

# 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 how they interact to shape demographic outcomes remains poorly understood. Such interactions may alter dynamics of populations in non-additive ways, making demographic predictions challenging when focusing on only one disturbance. 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 field data across 20 populations, encompassing 2435 individuals of an endangered herb, *Liatris ohlingerae*. We examined interactive effects of vertebrate herbivory, fire and anthropogenic activities (sand roads) on vital rates (e.g. survival, growth, reproduction, recruitment) and ultimately on population growth rates ( $\lambda$ ), to test the hypothesis that interactions amplify or dampen differences in  $\lambda$  depending on environmental contexts. We constructed megamatrices to determine coupled dynamics in individuals damaged vs. not damaged by herbivores in roadsides and in Florida scrub with different times since fire.

**3.** We identified strong interactive effects of fire with herbivory and habitat with herbivory on vital rates and on population growth rates in the IPM model. We also found different patterns of variation in  $\lambda$  between habitat and time-since-fire scenarios; population growth rates were higher in roadside populations compared to scrub populations and declined with increasing time since fire. Herbivory had interactive effects with both fire and human disturbances on  $\lambda$ . Herbivory resulted in decreased differences in  $\lambda$  due to anthropogenic disturbance and slightly increased differences in  $\lambda$  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 nonlinearities represent challenges in understanding and projecting of population dynamics. Here, we examined the effects of various sources of disturbance on the population dynamics of an endangered plant species, finding complex interactions affecting population growth rates. We argue that integration of multiple, interacting stressors in IPMs will allow more accurate estimation of the overall effects of ecological processes on species viability.

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

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## Introduction

Disturbances are critical drivers of many ecological processes, from local to global scales. They may be biotic (e.g. Goslee, Peters & Beck 2001; Rautio *et al.* 2005), 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 thus the local viability or invasiveness of organisms (Kercher & Zedler 2004). Consequently, 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; Mandl, Ticktin & Zuidema 2015; Ehrlén *et al.* 2016). Due to the complexities that potentially interactive disturbances may bring to population dynamics, here we first lay down a road map, which leads to our hypothesis of amplified vs. dampened population outcomes. This road map includes a brief account of how few studies have examined multiple disturbances, how anthropogenic and natural disturbances are difficult to examine in natural settings and how complex life cycles make this deciphering even more challenging.

A fairly small proportion of published studies using demographic models have explicitly considered environmental drivers such as disturbances (Crone *et al.* 2011). Most of these studies focus on a single driver (e.g. fire; Salguero-Gómez *et al.* 2015). However, interacting drivers can and do affect populations in ways that are not predictable when considering drivers in isolation. For example, the effects of predation and herbivory may be mediated by other biotic or abiotic factors (Bale *et al.* 2002; Byrnes *et al.* 2006). Furthermore, demographic effects of fire may interact with precipitation (Burgman & Lamont 1992), interspecific competition (Melgoza, Nowak & Tausch 1990) and herbivory (Hegland, Jongejans & Rydgren 2010). Fire and herbivory interactions have been invoked to explain species coexistence (Sankaran, Ratnam & Hanan 2004; Fuhlendorf *et al.* 2009), yet these effects have not been quantified demographically.

To further complicate this picture, both natural *a*/biotic 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). Roads are known to alter competitive plant interactions (Gelbard & Belnap 2003) and can cause genetic depression via habitat fragmentation (Keller & Lurgiader 2003; Jump & Peñuelas 2006). Anthropogenic disturbance along sandy roads can increase fecundity, likely due to reduced below-ground competition, and population instability (Quintana-Ascencio, Weekley & Menges 2007; Schafer *et al.* 2010; Oakley 2013). Anthropogenic disturbances can also

interact with other drivers, such as herbivory and fire, in affecting populations. For instance, reduced habitat heterogeneity interacts with bark beetle herbivory in increasing tree mortality, a process termed ‘anthropogenic amplification’ (Raffa *et al.* 2008). Anthropogenic disturbances can either hinder or amplify fire regimes. Deforestation may decrease humidity and thus increase fire frequency (Uhl & Kauffman 1990), but habitat fragmentation in pyrogenic landscapes often has a major depressing effect on fire frequencies and intensities (Duncan & Schmalzer 2004). In our study system, the Florida scrub, anthropogenic disturbances (roadsides) alter the rates and intensity of herbivory (Brudvig & Quintana-Ascencio 2003; Kettenring, Weekley & Menges 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 differently various 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 towards a successful management (Silvertown, Franco & Menges 1996; Caswell 2001).

