2.687	0.007209
Habitat:Herbivory	0.52503	0.1765	2.975	0.002933

Reproductive to Vegetative Growth(Habitat)

Model selection based on QAICc :(c-hat estimate = 3.73)

	k	Quasi.LL	QAICc	Delta_QAICc
Leaves(t+1) ~ Size + Habitat × Herbivory + Region + Rain + Size^2	9	-2015.67	4049.337	0
Leaves(t+1) ~ Size + Habitat + Herbivory + Region + Rain + Size^2	8	-2018.64	4053.282	3.945258
Leaves(t+1) ~ Size + Habitat × Herbivory + Region + Rain	8	-2019.41	4054.818	5.481673
Leaves(t+1) ~ Size + Habitat × Herbivory + Rain + Size^2	8	-2020.13	4056.259	6.922884
Leaves(t+1) ~ Size + Habitat + Herbivory + Region + Rain	7	-2022.16	4058.323	8.986125
Leaves(t+1) ~ Size + Habitat × Herbivory + Region + Size^2	8	-2022.36	4060.719	11.38254
Leaves(t+1) ~ Size + Habitat × Herbivory + Rain	7	-2023.44	4060.871	11.53413
Leaves(t+1) ~ Size + Habitat + Herbivory + Rain + Size^2	7	-2023.45	4060.905	11.56891
Leaves(t+1) ~ Size + Habitat + Herbivory + Region + Size^2	7	-2024.78	4063.55	14.21301
Leaves(t+1) ~ Size + Habitat + Herbivory + Rain	6	-2026.52	4065.04	15.70361
Leaves(t+1) ~ Size + Habitat × Herbivory + Region	7	-2026.34	4066.671	17.33437
Leaves(t+1) ~ Size + Habitat × Herbivory + Size^2	7	-2026.64	4067.284	17.94701
Leaves(t+1) ~ Size + Habitat + Herbivory + Region	6	-2028.53	4069.066	19.72931
Leaves(t+1) ~ Size + Habitat + Herbivory + Size^2	6	-2029.37	4070.74	21.40357
Leaves(t+1) ~ Size + Habitat × Herbivory	6	-2030.17	4072.343	23.00644
Leaves(t+1) ~ Size + Habitat + Herbivory	5	-2032.66	4075.327	25.99046
Leaves(t+1) ~ Size + Herbivory + Size^2	5	-2034.2	4078.398	29.06173
Leaves(t+1) ~ Size + Herbivory	4	-2036.19	4080.379	31.04262
Leaves(t+1) ~ Size + Rain + Size^2	5	-2052.54	4115.088	65.75143
Leaves(t+1) ~ Size + Region + Size^2	5	-2053.29	4116.582	67.24499
Leaves(t+1) ~ Size + Habitat + Size^2	5	-2056.15	4122.301	72.96448
Leaves(t+1) ~ Size + Rain	4	-2057.19	4122.377	73.04051
Leaves(t+1) ~ Size + Size^2	4	-2060.09	4128.182	78.84565
Leaves(t+1) ~ Size + Region	4	-2060.95	4129.895	80.55868
Leaves(t+1) ~ Size + Habitat	4	-2063.76	4135.52	86.18359
Leaves(t+1) ~ Size	3	-2065.77	4137.536	88.19917
Leaves(t+1) ~ 1	2	-5238.87	10481.73	6432.393

Reproductive to Vegetative Size (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.02018	0.22406	4.553	5.28E-06
Size	-0.11849	0.09256	-1.28	0.200521
Size^2	0.04258	0.01575	2.704	0.006851
Habitat	0.26393	0.08701	3.033	0.002418
Herbivory	0.55522	0.15206	3.651	0.000261
Region	-0.15945	0.05244	-3.041	0.002359
Rain	0.18544	0.05019	3.695	0.00022
Habitat:Herbivory	-0.26656	0.10893	-2.447	0.014404

Reproductive to Reproductive Growth (Habitat)

Model selection based on AICc

	K	AICc	Delta_AICc	LL
Size(t+1) ~ Size + Habitat × Herbivory + Rain+ Size^2	8	12885.29	0	-6434.63
Size(t+1) ~ Size + Habitat × Herbivory + Region + Rain+ Size^2 *	9	12885.39	0.1	-6433.67
Size(t+1) ~ Size + Habitat + Herbivory + Region + Rain+ Size^2	8	12887.26	1.97	-6435.61
Size(t+1) ~ Size + Habitat + Herbivory + Rain+ Size^2	7	12887.48	2.19	-6436.73
Size(t+1) ~ Size + Habitat × Herbivory+ Size^2	7	12894.21	8.92	-6440.09
Size(t+1) ~ Size + Habitat × Herbivory + Region+ Size^2	8	12894.34	9.06	-6439.16
Size(t+1) ~ Size + Habitat + Herbivory + Region+ Size^2	7	12895.78	10.49	-6440.88
Size(t+1) ~ Size + Habitat + Herbivory+ Size^2	6	12895.94	10.65	-6441.96
Size(t+1) ~ Size + Herbivory+ Size^2	5	12906.97	21.68	-6448.48
Size(t+1) ~ Size + Habitat+ Size^2	5	12942.36	57.07	-6466.17
Size(t+1) ~ Size + Rain+ Size^2	5	12947.07	61.79	-6468.53
Size(t+1) ~ Size + Size^2	4	12953.88	68.59	-6472.93
Size(t+1) ~ Size + Region+ Size^2	5	12955.59	70.3	-6472.79
Size(t+1) ~ Size + Habitat × Herbivory + Rain	7	13069.95	184.66	-6527.96
Size(t+1) ~ Size + Habitat × Herbivory + Region + Rain	8	13071.69	186.4	-6527.83
Size(t+1) ~ Size + Habitat + Herbivory + Rain	6	13073.1	187.81	-6530.54
Size(t+1) ~ Size + Habitat + Herbivory + Region + Rain	7	13074.7	189.41	-6530.34
Size(t+1) ~ Size + Habitat × Herbivory	6	13080.92	195.63	-6534.45
Size(t+1) ~ Size + Habitat × Herbivory + Region	7	13082.68	197.39	-6534.33
Size(t+1) ~ Size + Habitat + Herbivory	5	13083.51	198.23	-6536.75
Size(t+1) ~ Size + Habitat + Herbivory + Region	6	13085.15	199.86	-6536.56
Size(t+1) ~ Size + Herbivory	4	13116.57	231.28	-6554.28
Size(t+1) ~ Size + Habitat	4	13147.08	261.8	-6569.54
Size(t+1) ~ Size + Rain	4	13178.43	293.14	-6585.21
Size(t+1) ~ Size	3	13184.31	299.03	-6589.15
Size(t+1) ~ Size + Region	4	13184.93	299.65	-6588.46
Size(t+1) ~ 1	2	20964.26	8078.97	-10480.1

* Region was retained in all of the top models in the TSF version of this vital rate and this model is equivalent to the top model. Thus Region was retained here for consistency.

