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A comprehensive assessment of *Liatris helleri* demography: Insights from 16 years of observations and modeling

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Abstract

We analyzed demographic data for the endangered Blue Ridge endemic *Liatris helleri* (16 years, 6 sites, 982 plants, and 15,697 annual transitions). We recorded survival, growth, flowering, and recruitment. We evaluated effects of poaching, trampling, browsing, and fire which are potential population drivers for this species. Population size exhibited quasi stable trends, with some population changes attributable to fire or browsing. Survival, growth, and number of heads per plant varied among populations, increased with plant diameter, and were affected by browsing and fire (including overcompensation). Recruits were rarely observed but their numbers increased after fire. We built a projection model including seedlings, second year recruits, adults, and dormant plants. Populations were projected for 50 years. Decadal fires maintained sustainable recruitment rates. Browsing probabilities varied among populations and years; browsing increased the uncertainty of stochastic population growth and boosted extinction probability. Consideration of long-term, spatially replicated data and multiple drivers permitted us to evaluate demographic threats of a relatively long-lived species. Overall, these models suggested that *L. helleri* populations are likely to persist in the near term under current conditions. However, given their population growth rates near one and poor recruitment, any drivers that reduce their survival are threats to this species.

KEYWORDS

augmentation, browsing, fire, management, poaching, population viability

1 | INTRODUCTION

Wild plants with few individuals scattered across fragmented and isolated populations face multiple threats, including habitat loss, stochasticity (genetic, environmental, and demographic), changes in the interactions with other organisms, altered disturbance regimes and reduced metapopulation dynamics (Schemske et al., 1994; Wilcove et al., 1998). Population modeling based on demographic data collected from these populations can provide insights into the endangerment of these species and potential ways to alleviate threats to their

persistence. In particular, understanding the effects of drivers of population change can lead to management solutions to population endangerment.

Most such demographic studies have included few sampling years and populations (Crone et al., 2011; Menges, 2000; Salguero-Gómez et al., 2015). Short-term studies make analyses of long-lived species difficult and limited spatial and temporal sampling constrains the inferences that can be drawn on the effects of drivers on populations. Until recently, most population modeling summarized vital rates from data collected without regard to temporal and spatial environmental variation

(Ehrlén & Morris, 2015). Published studies examined a mean of 1.3 drivers with more than 70% including only one driver (Ehrlén et al., 2016). However, there has been a trend toward modeling population viability by incorporating multiple drivers of resultant demography. Drivers can also interact with each other in their effects on vital rates and population dynamics (e.g., Doak & Morris, 2010; Eckhart et al., 2011; Tye et al., 2016). Data on environmental drivers are often easier to access (e.g., weather data) or collect (e.g., disturbance history) than demographic data. However, linking environmental drivers to population dynamics may still be challenging given the number of drivers, the complexity of population responses, and the effort required collecting intensive demographic data across a range of environments (Quintana-Ascencio et al., 2021).

The viability of populations in highly visited, publicly accessible areas is increasingly threatened by trampling, poaching, and changes in species interactions and disturbance regimes. Public awareness, population augmentations, and prescribed fires are some management actions that can alleviate some of risks associated with the increasing use of these areas. Many potential drivers could affect population dynamics. Relatively well-studied drivers include fire (e.g., Menges et al., 2006; Quintana-Ascencio et al., 2018) and herbivory (e.g., Maron & Crone, 2006). Less work has been done on drivers such as harvesting/poaching (e.g., Gaoue & Ticktin, 2010), trampling (Maschinski et al., 1997), and augmentation (Halsey et al., 2017). One advantage of relating demography to drivers is that projections of population dynamics with changes in environmental driver regimes are possible. Examples include the effects of changing climate (Backus et al., 2023; Gotelli & Ellison, 2006) and altered disturbance regimes (Quintana-Ascencio et al., 2021).