We studied the importance (magnitude) and direction (negative/positive) of the effects of herbivory, fire, and anthropogenic disturbance on the population dynamics of an endangered endemic Florida scrub species, *Liatrix ohlingerae* (Asteraceae). This perennial plant can resprout after fire, and thus, its population dynamics is likely to be more resilient to stressors than co-occurring, shorter-lived herbaceous species that rely on a seed bank to recover after fire (Franco & Silvertown 2004; Paula *et al.* 2009). We tested the hypothesis that interactions among these disturbances amplify or dampen differences in population growth rate ( $\lambda$ ) depending on environmental contexts, with particular attention to the anthropogenic amplification hypothesis (above; Raffa *et al.* 2008), which would result in a magnified – rather than additive – effect on  $\lambda$  by interactive stressing factors. We expected that the cascading, negative effects of herbivory on survival and fecundity, and ultimately on  $\lambda$ , would be modulated by habitat type (Menges & Weekley 2005; Kettenring, Weekley & Menges 2009). Fire in recently burned scrub and mowing along roadsides, respectively, may lower survival directly; however, openness created by these disturbances could also increase fecundity and survival due to reduced competition. The relative effects of these disturbances on  $\lambda$  can vary. Positive effects of reduced competition on survival can be reduced if herbivory is higher in more disturbed communities. To test this hypothesis, we built hierarchical integral projection models (IPM) to evaluate the influence of these disturbances through their effects on the underlying vital rates of survival, growth, plant dormancy, reproduction and recruitment, and the combined effect of these vital rates on population growth rate. Differential responses of the vital rates to the same

stressors can result in additional complex synergies with consequences for  $\lambda$ .

## Materials and 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 subtropical and is typically defined by a warmer rainy season and a cooler dry season. Soils are xeric, nutrient poor and sandy. Florida scrub is characterized by denser patches of Florida rosemary (*Ceratiola ericoides*), xeric oaks (*Quercus* spp.) and palmettos (*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 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, Weekley & Menges 2009).

*Liatis ohlingerae* S.F. Blake B.L. Rob. (Asteraceae) is a perennial (maximum observed life span >10 years) herbaceous species endemic to the Lake Wales Ridge (Evans, Menges & Gordon 2003). Individuals form a corm from which above-ground biomass is produced yearly (Dolan *et al.* 1999), typically dying back in the winter. Flowering scapes are developed in mature individuals during June–September (Evans, Menges & Gordon 2003). Individuals are self-incompatible (Evans, Menges & Gordon 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 persistent seed bank (Weekley *et al.* 2008; Stephens, Castro-Morales & Quintana-Ascencio 2012), although its recruitment is typically low (Menges *et al.* 2010). Potential positive effects of fire 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* was slightly higher in patches with larger 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 reported higher rates of herbivory occurring in recently burned and non-roadside habitats (Kettenring, Weekley & Menges 2009).

The life cycle of *L. 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 above-ground biomass in a given year (Shefferson 2009) and instead remain alive exclusively below-ground. This species has no clonal reproduction. All possible transitions between these stages may occur between years (Fig. 1a).

### 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, Tye *et al.* 2016) through 2012 for 20 populations, resulting in a total of 2345 individuals. At each population, we established permanent plots ranging from 5 and 600 m<sup>2</sup>. 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°09' N; Table S1) 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>).

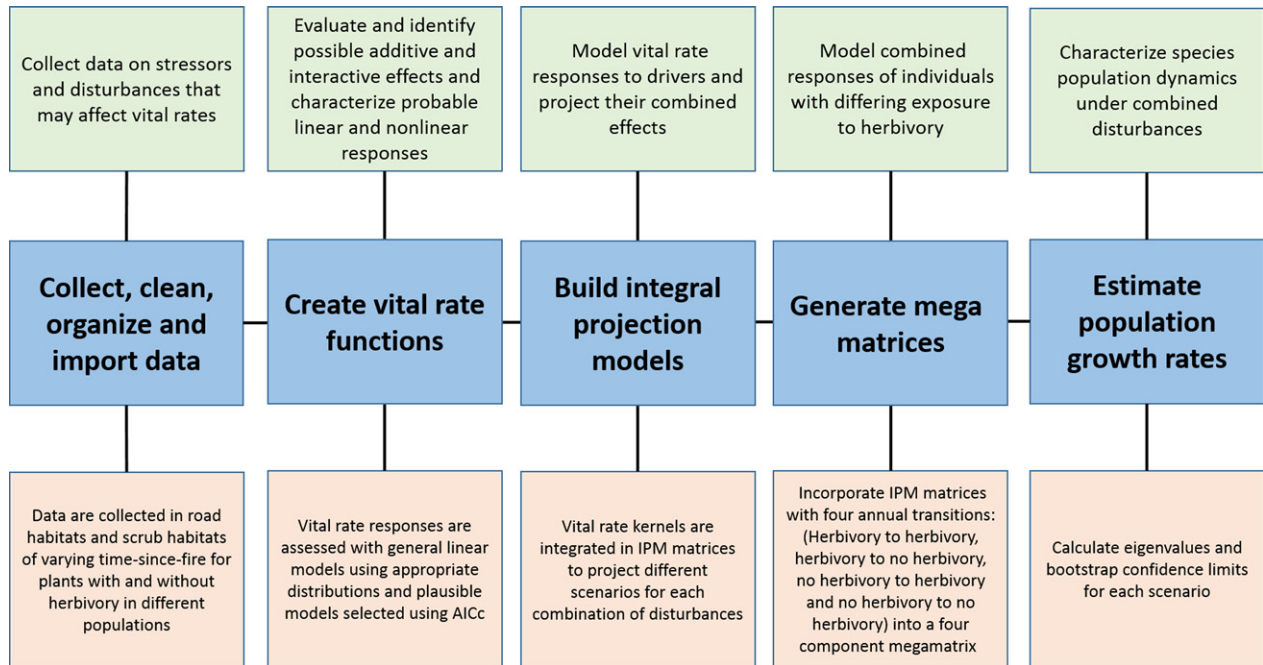
We individually marked each established individual and new seedlings with a unique identifier *in situ*. Seedlings were distinguished from established individuals awakening from vegetative dormancy through anatomic features related to leaf size and number. Data collected for reproductive individuals 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 above-ground for 1 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 (E. S. Menges, S. A. Smith & C. W. Weekley, unpubl. data).