Reproductive to Reproductive Size (Habitat)				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.538725	0.144365	24.512	< 2e-16
Size	-0.40056	0.064876	-6.174	7.23E-10
Size^2	0.136266	0.009836	13.854	< 2e-16
Habitat	-0.20821	0.048563	-4.287	1.84E-05
Herbivory	-0.17565	0.090721	-1.936	0.052911
Region	-0.04286	0.031051	-1.38	0.167523
Rain	-0.1014	0.03063	-3.31	0.000939
Habitat:Herbivory	0.127361	0.06468	1.969	0.049003

Reproductive to Dormancy Probability (Habitat)

Model selection based on AICc :(c-hat estimate = 1.013)

	K	AICc	Delta_AICc	LL
Dormancy ~ Size + Habitat + Herbivory + Rain	5	2350.46	0	-1170.22
Dormancy ~ Size + Habitat × Herbivory + Rain	6	2350.72	0.26	-1169.35
Dormancy ~ Size + Habitat + Herbivory + Rain + Size^2	6	2352.08	1.62	-1170.03
Dormancy ~ Size + Habitat + Herbivory + Region + Rain	6	2352.1	1.64	-1170.04
Dormancy ~ Size + Habitat × Herbivory + Region + Rain	7	2352.3	1.85	-1169.14
Dormancy ~ Size + Habitat × Herbivory + Rain + Size^2	7	2352.39	1.94	-1169.19
Dormancy ~ Size + Habitat + Herbivory + Region + Rain + Size^2	7	2353.76	3.31	-1169.87
Dormancy ~ Size + Habitat × Herbivory + Region + Rain + Size^2	8	2354.03	3.57	-1169
Dormancy ~ Size + Habitat + Herbivory	4	2356.21	5.75	-1174.1
Dormancy ~ Size + Habitat × Herbivory	5	2356.71	6.26	-1173.35
Dormancy ~ Size + Habitat + Herbivory + Size^2	5	2357.66	7.2	-1173.82
Dormancy ~ Size + Habitat + Herbivory + Region	5	2357.85	7.4	-1173.92
Dormancy ~ Size + Habitat × Herbivory + Size^2	6	2358.22	7.76	-1173.1
Dormancy ~ Size + Habitat × Herbivory + Region	6	2358.31	7.86	-1173.15
Dormancy ~ Size + Habitat + Herbivory + Region + Size^2	6	2359.36	8.91	-1173.67
Dormancy ~ Size + Habitat × Herbivory + Region + Size^2	7	2359.88	9.43	-1172.93
Dormancy ~ Size + Habitat	3	2362.41	11.95	-1178.2
Dormancy ~ Size × Habitat	4	2362.88	12.42	-1177.43
Dormancy ~ Size + Herbivory	3	2362.94	12.48	-1178.47
Dormancy ~ Size + Habitat + Size^2	4	2363.09	12.63	-1177.54
Dormancy ~ Size + Rain	3	2363.88	13.42	-1178.94
Dormancy ~ Size + Herbivory + Size^2	4	2364.93	14.48	-1178.46
Dormancy ~ Size + Rain + Size^2	4	2365.64	15.19	-1178.82
Dormancy ~ Size	2	2369.03	18.58	-1182.52
Dormancy ~ Size + Size^2	3	2370.8	20.35	-1182.4
Dormancy ~ Size + Region	3	2371	20.54	-1182.5
Dormancy ~ Size + Region + Size^2	4	2372.73	22.28	-1182.36
Dormancy ~ 1	1	4270.41	1919.95	-2134.21

Reproductive Dormancy (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.92729	0.34113	-5.65	1.61E-08
Size	-0.24969	0.05345	-4.671	2.99E-06
Habitat	-0.38041	0.13807	-2.755	0.00587
Herbivory	-0.27391	0.12551	-2.182	0.02908
Rain	0.34538	0.12571	2.747	0.00601

Reproductive Survival (Habitat)

Model selection based on AICc: (c-hat estimate = 1.041)

	K	AICc	Delta_AICc	LL
Survival ~ Size + Habitat + Herbivory + Region	5	3538.12	0	-1764.05
Survival ~ Size + Habitat + Herbivory + Region + Rain	6	3539.61	1.5	-1763.8
Survival ~ Size + Habitat × Herbivory + Region	6	3540.05	1.94	-1764.02
Survival ~ Size + Habitat + Herbivory + Region + Size^2	6	3540.08	1.96	-1764.03
Survival ~ Size + Habitat × Herbivory + Region + Rain	7	3541.56	3.45	-1763.77
Survival ~ Size + Habitat + Herbivory + Region + Rain + Size^2	7	3541.57	3.45	-1763.77
Survival ~ Size + Habitat × Herbivory + Region + Size^2	7	3542.02	3.91	-1764
Survival ~ Size + Habitat × Herbivory + Region + Rain + Size^2	8	3543.52	5.41	-1763.75
Survival ~ Size + Habitat + Herbivory	4	3548.07	9.95	-1770.03
Survival ~ Size + Herbivory	3	3549.28	11.17	-1771.64
Survival ~ Size + Habitat + Herbivory + Rain	5	3549.62	11.51	-1769.81
Survival ~ Size + Habitat + Herbivory + Size^2	5	3549.85	11.73	-1769.92
Survival ~ Size + Habitat × Herbivory	5	3550.03	11.92	-1770.01
Survival ~ Size + Herbivory + Size^2	4	3551.29	13.17	-1771.64
Survival ~ Size + Habitat + Herbivory + Rain + Size^2	6	3551.38	13.26	-1769.68
Survival ~ Size + Habitat × Herbivory + Rain	6	3551.6	13.48	-1769.79
Survival ~ Size + Habitat × Herbivory + Size^2	6	3551.82	13.71	-1769.9
Survival ~ Size + Habitat × Herbivory + Rain + Size^2	7	3553.36	15.24	-1769.67
Survival ~ Size + Region	3	3568.4	30.28	-1781.2
Survival ~ Size + Region + Size^2	4	3570.38	32.26	-1781.19
Survival ~ Size + Habitat	3	3574.3	36.18	-1784.15
Survival ~ Size	2	3574.89	36.77	-1785.44
Survival ~ Size + Habitat + Size^2	4	3575.78	37.66	-1783.89
Survival ~ Size + Rain	3	3576.28	38.16	-1785.14
Survival ~ Size + Size^2	3	3576.8	38.69	-1785.4
Survival ~ Size + Rain + Size^2	4	3578.19	40.08	-1785.09
Survival ~ 1	1	6447.41	2909.3	-3222.71