In this paper, we evaluate the effects of multiple drivers affecting viability and population dynamics of *Liatris helleri*. This species is a perennial plant endemic to the Blue Ridge Mountains of the southern Appalachians, USA, restricted to five counties in North Carolina (extirpated in one county). It has only 11 known populations, eight of which are protected (United States Fish and Wildlife Service, 2013) and is considered a threatened species by the USFWS. *L. helleri* is pollinated by a variety of bees, butterflies, and moths and its seeds are dispersed by wind (Clark, 2019). Population trends are poorly known (United States Fish and Wildlife Service, 2013). The species occurs only at mid- to high-elevations (1000–2000 m. asl) and grows on rocky outcrops, cliffs, or ledges in full sun (United States Fish and Wildlife Service, 2013). The Blue Ridge Mountains are a biodiversity hotspot for plants and other organisms. High elevation cliffs and outcrops in the southern Appalachian Mountains support dozens of rare plant species, many of

which have related species found above tree line in the northern Appalachians (Wiser, 1994). One example of a high-elevation endemic is *Geum radiatum*, which is threatened by climate change (Ulrey et al., 2016).

Of concern is the potential decline of *L. helleri* due to recreational use of its habitat, herbivory, poaching, and shrub encroachment (United States Fish and Wildlife Service, 2013). Current active management is primarily limited to educating the public in an attempt to reduce trampling at these sites. Poaching has not been often documented, although two subpopulations were poached with 10%–60% of adult plants removed (United States Fish and Wildlife Service, 2013). Herbivores such as rabbits and deer can reduce plant biomass, survival, recruitment, and population size of many plant species (Edenius & Ericsson, 2015; Maron & Crone, 2006) but has not been thoroughly studied for *L. helleri*. Prescribed fires have been used at some *L. helleri* sites to reduce the dominance of encroaching shrubs with some success, including increased flowering of *L. helleri* (North Carolina Natural Heritage Program, 2010; Ulrey, unpublished data). Climate change may also have deleterious effects on *L. helleri*, especially if it leads to warmer and wetter conditions in extant populations.

Augmentation of existing *L. helleri* populations has occurred on multiple sites and multiple occasions. However, the success of most of these augmentations has not been consistently monitored (United States Fish and Wildlife Service, 2013). One well-documented augmentation had low survival (28% after 2 years; United States Fish and Wildlife Service, 2013), likely due to dry, hot conditions at the time of transplanting. Earlier allozyme studies by Godt and Hamrick (1995; 1996) found high levels of genetic diversity in this species compared with most endemic plants. Gene flow was low, which was expected based on the scattered pattern of its rock outcrop sites.

In this paper, we analyze 16 years of *L. helleri* demographic data (2003–2019). We summarize data from individually marked and mapped aboveground individuals in six sites. We examine the potential roles of fire, poaching, herbivory, and augmentation on population dynamics, and project trajectories for these populations into the near future. We aim to identify the risks of population decline with known drivers and elucidate more effective management practices.

2 | METHODS

2.1 | Study sites and field sampling

We analyzed the demography of *L. helleri* at six sites (numbered A–F to minimize poaching) in the

Grandfather Mountain area in the Blue Ridge Mountains in North Carolina, USA. Study sites were associated with flat or sloping rock outcrops at high elevations. The study sites were in a matrix of shrubby Ericaceous vegetation and forest. Management at these sites has included the construction of boardwalks and fencing to limit human encroachment and trampling, prescribed fire, and augmentation. At least one site was affected by poaching of *L. helleri* plants.

We censused, within areas with naturally demarcated boundaries, all newly found and previously monitored live plants annually in late July or early August, from 2003 through 2019. Plants in each of these populations were mapped using combinations of surveying with laser rangefinder and field measurements of distances and directions among plants. Plants were marked with a metal nail and with a numbered tag. Smaller plants were marked with color coded pins. We also visited some populations earlier in the growing season in April to search for any seedlings within the study area. Seedlings were identified as such by the presence of cotyledons. Seedlings and second year recruits were rarely observed directly. We collected data on survival status (survived, died, plant not found, new adult, and new seedling), plant diameter, number of rosettes, width of the widest leaf and (for reproductive plants) number of reproductive stems, height of reproductive stems, and the number of flowering heads in a single stem chosen haphazardly. Reproductive measurements were scaled up to the plant level for analyses by multiplying number of stems by the average number of heads per stem.