### DEMOGRAPHIC MODELLING

Our modelling approach combined standard procedures for estimating the effects of disturbances and stressors on vital rates, integrated these responses into integral projection models (IPMs) and built megamatrices to assess interacting effects of disturbance on population dynamics (Fig. 1). We constructed three-stage 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, Vienna, Austria). 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): (i) four continuous kernel functions:  $K_{v,v}$ ,  $K_{v,r}$ ,  $K_{r,v}$  and  $K_{r,r}$ , where  $K_{ij}$  represents transitions from stage  $j$  (v or r) in time  $t$  to stage  $i$  in  $t + 1$  (Caswell 2001); (ii) four vectors describing transitions involving dormancy as the origin or end stage:  $D_v$ ,  $D_r$ ,  $V_d$  and  $R_d$ ; and (iii) a scalar quantity  $D_d$  indicating the probability of stasis for dormant individuals (eqn 1 and Fig. 2B):

$$\begin{pmatrix} V_d & R_d & D_d \\ P_{r,v} & P_{r,r} & D_r \\ P_{v,v} & P_{v,r} & D_v \end{pmatrix} \quad \text{eqn 1}$$

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 traditional matrix population models (Caswell 2001) and IPMs (Easterling, Ellner & Dixon 2000), our hybrid model’s eigen structure 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). Our



**Fig. 1.** A workflow describing the steps used to construct the overall models of the population dynamics of *Liatris ohlingearae* and the effects of a/biotic factors on its population growth rates. The blue centre boxes describe the steps involved. The green and orange boxes describe the rationale and methods in each step, respectively.

model allows us to examine the interactive effects of the parameters linking size, a/biotic factors and their interactions to all vital rates through the estimation of their responses with generalized linear models (Merow *et al.* 2014; Zambrano & Salguero-Gómez 2014). We integrated these responses in the IPMs for individuals with and without herbivory under different scenarios of the disturbances. Our megamatrices (see below) linked the coupled dynamics of these two states per disturbance scenario using estimates of probability of herbivory for plants previously non-consumed and consumed.

We carried out model selection to identify the most plausible combination of studied environmental variables (TSF, herbivory, site, precipitation and roads) and their interactions explaining variation of 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 distributions for survival ( $\sigma$ ) and probability of transitioning between stages ( $T$ ), and a normal distribution for changes in size of reproductive plants ( $\gamma_{r,r}$ ,  $\gamma_{v,r}$ ). We adjusted by quasi-Poisson for changes in number of leaves of vegetative plants ( $\gamma_{v,v}$ ) and used negative binomial distributions for flower counts ( $\phi_1$ ) and changes in number of leaves of vegetative plants ( $\gamma_{r,v}$ ). We used Akaike Information 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 proceeded 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<sup>-1</sup>). 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. In our model, vegetative plants were not affected by herbivory (topping) and this allocation does not affect the simulations.

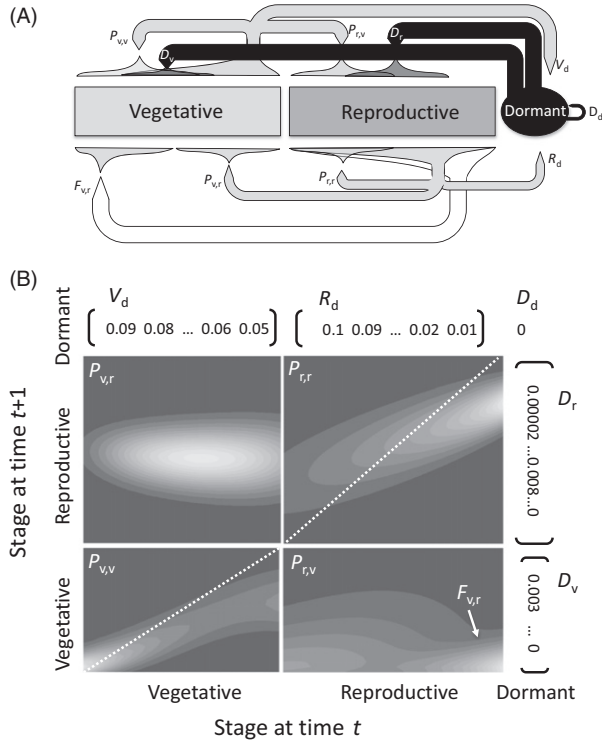
Because fires do not take place on/nearby roads, we constructed two separate IPMs. The *habitat model* was parameterized with data from all populations, while the *time-since-fire (TSF) model* was parameterized with Florida scrub population data only. In one case, where the most plausible models for 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 eqns 2 and 3