Rep Survival (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.17087	0.27721	0.616	0.53763
Size	0.41733	0.03814	10.942	< 2e-16
Habitat	0.28095	0.10385	2.705	0.00682
Herbivory	-0.10749	0.09837	-1.093	0.27451
Region	0.33078	0.09601	3.445	0.00057

Fecundity(Habitat) Model selection based on QAICc :(c-hat estimate = 1.8745)				
	k	sumlogL	sumaic	delta
Heads ~ Size + Habitat + Herbivory + Region	6	-13339.5	26691.01	0
Heads ~Size + Habitat + Herbivory + Region + Rain	7	-13338.9	26691.76	0.749858
Heads ~Size + Habitat * Herbivory + Region	7	-13338.9	26691.78	0.763781
Heads ~Size + Habitat + Herbivory	5	-13341.1	26692.23	1.217328
Heads ~Size + Habitat * Herbivory + Region + Rain	8	-13338.2	26692.45	1.439016
Heads ~Size + Habitat + Herbivory + Rain	6	-13340.4	26692.77	1.753908
Heads ~Size + Habitat * Herbivory	6	-13340.5	26692.9	1.885648
Heads ~Size + Habitat * Herbivory + Rain	7	-13339.7	26693.36	2.3445
Heads ~Size + Habitat	4	-13348	26704.07	13.06154
Heads ~Size + Herbivory	4	-13491.3	26990.58	299.5633
Heads ~Size	3	-13494.8	26995.6	304.5925
Heads ~Size + Region	4	-13494.3	26996.54	305.5281
Heads ~Size + Rain	4	-13494.6	26997.21	306.1996
Heads ~1	2	-16741.6	33487.16	6796.149

Fecundity (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-5.67919	0.10521	-53.978	< 2e-16
Size	1.53366	0.01848	82.983	< 2e-16
Habitat	0.49733	0.02919	17.036	< 2e-16
Herbivory	-0.07813	0.02529	-3.089	0.00201
Region	0.04496	0.02537	1.772	0.07635

Herbivory Rate (Habitat)

Model selection based on AICc : (c-hat estimate = 1.13)

	K	AICc	Delta_AICc	LL
Herbivory(t+1) ~ Size +Size2+ Habitat + Herbivory + Rain + Region	7	5554.68	0	-2770.33
Herbivory(t+1) ~ Size +Size2+ Habitat * Herbivory + Rain + Region	8	5556.69	2.01	-2770.33
Herbivory(t+1) ~ Size +Size2+ Habitat + Herbivory + Region	6	5565.38	10.69	-2776.68
Herbivory(t+1) ~ Size +Size2+ Habitat + Herbivory + Rain	6	5567.18	12.5	-2777.58
Herbivory(t+1) ~ Size +Size2+ Habitat * Herbivory + Region	7	5567.37	12.68	-2776.67
Herbivory(t+1) ~ Size +Size2+ Habitat + Herbivory	5	5576.85	22.16	-2783.42
Herbivory(t+1) ~ Size +Size2+ Habitat * Herbivory	6	5578.85	24.16	-2783.41
Herbivory(t+1) ~ Size +Size2+ Herbivory	4	5579.2	24.52	-2785.6
Herbivory(t+1) ~ Size + Habitat + Herbivory + Region + Rain	6	5635.18	80.49	-2811.58
Herbivory(t+1) ~ Size + Habitat * Herbivory + Region + Rain	7	5637.17	82.49	-2811.57
Herbivory(t+1) ~ Size + Habitat + Herbivory + Region	5	5645.41	90.73	-2817.7
Herbivory(t+1) ~ Size + Habitat * Herbivory + Region	6	5647.42	92.73	-2817.7
Herbivory(t+1) ~ Size + Habitat + Herbivory + Rain	5	5648.66	93.97	-2819.32
Herbivory(t+1) ~ Size + Habitat * Herbivory + Rain	6	5650.56	95.88	-2819.27
Herbivory(t+1) ~ Size + Herbivory	3	5657.02	102.34	-2825.51
Herbivory(t+1) ~ Size + Habitat + Herbivory	4	5657.9	103.22	-2824.95
Herbivory(t+1) ~ Size + Habitat * Herbivory	5	5659.85	105.17	-2824.92
Herbivory(t+1) ~ Size +Size2+ Habitat	4	9114.16	3559.47	-4553.08
Herbivory(t+1) ~ Size +Size2+ Rain	4	9121.55	3566.87	-4556.77
Herbivory(t+1) ~ Size +Size2+ Region	4	9137.54	3582.85	-4564.77
Herbivory(t+1) ~ Size +Size2	3	9135.8	3581.11	-4564.9
Herbivory(t+1) ~ Size + Habitat	3	9134.7	3580.02	-4564.35
Herbivory(t+1) ~ Size + Rain	3	9135.61	3580.92	-4564.8
Herbivory(t+1) ~ Size + Region	3	9151.12	3596.43	-4572.56
Herbivory(t+1) ~ Size	2	9149.82	3595.13	-4572.91
Herbivory(t+1) ~ 1	1	9833.33	4278.64	-4915.66

Herbivory Rate (Habitat)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.73064	0.38944	9.579	< 2e-16
Herbivory	0.54738	0.06496	8.426	< 2e-16
Size	-2.28448	0.19706	-11.593	< 2e-16
Size^2	0.23897	0.02771	8.624	< 2e-16
Habitat	0.24927	0.07476	3.334	0.000855
Region	0.25417	0.06689	3.8	0.000145
Rain	0.23133	0.06502	3.558	0.000374

Vegetative Survival (TSF)

Model selection based on AICc : (c-hat estimate = 1.006)