For each plant, we also categorized whether it suffered mammalian herbivory or had been trampled in each year. We also noted whether individual plants were poached, planted as an augmentation, or growing in sites prescribed-burned. We assessed browsing by mammals, mostly rabbits and deer, during each sample period. Removal of flowering stems was common and obvious from the clean breaks from mammal bites. We also documented trampling damage to living plants (often breakage of flowering stems). Populations B and C were augmented with plants in 2007. A total of 85 plants were added and monitored in a similar manner to wild plants. In 2009, we observed poaching of 11 plants at population as evident from holes dug in the soil. Prescribed burns were accomplished by NPS staff at populations A and C in 2005 and in populations A, B, and C in 2007. Fires were completed using a propane torch.

2.2 | Analysis and modeling building

We built an integral projection model (IPM) to evaluate *L. helleri* viability in the six studied populations and its

population dynamics in response to fire, augmentation, poaching, browsing, and the random effect of year variation. This model comprised submodels estimating vital rate variation as a function of the different drivers. We recognized five life history stages (seedling, second year recruit, adult, and two dormant plant stages). We modeled vital rate variation of adult plants (>2 years old) using generalized linear mixed models (GLMMs) with the natural logarithm of individual plant diameter as the continuous state variable. Variation of among years was included as a random effect on the intercept of all these models ($\alpha_{s(y_i)}$). We used binomial error distributions for survival (σ) and probability of reproduction (φ_0), and normal distributions for changes in size of adults (γ) and counts of reproductive structures (φ_1). We chose a lognormal distribution instead of Poisson or negative binomial for the number of reproductive structures because this likelihood is more consistent with data summarizing plant reproductive output (Quintana-Ascencio et al., 2022). The effects of browsing on diameter change were confounded with population effects probably because the uneven rates of herbivory among locations; thus, population and herbivory effects on plant growth were analyzed independently. We did not attempt to evaluate density dependence in our models since we did not have any prior evidence of its potential effects on *L. helleri* demography; recruitment was scarce and intraspecific densities were quite low. Fire did not occur in all populations and was also analyzed independently for burned populations. We tested for evidence of overcompensation in plants burned and browsed.

The Bayesian hierarchical models describing survival (σ), growth (γ), probability of flowering (φ_0), and fecundity (φ_1) of adults were defined in general as follows:

$$G(\mu_{j(ky_i)}) = \alpha_0 + \alpha_{s(y_i)} + \alpha_1 \times \text{size}_j + \alpha_2 [\text{site}_i] + \sum_k^n (\beta_{kj} \times \text{driver}_{kj}) + \sum_k^n (\beta_{km} \times \text{driver}_{k1j} \times \text{driver}_{k2j}) + \varepsilon, \quad (1)$$

where α and β are linear coefficients for data at individual (j) and population (i) levels and for each driver (k) and their interactions ($m = \text{different } k_s$). The terms (β_{k_m} and β_{k_v}) include additive and interactive effects among drivers. The error term (ε) was explicitly included only in models with normal distributions. We used model selection based on Watanabe Akaike Information Criterion (WAIC; Watanabe, 2013) to identify the most plausible combination of these drivers and their interactions in explaining variation of each vital rate of aboveground individuals (survival, growth, probability of reproduction,

and fecundity). We preserved in the combined Integral projection model (IPM) the particular variable structure (e.g., the set of variables and interactions) for the most likely submodel of each vital rates allowing any terms with clear effects on the vital rates to influence the projection outcomes of the merged model.

We modeled seedlings and second year recruits independently. We assumed that seedlings and recruits lasted as such only 1 year each and did not reproduce. We also assumed that seeds had no persistent seed bank based on experiments indicating strong germination during the first year and low viability of older seeds (Chris Ulrey, unpublished data). We allocated annual seed production to seedlings corrected by estimates of survival of seedlings and first year recruits as described below. Seedlings and recruits were difficult to find in the field and their numbers were probably underestimated. Therefore, we used observed survival from seedlings to recruits and from recruits to adults, and the number of recruits and small adult plants to estimate “corrected” seedling and recruit abundances. We evaluated the variation of seedling (S) abundance as function of survival of the total available seeds the previous year (α_3), time-since-fire (fire-year, year after fire and no burn year) and population. To obtain the total of number of seeds per population and year we used estimates of fecundity and multiplied the estimated number of heads by the average number of seeds per head ($\bar{X} = 2.72$ seeds, $n = 60$ heads).