$$P_{v,v}(x,y) = \sigma_v(x) \times (1 - T_{v,r}(x,y)) \times \gamma_{v,v}(x,y) \quad \text{eqn 2}$$

$$P_{r,v}(x,y) = \sigma_v(x) \times (T_{r,v}(x,y)) \times \gamma_{r,v}(x,y), \quad \text{eqn 3}$$

where  $P$ , following standard IPM notation (Easterling, Ellner & Dixon 2000), indicates the kernel of each submatrix,  $\sigma$  indicates survival of an individual of size  $x$  in year  $t$  to the next year  $t+1$ ,  $T_{ij}$  indicates the probability of transitioning from stage  $j$  in time  $t$  to stage





**Fig. 2.** (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 grey, dark grey and black arrows indicate transition probabilities from individuals in stages v, r and d, respectively. Rates of dormancy:  $V_d$ ,  $R_d$  and  $D_d$ ; Survival-size change kernels within and between vegetative and reproductive individuals:  $P_{v,v}$ ,  $P_{r,v}$ ,  $P_{r,r}$  and  $P_{v,r}$ ; Vectors of emergence from vegetative dormancy into vegetative and reproductive stages:  $D_r$  and  $D_v$ . The white arrow corresponds to the kernel of reproduction,  $F_{v,r}$ . (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. The white dotted, diagonal line represents no changes in size within v and r.

$i$  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 Poisson (vegetative to vegetative) or negative binomial (reproductive to vegetative) 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 ( $F_{i,j}$ ; eqn 4). Reproduction was modelled as the number of heads per capita ( $\phi_1$ , with negative binomial error), and five constants quantified elsewhere for the same species and field sites (Stephens, Castro-Morales & Quintana-Ascencio 2012; Weekley *et al.* 2008; E. S. Menges, S. A. Smith & C. W. Weekley, unpubl. data): number of seeds per head ( $\phi_2$ ), pre- and post-dispersal seed predation collected from estimates of boring insect damage and experimental data on seed removal ( $\phi_3$ ,  $\phi_4$ ), seed viability and germination rates based on growth chamber trials ( $\phi_5$ ,  $\phi_6$ ). 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 ( $\phi_7$ ) that adjusts the estimated value to be more consistent with the observed number of germinants in the field (cf. Quintana-Ascencio, Menges & Weekley 2003; Rose, Louda & Rees 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 follows:

$$K_{i,j} = P_{i,j} + F_{i,j} \quad \text{eqn 4}$$

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

$$F_{v,r}(x,y) = (\phi_1 \times \phi_2 \times \phi_3 \times \phi_4 \times \phi_5 \times \phi_6 \times \phi_7) + (\sigma_r(x) \times (1 - T_{r,r}(x,y)) \times \gamma_{v,r}(x,y)). \quad \text{eqn 6}$$

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 ( $D_d$ ) more than a year was assumed to be zero as it occurred infrequently ( $D_{d(t=0, t \geq 2)} = 0.016$ ), and the sensitivity of population growth rate ( $\lambda$ ) to  $D_d$  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 rate were summarized in Table 1 (details and plots were shown in Figs S1 and S2 and Table S2). Models with the lowest AICc in the set occasionally included variables with marginally significant or non-significant coefficients (Table 1). Below, we only describe variables for which we have evidence of the coefficients being significantly different from zero.

Survival of vegetative plants was significantly higher in roadside plots than in scrub and relatively high in years with higher precipitation. Survival of reproductive individuals was also higher in roadside, increased significantly with plant total stem length, and in the northern sector.

Change in size and fecundity were affected by initial size, habitat and herbivory. Large vegetative plants and larger reproductive plants that transitioned to vegetative produced more leaves. The number of leaves for vegetative plants that previously reproduced was higher in the scrub and with higher precipitation. There was a significantly higher probability of becoming reproductive from the vegetative stage for plants with more leaves, with a small decline for the largest vegetative plants; the shape of the parabolic response varied by time since fire (Table 1). In both models, dormancy of reproductive individuals decreased with total stem length and increased with precipitation (Table 1). Number of