	K	AICc	Delta_AICc	LL
Survival ~ Leaves+ Leaves^2	3	1465.3	0	-729.64
Survival ~ Leaves + Leaves^2 + Rain	4	1465.33	0.03	-728.65
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Region + Rain*	6	1465.66	0.36	-726.8
Survival ~ Leaves	2	1465.77	0.48	-730.88
Survival ~ Leaves+ Leaves^2 + Region	4	1465.88	0.59	-728.93
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Region	5	1465.9	0.6	-727.93
Survival ~ Leaves + Rain	3	1466.15	0.86	-730.07
Survival ~ Leaves + Time-Since-Fire + Region	4	1466.19	0.89	-729.08
Survival ~ Leaves + Region	3	1466.29	0.99	-730.14
Survival ~ Leaves + Time-Since-Fire + Region + Rain	5	1466.3	1	-728.13
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Region + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	8	1466.63	1.33	-725.26
Survival ~ Leaves × Time-Since-Fire + Region + Rain	6	1466.71	1.41	-727.32
Survival ~ Leaves × Time-Since-Fire + Region	5	1466.73	1.43	-728.34
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Rain	5	1466.73	1.43	-728.34
Survival ~ Leaves + Region + Rain	4	1466.89	1.59	-729.43
Survival ~ Leaves + Leaves^2 + Time-Since-Fire	4	1466.97	1.67	-729.47
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Region + Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	1467.05	1.75	-726.48
Survival ~ Leaves + Time-Since-Fire	3	1467.42	2.12	-730.7
Survival ~ Leaves + Time-Since-Fire + Rain	4	1467.54	2.24	-729.76
Survival ~ Leaves + Leaves^2 + Time-Since-Fire + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	1467.88	2.59	-726.9
Survival ~ Leaves × Time-Since-Fire + Rain	5	1468.1	2.81	-729.03
Survival ~ Leaves × Time-Since-Fire	4	1468.11	2.81	-730.04
Survival ~ Leaves + Leaves^2 + Time-Since-Fire+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	6	1468.31	3.01	-728.12
Survival ~ 1	1	4612.81	3147.52	-2305.41

Veg Survival (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.256813	0.430267	0.597	0.5506
leaves	-0.05344	0.045459	-1.176	0.2398
Leaves^2	0.003516	0.002431	1.447	0.148
Time Since Fire	0.147268	0.093214	1.58	0.1141
Region	0.266959	0.15142	1.763	0.0779
Rain	0.197956	0.131544	1.505	0.1324

*We retained this model for consistency with the vital rate in Habitat model.

Vegetative Growth(TSF)

Model selection based on QAICc :(c-hat estimate = 1.549071)

	K	QAICc	Delta_QAICc	Quasi.LL
Leaves(t+1) ~ Leaves+ Leaves^2 + Region	5	1539.62	0	-764.75
Leaves(t+1) ~ Leaves+ Leaves^2	4	1540.93	1.31	-766.43
Leaves(t+1) ~ Leaves + Leaves^2 + Time-Since-Fire	5	1541.12	1.5	-765.5
Leaves(t+1) ~ Leaves + Leaves^2 + Time-Since-Fire + Region	6	1541.54	1.92	-764.69
Leaves(t+1) ~ Leaves + Leaves^2 + Time-Since-Fire + Rain	6	1542.71	3.09	-765.28
Leaves(t+1) ~ Leaves + Leaves^2 + Rain	5	1542.73	3.12	-766.31
Leaves(t+1) ~ Leaves + Leaves^2 + Time-Since-Fire + Region + Rain	7	1543.13	3.51	-764.46
Leaves(t+1) ~ Leaves + Region	4	1576.59	36.97	-784.26
Leaves(t+1) ~ Leaves + Region + Rain	5	1578.11	38.5	-784
Leaves(t+1) ~ Leaves + Time-Since-Fire + Region	5	1578.52	38.9	-784.2
Leaves(t+1) ~ Leaves + Time-Since-Fire	4	1579.56	39.94	-785.74
Leaves(t+1) ~ Leaves + Time-Since-Fire + Region + Rain	6	1579.98	40.36	-783.91
Leaves(t+1) ~ Leaves	3	1580.4	40.79	-787.18
Leaves(t+1) ~ Leaves + Time-Since-Fire + Rain	5	1580.98	41.36	-785.43
Leaves(t+1) ~ Leaves + Rain	4	1582.15	42.54	-787.04
Leaves(t+1) ~ 1	2	5221.86	3682.25	-2608.93

Vegetative to Vegetative Growth (TSF)

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.900626	0.11099	8.114	3.30E-15
leaves	0.156894	0.014142	11.094	< 2e-16
Leaves^2	-0.00307	0.000525	-5.846	8.69E-09
Region	-0.10222	0.056492	-1.809	0.0709

Vegetative to Reproductive Growth(TSF)
Model selection based on AICc

	K	AICc	Delta_AICc	LL
Size(t+1) ~ Leaves + Region	4	1089.74	0	-540.81
Size(t+1) ~ Leaves+Leaves^2 + Region	5	1091.31	1.57	-540.57
Size(t+1) ~ Leaves * Time-Since-Fire + Region	6	1091.36	1.61	-539.55
Size(t+1) ~ Leaves + Time-Since-Fire + Region	5	1091.8	2.06	-540.81
Size(t+1) ~ Leaves	3	1092.05	2.31	-542.99
Size(t+1) ~ Leaves * Time-Since-Fire	5	1092.2	2.45	-541.01
Size(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region +Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	8	1092.8	3.05	-538.19
Size(t+1) ~ Leaves * Time-Since-Fire + Region + Rain	7	1093.04	3.3	-539.36
Size(t+1) ~ Leaves + Time-Since-Fire	4	1093.07	3.33	-542.48
Size(t+1) ~ Leaves + Rain	4	1093.37	3.62	-542.62
Size(t+1) ~ Leaves+Leaves^2 + Time-Since-Fire + Region	6	1093.38	3.64	-540.57
Size(t+1) ~ Leaves + Time-Since-Fire + Region + Rain	6	1093.48	3.74	-540.62
Size(t+1) ~ Leaves * Time-Since-Fire + Rain	6	1093.71	3.97	-540.73
Size(t+1) ~ Leaves+Leaves^2 + Time-Since-Fire+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	1093.82	4.07	-539.74
Size(t+1) ~ Leaves +Leaves^2	4	1093.82	4.08	-542.85
Size(t+1) ~ Leaves + Time-Since-Fire + Rain	5	1094.57	4.82	-542.2
Size(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain +Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	9	1094.78	5.03	-538.12
Size(t+1) ~ Leaves+Leaves^2 + Time-Since-Fire	5	1094.8	5.05	-542.31
Size(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain	7	1095.18	5.43	-540.42
Size(t+1) ~ Leaves +Leaves^2 + Rain	5	1095.24	5.5	-542.53
Size(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Rain +Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	8	1095.67	5.93	-539.62
Size(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Rain	6	1096.4	6.66	-542.08
Size(t+1) ~ 1	2	13489.1	12399.36	-6742.55

Vegetative to Reproductive Growth(TSF)				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.45019	0.21636	15.947	<2e-16
Leaves	-0.02128	0.01414	-1.505	0.1333
Region	-0.2634	0.12638	-2.084	0.0379

Vegetative to Reproductive Transition Probability (TSF)

Model selection based on AICc : (c-hat estimate = 1.04028)