**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 Fig. 2, for further reference on demographic processes)

Vital rate	Explanatory variable	Habitat model	TSF model	
		Estimate (SE)	Estimate (SE)	
Vegetative survival ( $\sigma_v$ )	<i>Intercept</i>	0.196 (0.279)	0.257 (0.430)	
	<i>Leaves</i>	-0.067 (0.040)	-0.053 (0.045)	
	<i>Leaves</i> <sup>2</sup>	0.004 (0.002)	0.003 (0.002)	
	<i>Habitat</i>	<b>0.704 (0.139)</b>	NA	
	<i>Time-Since-Fire</i>	NA	0.147 (0.093)	
	<i>Region</i>	-	<b>0.267 (0.151)</b>	
	<i>Precipitation</i>	<b>0.235 (0.115)</b>	0.198 (0.131)	
Reproductive survival ( $\sigma_r$ )	<i>Intercept</i>	0.171 (0.277)	0.122 (0.329)	
	<i>Length</i>	<b>0.417 (0.038)</b>	<b>0.498 (0.044)</b>	
	<i>Habitat</i>	<b>0.281 (0.104)</b>	NA	
	<i>Herbivory</i>	-0.107 (0.098)	-0.043 (0.119)	
	<i>TSF</i>	NA	-0.030 (0.080)	
	<i>Region</i>	<b>0.331 (0.096)</b>	<b>0.409 (0.111)</b>	
	<i>Intercept</i>	<b>0.945 (0.090)</b>	0.901 (0.111)	
Vegetative-vegetative growth ( $\gamma_{vv}$ )	<i># leaves</i>	<b>0.149 (0.013)</b>	0.157 (0.014)	
	<i># leaves</i> <sup>2</sup>	<b>-0.003 (0.001)</b>	<b>-0.003 (0.001)</b>	
	<i>Region</i>	<b>-0.112 (0.048)</b>	<b>-0.102 (0.056)</b>	
Vegetative-reproductive growth ( $\gamma_{vr}$ )	<i>Intercept</i>	<b>3.717 (0.253)</b>	<b>3.450 (0.216)</b>	
	<i># leaves</i>	-0.034 (0.026)	-0.021 (0.014)	
	<i># leaves</i> <sup>2</sup>	-0.001 (0.001)	-	
	<i>Region</i>	<b>-0.280 (0.099)</b>	<b>-0.263 (0.126)</b>	
	<i>Habitat</i>	<b>-0.216 (0.103)</b>	-	
	<i>Intercept</i>	<b>-1.781 (0.282)</b>	-0.281 (0.499)	
Vegetative → reproductive ( $T_{r,v}$ )	<i># leaves</i>	<b>0.226 (0.035)</b>	0.026 (0.103)	
	<i># leaves</i> <sup>2</sup>	<b>-0.006 (0.001)</b>	-0.007 (0.005)	
	<i>Habitat</i>	0.229 (0.124)	NA	
	<i>Precipitation</i>	0.202 (0.118)	-	
	<i>Region</i>	-	-0.312 (0.171)	
	<i>Time since fire</i>	NA	-0.321 (0.219)	
	<i>Leaves × TSF</i>	NA	<b>0.153 (0.072)</b>	
Vegetative → dormancy ( $V_d$ )	<i>Intercept</i>	<b>-2.263 (0.145)</b>	-2.17 (0.172)	
	<i>Leaves</i>	-0.025 (0.027)	-0.031 (0.032)	
	Reproductive → reproductive ( $T_{r,r}$ )	<i>Intercept</i>	-0.028 (0.271)	0.386 (0.248)
		<i>Length</i>	0.018 (0.154)	-0.069 (0.172)
		<i>Length</i> <sup>2</sup>	<b>0.104 (0.027)</b>	<b>0.117 (0.030)</b>
	<i>Habitat</i>	<b>0.270 (0.134)</b>	NA	
	<i>Herbivory</i>	<b>-0.657 (0.244)</b>	-0.146 (0.101)	
<i>Habitat × Herb</i>	<b>0.525 (0.177)</b>	NA		
Reproductive-vegetative growth ( $\gamma_{rv}$ )	<i>Intercept</i>	<b>1.020 (0.224)</b>	<b>1.362 (0.238)</b>	
	<i>Length</i>	-0.118 (0.093)	<b>-0.227 (0.104)</b>	
	<i>Length</i> <sup>2</sup>	<b>0.043 (0.016)</b>	<b>0.056 (0.017)</b>	
	<i>Habitat</i>	<b>0.264 (0.087)</b>	NA	
	<i>Precipitation</i>	<b>0.185 (0.050)</b>	<b>0.213 (0.060)</b>	
	<i>TSF</i>	NA	-0.008 (0.045)	
	<i>Region</i>	<b>-0.159 (0.052)</b>	<b>-0.102 (0.065)</b>	
	<i>Herbivory</i>	<b>0.555 (0.152)</b>	<b>0.249 (0.065)</b>	
	<i>Habitat × Herb</i>	<b>-0.267 (0.110)</b>	NA	
Reproductive-reproductive growth ( $\gamma_{rr}$ )	<i>Intercept</i>	<b>3.539 (0.144)</b>	<b>3.646 (0.169)</b>	
	<i>Length</i>	<b>-0.401 (0.065)</b>	<b>-0.445 (0.078)</b>	
	<i>Length</i> <sup>2</sup>	<b>0.136 (0.010)</b>	<b>0.140 (0.011)</b>	
	<i>Habitat</i>	<b>-0.208 (0.049)</b>	NA	
	<i>TSF</i>	NA	-0.044 (0.029)	
	<i>Precipitation</i>	<b>-0.101 (0.031)</b>	<b>-0.109 (0.038)</b>	
	<i>Region</i>	<b>-0.043 (0.031)</b>	<b>-0.124 (0.042)</b>	
	<i>Herbivory</i>	<b>-0.176 (0.091)</b>	-0.053 (0.038)	
	<i>Habitat × Herb</i>	<b>0.127 (0.065)</b>	-	

(continued)

**Table 1.** (continued)

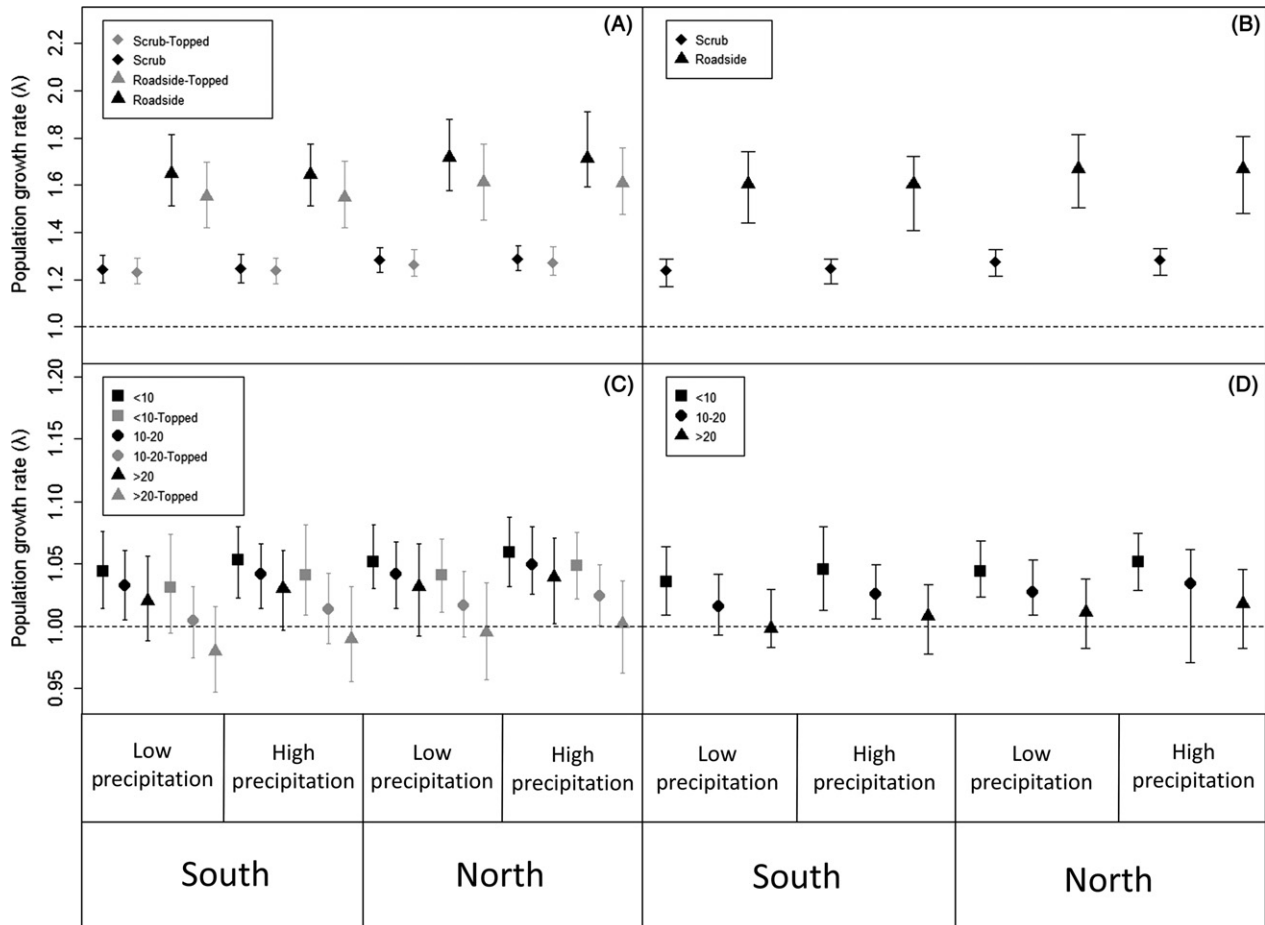
Vital rate	Explanatory variable	Habitat model	TSF model
		Estimate (SE)	Estimate (SE)
Reproductive → dormant ( $R_d$ )	<i>Intercept</i>	<b>-1.927 (0.341)</b>	<b>-1.815 (0.474)</b>
	<i>Length</i>	<b>-0.250 (0.053)</b>	<b>-0.296 (0.060)</b>
	<i>Habitat</i>	<b>-0.380 (0.138)</b>	NA
	<i>TSF</i>	NA	-0.051 (0.104)
	<i>Region</i>	-	<b>-0.291 (0.153)</b>
	<i>Herbivory</i>	<b>-0.274 (0.126)</b>	-0.207 (0.146)
	<i>Precipitation</i>	<b>0.345 (0.126)</b>	<b>0.450 (0.150)</b>
Fecundity ( $\phi_1$ )	<i>Intercept</i>	<b>-5.678 (0.105)</b>	<b>-4.788 (0.123)</b>
	<i>Length</i>	<b>1.534 (0.105)</b>	<b>1.491 (0.023)</b>
	<i>Habitat</i>	<b>0.497 (0.030)</b>	NA
	<i>Herbivory</i>	<b>-0.078 (0.025)</b>	0.089 (0.067)
	<i>Region</i>	0.045 (0.025)	<b>-0.065 (0.032)</b>
	<i>TSF</i>	NA	-0.028 (0.027)
	<i>TSF × Herb</i>	NA	<b>-0.089 (0.043)</b>
Herbivory rate ( $X$ )	<i>Intercept</i>	<b>3.731 (0.389)</b>	<b>4.631 (0.551)</b>
	<i>Length</i>	<b>-2.280 (0.197)</b>	<b>-2.620 (0.270)</b>
	<i>Length</i> <sup>2</sup>	<b>0.239 (0.027)</b>	<b>0.272 (0.036)</b>
	<i>Habitat</i>	<b>0.249 (0.075)</b>	NA
	<i>Herbivory</i>	<b>0.547 (0.065)</b>	<b>0.571 (0.082)</b>
	<i>(Previous Year)</i>	-	-
	<i>Region</i>	<b>0.254 (0.067)</b>	<b>0.323 (0.092)</b>
	<i>Precipitation</i>	<b>0.231 (0.065)</b>	<b>0.201 (0.084)</b>
	<i>TSF</i>	NA	0.039 (0.063)