	K	AICc	Delta_AICc	LL
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	1156.08	0	-570.98
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	6	1157.37	1.29	-572.64
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	8	1157.66	1.57	-570.75
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	1158.92	2.84	-572.4
Reproduction(t+1) ~ Leaves +Leaves^2 + Region	4	1163.18	7.1	-577.57
Reproduction(t+1) ~ Leaves+Leaves^2	3	1165.07	8.99	-579.52
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region	5	1165.14	9.06	-577.54
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain	6	1166.13	10.04	-577.02
Reproduction(t+1) ~ Leaves +Leaves^2 + Rain	4	1166.22	10.14	-579.09
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire	4	1166.33	10.25	-579.14
Reproduction(t+1) ~ Leaves +Leaves^2 + Time-Since-Fire + Rain	5	1167.29	11.21	-578.61
Reproduction(t+1) ~ Leaves + Region	3	1172.23	16.15	-583.1
Reproduction(t+1) ~ Leaves + Time-Since-Fire + Region	4	1174.17	18.09	-583.06
Reproduction(t+1) ~ Leaves + Time-Since-Fire + Region + Rain	5	1174.45	18.37	-582.19
Reproduction(t+1) ~ Leaves	2	1174.63	18.55	-585.31
Reproduction(t+1) ~ Leaves × Time-Since-Fire + Region	5	1174.89	18.81	-582.41
Reproduction(t+1) ~ Leaves + Rain	3	1175.12	19.04	-584.55
Reproduction(t+1) ~ Leaves × Time-Since-Fire + Region + Rain	6	1175.36	19.27	-581.63
Reproduction(t+1) ~ Leaves + Time-Since-Fire	3	1175.81	19.73	-584.89
Reproduction(t+1) ~ Leaves + Time-Since-Fire + Rain	4	1176.03	19.95	-583.99
Reproduction(t+1) ~ Leaves × Time-Since-Fire	4	1176.72	20.63	-584.34
Reproduction(t+1) ~ Leaves × Time-Since-Fire + Rain	5	1177.1	21.02	-583.52
Reproduction(t+1) ~ 1	1	6610.5	5454.42	-3304.25

Vegetative to Reproductive Transition Probability (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.28158	0.498623	-0.565	0.57226
Leaves	0.02589	0.102738	0.252	0.80104
Leaves^2	0.007398	0.005221	1.417	0.15647
Time Since Fire	-0.32123	0.218926	-1.467	0.14229
Region	-0.31214	0.171069	-1.825	0.06806
Leaves:Time Since Fire	0.152722	0.072326	2.112	0.03472
Leaves^2 :Time Since Fire	-0.01152	0.004453	-2.587	0.00969

Vegetative to Dormancy (TSF)

Model selection based on AICc : (c-hat estimate = 1.002)

	K	AICc	Delta_AICc	LL
Dormancy ~ Leaves	2	599.48	0	-297.74
Dormancy ~ Leaves + Region	3	599.67	0.18	-296.82
Dormancy ~ Leaves + Rain	3	600.87	1.39	-297.42
Dormancy ~ Leaves + Region + Rain	4	600.98	1.5	-296.47
Dormancy ~ Leaves + Time-Since-Fire + Region	4	601.01	1.52	-296.48
Dormancy ~ Leaves + Time-Since-Fire	3	601.49	2.01	-297.73
Dormancy ~ Leaves+Leaves^2	3	601.5	2.01	-297.74
Dormancy ~ Leaves +Leaves^2 + Region	4	601.68	2.2	-296.82
Dormancy ~ Leaves + Time-Since-Fire + Region + Rain	5	602.45	2.97	-296.2
Dormancy ~ Leaves + Time-Since-Fire + Rain	4	602.87	3.39	-297.41
Dormancy ~ Leaves +Leaves^2 + Rain	4	602.88	3.4	-297.42
Dormancy ~ Leaves × Time-Since-Fire + Region	5	602.99	3.51	-296.46
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Region	5	603.02	3.54	-296.48
Dormancy ~ Leaves × Time-Since-Fire	4	603.49	4	-297.72
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire	4	603.51	4.03	-297.73
Dormancy ~ Leaves × Time-Since-Fire + Region + Rain	6	604.45	4.97	-296.18
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain	6	604.47	4.99	-296.19
Dormancy ~ Leaves × Time-Since-Fire + Rain	5	604.88	5.4	-297.41
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Rain	5	604.89	5.4	-297.41
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Region+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	606.89	7.41	-296.39
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	6	607.4	7.92	-297.66
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Region + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	8	608.33	8.85	-296.09
Dormancy ~ Leaves +Leaves^2 + Time-Since-Fire + Rain+ Leaves:Time-Since-Fire+Leaves^2 :Time-Since-Fire	7	608.77	9.29	-297.33
Dormancy ~ 1	1	3023.14	2423.66	-1510.57

Vegetative to Dormancy (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.17314	0.17169	-12.657	<2e-16
leaves	-0.03099	0.03265	-0.949	0.342

Reproductive Survival (TSF)

Model selection based on AICc : (c-hat estimate = 1.064)

	K	AICc	Delta_AICc	LL
Survival ~ Size + Region	3	2404.36	0	-1199.18
Survival ~ Size + Time-Since-Fire + Herbivory + Region*	5	2404.71	0.35	-1197.35
Survival ~ Size +Size^2+ Region	4	2405.79	1.43	-1198.89
Survival ~ Size +Size^2+ Time-Since-Fire + Herbivory + Region	6	2406.15	1.79	-1197.07
Survival ~ Size + Time-Since-Fire × Herbivory + Region	6	2406.36	2	-1197.17
Survival ~ Size + Time-Since-Fire + Herbivory + Region + Rain	6	2406.48	2.12	-1197.23
Survival ~ Size +Size^2+ Time-Since-Fire × Herbivory + Region	7	2407.81	3.45	-1196.89
Survival ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain + Region	7	2407.87	3.51	-1196.92
Survival ~ Size + Time-Since-Fire × Herbivory + Region + Rain	7	2408.17	3.81	-1197.07
Survival ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain + Region	8	2409.57	5.21	-1196.77
Survival ~ Size + Time-Since-Fire + Herbivory	4	2412.32	7.96	-1202.16
Survival ~ Size +Size^2+ Time-Since-Fire + Herbivory	5	2413.48	9.12	-1201.74
Survival ~ Size + Time-Since-Fire	3	2413.82	9.46	-1203.91
Survival ~ Size + Time-Since-Fire × Herbivory	5	2414.13	9.77	-1202.06
Survival ~ Size + Time-Since-Fire + Herbivory + Rain	5	2414.17	9.81	-1202.08
Survival ~ Size + Herbivory	3	2414.23	9.87	-1204.11
Survival ~ Size +Size^2+ Time-Since-Fire	4	2415.02	10.67	-1203.51
Survival ~ Size +Size^2+ Herbivory	4	2415.03	10.67	-1203.51
Survival ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain	6	2415.27	10.91	-1201.62
Survival ~ Size +Size^2+ Time-Since-Fire × Herbivory	6	2415.29	10.94	-1201.64
Survival ~ Size	2	2415.82	11.46	-1205.91
Survival ~ Size + Time-Since-Fire × Herbivory + Rain	6	2416	11.64	-1201.99
Survival ~ Size +Size^2	3	2416.69	12.33	-1205.34
Survival ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain	7	2417.11	12.75	-1201.54
Survival ~ Size + Rain	3	2417.46	13.1	-1205.73
Survival ~ Size +Size^2+ Rain	4	2418.23	13.87	-1205.11
Survival ~ 1	1	4612.81	2208.45	-2305.41

*We retained this model for consistency with the vital rate in the Habitat model.