reproductive heads increased with increasing stem length. In the habitat model, fecundity increased in the roadside and decreased with herbivory. In the TSF model, the number of reproductive heads decreased with latitude.

Herbivory rates were generally high across all environmental conditions (~50%; Fig. S3). Herbivory was higher for previously damaged plants, lowest for intermediate size plants (quadratic relationship) and increased with precipitation (Table 1). Roadside populations consistently experienced higher herbivory rate compared to scrub populations. There was variation in herbivory rate by sector. Herbivory reduced the probability of reproductive individuals remaining reproductive. In the habitat model, there was a significant interaction between habitat and herbivory. Without herbivory, the probability of remaining reproductive was higher in the roadside habitat. The number of leaves increased for individuals affected by herbivory, but this increase was lower at roadside populations. The rate of dormancy from the reproductive stage was significantly lower in the roadside habitat and with herbivory. There was a significant interaction between TSF and herbivory. The effect of herbivory on fecundity decreased with time since fire.

#### POPULATION GROWTH RATES

In the habitat model, population growth rates ( $\lambda$ ) ranged between 1.23 and 1.71 (Fig. 3a). Roadside populations exhibited higher and more variable  $\lambda$  across all sets of environmental conditions. This trend was less pronounced for herbivory scenarios, where differences in  $\lambda$  between road and scrub ranged between 0.31 and 0.35 as compared to 0.40–0.43 in



**Fig. 3.** Population growth rates ( $\lambda$ ) predicted by (a) the habitat model under varying environmental conditions (low or high precipitation), (b) the herbivory megamatrix for habitat, (c) the time-since-fire model under varying environmental conditions and (d) the herbivory megamatrix for time since fire. Error bars represent bootstrapped 95% confidence intervals (200 iterations). Note differing y-axis scales between a–b and c–d panels. Horizontal dashed lines represent  $\lambda = 1$ , where populations are neither increasing nor declining on the long term.

scenarios without herbivory. This is due to a marked decline in  $\lambda$  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  $\lambda$  than southern populations. High precipitation also produced consistent but modest improvements in  $\lambda$ .

In the habitat megamatrix, roadside populations once again outperformed scrub populations across all combinations of region and rainfall, despite higher rates of herbivory (Fig. 3b). These differences were relatively uniform, ranging at  $\lambda = 0.36$ – $0.39$ . 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  $\lambda$  than populations in southern sites. Populations in high rainfall years had marginally higher  $\lambda$  than those in low rainfall years.

In the time-since-fire model,  $\lambda$  varied only a small amount and ranged only between 0.97 and 1.06 (Fig. 3c). In all scenarios,  $\lambda$  decreased with increasing time since fire. The difference in  $\lambda$  between the highest and lowest time-since-fire classes ranged 0.02–0.05. However, herbivory increased the

difference in  $\lambda$  due to time since fire. Northern populations had marginally higher  $\lambda$  than southern populations. High precipitation led to a small but consistent improvement in  $\lambda$  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. 3d). The differences in  $\lambda$  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, Woodward & Midgley 2004). Such disturbances typically occur in concert, rather than in an isolated manner, thus giving rise to potential amplification or dampening in ecological outcomes (Dahlgren & Ehrlén 2009; Mandle, Ticktin & Zuidema 2015). Here, we have quantified the complex synergistic effects of herbivory, fire and anthropogenic disturbance along roadsides on what constitutes a *ménage à trois*

for the population dynamics of the endemic plant *L. 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, namely precipitation, played a secondary but significant role.

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 & Kohfeldt 1995; Abrahamson & Abrahamson 2009). The more stable demography of *L. ohlingerae*, compared with other species in the same ecosystem (Quintana-Ascencio, Menges & Weekley 2003; Menges & Quintana-Ascencio 2004), supports our first hypothesis. The moderate effect of time-since-fire on *L. ohlingerae* population growth rates is reinforced by the occurrence of this species in Florida rosemary patches with different times-since-fire (Miller *et al.* 2012). The relatively smaller effect of fire on *L. ohlingerae*, in comparison with other endemic herbs in the same system (e.g. Quintana-Ascencio, Menges & Weekley 2003), underscores the importance of fully understanding the life-history strategies of a species as well as its interactions with the environment.

Population growth rates of *L. ohlingerae* were less affected by differences among time-since-fire states than between habitats. Increasing time-since-fire had a consistent but moderate negative effect on population growth rates, as hypothesized. The moderate fire effects on *L. ohlingerae* contrast with several other co-occurring, well-documented species of the Florida scrub such as *Hypericum cumulicola*, *Eriogonum longifolium* var. *gnaphalifolium*, *Eryngium cuneifolium* and *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).

*Liatrix ohlingerae* in sandy roads experienced higher population growth than in scrub, probably due to higher survival in both vegetative and reproductive stages, as well as higher fecundity than those in scrub. Shorter-lived scrub endemics of the same region, such as *Hypericum cumulicola* and *Paronychia chartacea* (Quintana-Ascencio, Weekley & Menges 2007; Schafer *et al.* 2010; Oakley 2013), experienced higher fecundity but more variable survival in roadsides. Higher survival rates in *L. ohlingerae* and increasing fecundity in roadsides may result from decreased competition in this human-disturbed habitat (Petru & Menges 2003). Despite 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 short-term benefits

associated with roadsides (Quintana-Ascencio, Weekley & Menges 2007).

The differences in population growth rate  $\lambda$  due 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 have 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).

*Liatrix ohlingerae* in roadsides had higher  $\lambda$  than scrub populations and recently burned populations had higher  $\lambda$  compared to long-unburned scrub under all herbivory conditions. However, the magnitude of the differences between roadside and scrub populations was reduced with herbivory while differences between recently and long-unburned populations were increased with herbivory. Contrasting with Kettenring, Weekley & Menges (2009), individuals in our roadside populations and long-unburned plots generally experienced higher levels of herbivory (Fig. S1). Changes in herbivory with habitat support our hypothesis, which suggests that the negative effects of herbivory serve to either amplify or dampen the positive effects of openness onto  $\lambda$ . Between road and scrub, more frequent herbivory occurred in the more open road populations leading to lower net difference in  $\lambda$  with herbivory. With TSF, more frequent herbivory tended to occur in less open habitats leading to higher net differences in population growth rate.

Our study highlights the advantages of combining environmental interactions with a fine-scale approach to modelling (e.g. Dahlgren & Ehrlén 2011; Mandle, Tickin & Zuidema 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, studies include one or more discrete stages with a single continuous stage rather than multiple continuous stages (e.g. 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 it involved several phases between seed production and establishment for which we had only point estimates. Consequently, our  $\lambda$  estimates should be taken as relative responses more than actual values. 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 assess the effects of 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 as result of herbivory by vertebrates in vegetative or reproductive plants.

Observed differences in the response of *L. ohlingerae* 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, Menges & Weekley 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.

## Acknowledgements

We thank J. Fauth and A. Nevai for comments on earlier versions of this manuscript, as well as the numerous Archbold Biological Station interns and research assistants who contributed to data collection. This work was partially funded by NSF-DEB 1347247 and NSF-DEB 0812753 and grants from the Florida Division of Plant Industry, advised by the Endangered Plant Advisory Council. R.S.G. was supported by DECRA # 140100505 of the Australian Research Council and NERC IRF R/142195-11-1. The demographic methodologies employed in this manuscript were developed with support by the Max Planck Institute for Demographic Research (Rostock, Germany). The authors stated that they have no conflict of interest related to this work.

## Data accessibility

Data supporting this article available at Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.8q57v> (Tye *et al.* 2016).

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Received 4 April 2016; accepted 7 July 2016

Handling Editor: Richard Shefferson

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Summary of the populations of *Liatrix ohlingearae* 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.

**Figure S1.** Vital rates of *Liatrix 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 reproduc-

tive. (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.

**Figure S2.** Vital rates of *Liatrix ohlingearae* are affected by the size of its individuals and time since fire (TSF) (black  $\leq 10$ , dark grey = 10–20, and light grey  $\geq 20$  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)

**Figure S3.** Proportion of reproductive individuals damaged by herbivores in differing environmental conditions (high vs. low precipitation and north vs. south site).