Reproductive Survival (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.12232	0.32891	0.372	0.70997
Size	0.49831	0.04374	11.393	< 2e-16
Time Since Fire	-0.03074	0.08044	-0.382	0.70234
Herbivory	-0.04247	0.11984	-0.354	0.72305
Region	0.3877	0.12411	3.124	0.00179

Reproductive to Reproductive Transition Probability(TSF) Model selection based on AICc : (c-hat estimate = 1.064)				
	K	AICc	Delta_AICc	LL
Reproduction(t+1) ~ Size +Size^2+ Herbivory	4	2928.57	0	-1460.28
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Region	6	2930	1.43	-1458.99
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory	5	2930.21	1.64	-1460.09
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain + Region	7	2930.29	1.72	-1458.13
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain	6	2930.5	1.94	-1459.24
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Region	7	2931.8	3.24	-1458.89
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory	6	2931.95	3.39	-1459.97
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain + Region	8	2932.04	3.47	-1458
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain	7	2932.19	3.62	-1459.08
Reproduction(t+1) ~ Size +Size^2+ Region	4	2933.64	5.07	-1462.82
Reproduction(t+1) ~ Size +Size^2	3	2934.26	5.7	-1464.13
Reproduction(t+1) ~ Size +Size^2+ Rain	4	2934.36	5.79	-1463.17
Reproduction(t+1) ~ Size +Size^2+ Time-Since-Fire	4	2935.95	7.38	-1463.97
Reproduction(t+1) ~ Size + Herbivory	3	2942.49	13.92	-1468.24
Reproduction(t+1) ~ Size + Time-Since-Fire + Herbivory + Rain	5	2943.93	15.37	-1466.96
Reproduction(t+1) ~ Size + Time-Since-Fire + Herbivory + Region + Rain	6	2944.22	15.65	-1466.1
Reproduction(t+1) ~ Size + Time-Since-Fire + Herbivory	4	2944.42	15.86	-1468.21
Reproduction(t+1) ~ Size + Time-Since-Fire + Herbivory + Region	5	2944.76	16.19	-1467.37
Reproduction(t+1) ~ Size + Time-Since-Fire × Herbivory + Rain	6	2945.56	16.99	-1466.77
Reproduction(t+1) ~ Size + Time-Since-Fire × Herbivory + Region + Rain	7	2945.9	17.34	-1465.94
Reproduction(t+1) ~ Size + Time-Since-Fire × Herbivory	5	2946.13	17.57	-1468.06
Reproduction(t+1) ~ Size + Time-Since-Fire × Herbivory + Region	6	2946.52	17.95	-1467.25
Reproduction(t+1) ~ Size + Rain	3	2948.84	20.27	-1471.42
Reproduction(t+1) ~ Size	2	2949.51	20.95	-1472.76
Reproduction(t+1) ~ Size + Region	3	2949.83	21.27	-1471.91
Reproduction(t+1) ~ Size + Time-Since-Fire	3	2951.46	22.89	-1472.73
Reproduction(t+1) ~ 1	1	6610.5	3681.93	-3304.25

Reproductive to Reproductive Transition Probability(TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.38612	0.2476	1.559	0.119
Size	-0.06921	0.17247	-0.401	0.688
Size^2	0.11695	0.02991	3.91	9.23E-05
Herbivory	-0.14609	0.10102	-1.446	0.148

Reproductive to Reproductive Size (TSF)
Model selection based on AICc

	K	AICc	Delta_AICc	LL
Size(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain + Region	8	8865.33	0	-4424.64
Size(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain + Region	9	8867.33	2	-4424.64
Size(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Region	7	8871.41	6.08	-4428.69
Size(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain	7	8872.08	6.75	-4429.02
Size(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Region	8	8873.38	8.05	-4428.67
Size(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain	8	8874.09	8.76	-4429.02
Size(t+1) ~ Size +Size^2+ Herbivory	5	8876.21	10.87	-4433.09
Size(t+1) ~ Size +Size^2+ Rain	5	8877.94	12.61	-4433.96
Size(t+1) ~ Size +Size^2+ Time-Since-Fire + Herbivory	6	8878.17	12.84	-4433.07
Size(t+1) ~ Size +Size^2+ Region	5	8879	13.67	-4434.49
Size(t+1) ~ Size +Size^2+ Time-Since-Fire × Herbivory	7	8880.17	14.84	-4433.07
Size(t+1) ~ Size +Size^2	4	8884.08	18.75	-4438.03
Size(t+1) ~ Size +Size^2+ Time-Since-Fire	5	8886.08	20.75	-4438.03
Size(t+1) ~ Size + Time-Since-Fire + Herbivory + Region + Rain	7	9009.74	144.41	-4497.85
Size(t+1) ~ Size + Time-Since-Fire × Herbivory + Region + Rain	8	9011.75	146.42	-4497.85
Size(t+1) ~ Size + Time-Since-Fire + Herbivory + Rain	6	9013.01	147.68	-4500.49
Size(t+1) ~ Size + Time-Since-Fire × Herbivory + Rain	7	9015.01	149.68	-4500.49
Size(t+1) ~ Size + Time-Since-Fire + Herbivory + Region	6	9018.6	153.27	-4503.29
Size(t+1) ~ Size + Time-Since-Fire × Herbivory + Region	7	9020.6	155.27	-4503.28
Size(t+1) ~ Size + Herbivory	4	9020.97	155.64	-4506.48
Size(t+1) ~ Size + Time-Since-Fire + Herbivory	5	9021.86	156.53	-4505.92
Size(t+1) ~ Size + Rain	4	9022.55	157.22	-4507.27
Size(t+1) ~ Size + Time-Since-Fire × Herbivory	6	9023.86	158.53	-4505.92
Size(t+1) ~ Size + Region	4	9030.37	165.04	-4511.18
Size(t+1) ~ Size	3	9031.13	165.8	-4512.56
Size(t+1) ~ Size + Time-Since-Fire	4	9032.26	166.93	-4512.12
Size(t+1) ~ 1	2	13489.1	4623.77	-6742.55

Reproductive to Reproductive Size (TSF)				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.6457	0.16922	21.544	< 2e-16
Size	-0.44547	0.0767	-5.808	6.96E-09
Size^2	0.14042	0.01148	12.232	< 2e-16
Time Since Fire	-0.04401	0.02886	-1.525	0.12732
Herbivory	-0.05346	0.03806	-1.405	0.16018
Region	-0.12433	0.04203	-2.958	0.00312
Rain	-0.10911	0.03838	-2.843	0.0045

Reproductive to Dormancy Probability (TSF)

Model selection based on AICc : (c-hat estimate = 1.018)

	K	AICc	Delta_AICc	LL
Dormancy ~ Size + Time-Since-Fire + Herbivory + Region + Rain	6	1722.66	0	-855.32
Dormancy ~ Size + Rain	3	1723.21	0.55	-858.6
Dormancy ~ Size + Time-Since-Fire + Herbivory + Rain	5	1724.18	1.52	-857.08
Dormancy ~ Size + Time-Since-Fire × Herbivory + Region + Rain	7	1724.5	1.84	-855.23
Dormancy ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain + Region	7	1724.67	2	-855.32
Dormancy ~ Size +Size^2+ Rain	4	1725.2	2.54	-858.6
Dormancy ~ Size + Time-Since-Fire × Herbivory + Rain	6	1726.06	3.4	-857.02
Dormancy ~ Size +Size^2+ Time-Since-Fire + Herbivory + Rain	6	1726.19	3.53	-857.08
Dormancy ~ Size +Size^2+ Time-Since-Fire × Herbivory + Rain + Region	8	1726.5	3.84	-855.23
Dormancy ~ Size + Region	3	1728.71	6.05	-861.35
Dormancy ~ Size + Herbivory	3	1729.66	7	-861.83
Dormancy ~ Size + Time-Since-Fire + Herbivory + Region	5	1729.98	7.32	-859.98
Dormancy ~ Size	2	1729.99	7.33	-862.99
Dormancy ~ Size +Size^2+ Region	4	1730.69	8.03	-861.34
Dormancy ~ Size +Size^2+ Herbivory	4	1731.59	8.93	-861.79
Dormancy ~ Size + Time-Since-Fire + Herbivory	4	1731.59	8.93	-861.79
Dormancy ~ Size +Size^2	3	1731.91	9.25	-862.95
Dormancy ~ Size + Time-Since-Fire × Herbivory + Region	6	1731.93	9.27	-859.95
Dormancy ~ Size + Time-Since-Fire	3	1731.95	9.29	-862.97
Dormancy ~ Size +Size^2+ Time-Since-Fire + Herbivory + Region	6	1731.97	9.31	-859.97
Dormancy ~ Size +Size^2+ Time-Since-Fire + Herbivory	5	1733.54	10.88	-861.76
Dormancy ~ Size + Time-Since-Fire × Herbivory	5	1733.56	10.9	-861.77
Dormancy ~ Size +Size^2+ Time-Since-Fire	4	1733.88	11.22	-862.94
Dormancy ~ Size +Size^2+ Time-Since-Fire × Herbivory + Region	7	1733.92	11.26	-859.94
Dormancy ~ Size +Size^2+ Time-Since-Fire × Herbivory	6	1735.51	12.85	-861.75
Dormancy ~ 1	1	3023.14	1300.48	-1510.57

Reproductive to Dormancy (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.8152	0.47368	-3.832	0.000127
Size	-0.2967	0.06021	-4.927	8.33E-07
Time Since Fire	-0.0515	0.1047	-0.492	0.622826
Herbivory	-0.20709	0.14648	-1.414	0.157427
Region	-0.29157	0.15389	-1.895	0.058136
Rain	0.44979	0.15047	2.989	0.002797

Reproductive to Vegetative Size (TSF)

Model selection based on QAICc :(c-hat estimate = 3.86)

	k	sumlogL	sumaic	delta
Leaves(t+1) ~ Size + TSF + Herbivory + Region + Rain + Size^2	8	-1442.49	2900.978	0
Leaves(t+1) ~ Size + TSF + Herbivory + Rain + Size^2	7	-1443.69	2901.38	0.401
Leaves(t+1) ~ Size + TSF × Herbivory + Region + Rain + Size^2	9	-1442.34	2902.68	1.701
Leaves(t+1) ~ Size + TSF × Herbivory + Rain + Size^2	8	-1443.51	2903.014	2.036
Leaves(t+1) ~ Size + TSF + Herbivory + Region + Rain	7	-1447.99	2909.983	9.005
Leaves(t+1) ~ Size + Herbivory + Size^2	5	-1449.99	2909.986	9.008
Leaves(t+1) ~ Size + TSF + Herbivory + Rain	6	-1449.1	2910.19	9.212
Leaves(t+1) ~ Size + TSF + Herbivory + Region + Size^2	7	-1448.5	2910.997	10.018
Leaves(t+1) ~ Size + TSF × Herbivory + Region + Rain	8	-1447.95	2911.904	10.926
Leaves(t+1) ~ Size + TSF + Herbivory + Size^2	6	-1449.97	2911.935	10.957
Leaves(t+1) ~ Size + TSF × Herbivory + Rain	7	-1449.04	2912.076	11.098
Leaves(t+1) ~ Size + TSF × Herbivory + Region + Size^2	8	-1448.49	2912.975	11.997
Leaves(t+1) ~ Size + TSF × Herbivory + Size^2	7	-1449.95	2913.896	12.917
Leaves(t+1) ~ Size + Rain + Size^2	5	-1453.46	2916.927	15.949
Leaves(t+1) ~ Size + Herbivory	4	-1455.37	2918.746	17.768
Leaves(t+1) ~ Size + TSF + Herbivory + Region	6	-1453.95	2919.893	18.915
Leaves(t+1) ~ Size + TSF + Herbivory	5	-1455.3	2920.591	19.612
Leaves(t+1) ~ Size + TSF × Herbivory + Region	7	-1453.94	2921.88	20.902
Leaves(t+1) ~ Size + TSF × Herbivory	6	-1455.29	2922.587	21.608
Leaves(t+1) ~ Size + Rain	4	-1460.15	2928.298	27.319
Leaves(t+1) ~ Size + Size^2	4	-1460.74	2929.485	28.506
Leaves(t+1) ~ Size + Region + Size^2	5	-1459.78	2929.557	28.578
Leaves(t+1) ~ Size + TSF + Size^2	5	-1460.74	2931.476	30.498
Leaves(t+1) ~ Size	3	-1467.62	2941.231	40.253
Leaves(t+1) ~ Size + Region	4	-1466.87	2941.747	40.769
Leaves(t+1) ~ Size + TSF	4	-1467.58	2943.151	42.173
Leaves(t+1) ~ 1	2	-3540.91	7085.817	4184.838

Reproductive to Vegetative Size (TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.361726	0.237762	5.727	1.02E-08
Size	-0.22704	0.103665	-2.19	0.028517
Size^2	0.056286	0.01725	3.263	0.001103
TSF	-0.00763	0.04499	-0.17	0.865288
Herbivory	0.249442	0.065085	3.833	0.000127
Region	-0.10196	0.065511	-1.556	0.119603
Rain	0.212828	0.060501	3.518	0.000435

Fecundity (TSF)
Model selection based on QAICc : (c-hat estimate = 2.1021)

	k	QAICc	Delta_QAICc	Quasi.LL
Heads ~ Size + TSF × Herbivory	6	11545.68	0	-5766.84
Heads ~ Size + TSF × Herbivory + Region*	7	11545.79	0.116	-5765.9
Heads ~ Size + TSF × Herbivory + Rain	7	11546.33	0.655	-5766.17
Heads ~ Size + TSF × Herbivory + Region + Rain	8	11546.5	0.829	-5765.25
Heads ~ Size + TSF	4	11549.09	3.411	-5770.54
Heads ~ Size + TSF + Region	5	11549.21	3.53	-5769.6
Heads ~ Size + TSF + Herbivory + Region	6	11549.58	3.909	-5768.79
Heads ~ Size + TSF + Herbivory	5	11549.71	4.033	-5769.85
Heads ~ Size + TSF + Herbivory + Region + Rain	7	11550.21	4.537	-5768.11
Heads ~ Size + TSF + Herbivory + Rain	6	11550.27	4.597	-5769.14
Heads ~ Size	3	17883.77	6338.097	-8938.89
Heads ~ Size + Herbivory	4	17884.19	6338.512	-8938.09
Heads ~ Size + Region	4	17884.47	6338.792	-8938.23
Heads ~ Size + Rain	4	17885.18	6339.5	-8938.59
Heads ~ 1	2	22338.31	10792.64	-11167.2

*We retained this model for consistency with the vital rate in the Habitat model.

<table>
<tr><th colspan="5">Fecundity (TSF)</th></tr>
<tr><th></th><th>Estimate</th><th>Std. Error</th><th>z value</th><th>Pr(>|z|)</th></tr>
<tr><td>(Intercept)</td><td>-4.7883</td><td>0.12317</td><td>-38.876</td><td><2e-16</td></tr>
<tr><td>Size</td><td>1.4906</td><td>0.02263</td><td>65.882</td><td><2e-16</td></tr>
<tr><td>Time Since Fire</td><td>-0.02809</td><td>0.0273</td><td>-1.029</td><td>0.3035</td></tr>
<tr><td>Herbivory</td><td>0.08868</td><td>0.0669</td><td>1.326</td><td>0.185</td></tr>
<tr><td>Region</td><td>-0.06532</td><td>0.03211</td><td>-2.034</td><td>0.0419</td></tr>
<tr><td>Time Since Fire:Herbivory</td><td>-0.08938</td><td>0.04282</td><td>-2.087</td><td>0.0369</td></tr>
</table>

Herbivory Rate (TSF) Model selection based on AICc: (c-hat estimate = 1.152)				
	K	AICc	Delta_AICc	LL
Herbivory(t+1) ~ Size + Size^2+ TSF + Herbivory + Rain + Region	7	3510.22	0	-1748.09
Herbivory(t+1) ~ Size + Size^2+ TSF × Herbivory + Rain + Region	8	3512.18	1.96	-1748.06
Herbivory(t+1) ~ Size + Size^2+ TSF + Herbivory + Region	6	3514	3.78	-1750.99
Herbivory(t+1) ~ Size + Size^2+ TSF × Herbivory + Region	7	3515.84	5.62	-1750.9
Herbivory(t+1) ~ Size + Size^2+ TSF + Herbivory + Rain	6	3520.68	10.46	-1754.32
Herbivory(t+1) ~ Size + Size^2+ Herbivory	4	3522.55	12.33	-1757.27
Herbivory(t+1) ~ Size + Size^2 TSF + Herbivory	5	3523.19	12.97	-1756.58
Herbivory(t+1) ~ Size + Size^2+ TSF × Herbivory	6	3525.13	14.91	-1756.55
Herbivory(t+1) ~ Size + TSF + Herbivory + Region + Rain	6	3570.55	60.33	-1779.26
Herbivory(t+1) ~ Size + TSF × Herbivory + Region + Rain	7	3572.45	62.23	-1779.21
Herbivory(t+1) ~ Size + TSF + Herbivory + Region	5	3574.72	64.5	-1782.35
Herbivory(t+1) ~ Size + TSF × Herbivory + Region	6	3576.46	66.24	-1782.22
Herbivory(t+1) ~ Size + TSF + Herbivory + Rain	5	3581.77	71.55	-1785.87
Herbivory(t+1) ~ Size + TSF × Herbivory + Rain	6	3583.75	73.53	-1785.86
Herbivory(t+1) ~ Size + Herbivory	3	3584.15	73.93	-1789.07
Herbivory(t+1) ~ Size + TSF + Herbivory	4	3584.61	74.39	-1788.3
Herbivory(t+1) ~ Size + TSF × Herbivory	5	3586.5	76.28	-1788.24
Herbivory(t+1) ~ Size +Size2+ TSF	4	5920.06	2409.84	-2956.02
Herbivory(t+1) ~ Size +Size2+ Rain	4	5910.16	2399.94	-2951.08
Herbivory(t+1) ~ Size +Size2+ Region	4	5914.02	2403.79	-2953
Herbivory(t+1) ~ Size +Size2	3	5918.11	2407.89	-2956.05
Herbivory(t+1) ~ Size + TSF	3	5920.65	2410.42	-2957.32
Herbivory(t+1) ~ Size + Rain	3	5910.95	2400.73	-2952.47
Herbivory(t+1) ~ Size + Region	3	5914.11	2403.89	-2954.05
Herbivory(t+1) ~ Size	2	5918.67	2408.45	-2957.33
Herbivory(t+1) ~ 1	1	6362.81	2852.59	-3180.41

Herbivory Rate(TSF)				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.63058	0.55056	8.411	< 2e-16
Size	-2.62143	0.27008	-9.706	< 2e-16
Size^2	0.27221	0.03682	7.392	1.44E-13
TSF	0.03921	0.06347	0.618	0.536751
Herbivory	0.57101	0.08194	6.969	3.20E-12
Rain	0.20076	0.08359	2.402	0.016319
Region	0.32289	0.09174	3.52	0.000432