$$S(\mu_t) = \alpha_{r0} + \alpha_1[\text{TSF}_i] + \alpha_2[\text{site}_i] + \alpha_3 \times \text{Total number of seed}_{t-1}. \quad (2)$$

To build the kernels of Integral Projection Models, we used Bayesian posteriors of fixed and random effects of plausible models assessing the responses of the different vital rates to the studied drivers (Easterling et al., 2000; Ellner et al., 2016; Ellner & Rees, 2006). The mid-point rule approximation to the continuous form of these IPMs (from Ellner et al., 2016) was a Goodman matrix (Goodman, 1969) model (with 84×84 cells) describing the population dynamics of five stages, four discrete stages (seedlings, second year recruits, short-term and long-term dormant plants) and one continuous stage based on variation in plant diameter (adults). The responses of coupled equations were integrated over $L = 0$ and $U = 4.38$ (logarithm values of 80 bins [1–80 cm in diameter]) using the mid-point approximation into $m = 80$ size classes of width $h = (U - L)/m$. The discrete form of the IPM is described as:

$$n(z_{jk}, t+1) = h \sum_{i=1}^m K(z_{jk}, z_{ik}) n(z_{ik}t), \quad (3)$$

where $n(z_{jk}, t+1)$ is the number of individuals in size class j and stage k at time $t+1$ from individuals in size class i and stage k at time t given the matrix kernel (K) and number of individuals at time t $n(z_{ik}t)$. We defined two continuous kernel functions for adults, one including survival and growth ($P_{j,i}$) and another for recruitment ($F_{j,i}$ for seedling recruitment [$\text{Seedlings}_{(j)}$]).

$$K_{z(j,i)} = P_{(j,i)} + F_{(j,i)}, \quad (4)$$

$$P_{(j,i)} = \sigma_{(i)} \times \gamma_{(j,i)}, \quad (5)$$

$$F_{(j,i)} = \text{Seedlings}_{(j)}, \quad (6)$$

where j is the index for the vector of size classes n at $t+1$, and i the index for size classes at time t . Seedling recruitment was estimated by probability of reproduction (ϕ) per plant size class (x), probability of heads >0 (ϕ_1), number of heads per plant (ϕ_2), number of seeds per head (s), and probability of annual survival of those that germinated (g),

$$\text{Seedling}(y, t+1) = \int_L^U \phi_0(x) \phi_1(x) \phi_2(x) g s \delta x. \quad (7)$$

We used ad-hoc distributions to allocate “newly appearing” plants in their IPM vectors (new adults and plants out of dormancy). Sizes of new adults were assigned using a gamma distribution of plant diameter obtained from the mean and variance of the observed size distribution of newly appearing plants (≤ 10 cm diameter). We assigned sizes of plants recovering from dormancy using a lognormal distribution of plant diameter, obtained with the mean and variance of observed previously dormant plants.

We used the eigen-structure of our models to quantify the stochastic population growth rate (λ) for each population. We calculated 400 posteriors for each modeled scenario bracketing observed variation of mean lambda per site. We used matrix projection to obtain predictions of extinction probability with no fires and with fires every 10 years. We started each simulation using the Stable Stage Distribution of each population. These values were commensurate to observed initial densities (20–70 adult plants).

Demographic drivers do not occur in isolation and the number of possible combinations of those in this

study is quite large. We decided to evaluate a sample of reasonable scenarios with management implications. In addition, the nature of these drivers is different. For example, while observed rates are reasonable baselines for herbivory levels, no poaching and no augmenting are acceptable baselines for treatments involving anthropogenic changes in numbers of plants. We simulate four reasonable combinations of scenarios: (1) variable browsing with no fire, (2) variable browsing and fire every 10 years, (3) observed browsing and different levels of poaching, and (4) observed browsing and different levels of augmentation.

We projected populations with observed browsing and reduced and increased browsing ($\times 0.6$, $\times 0.8$, $\times 1.0$, $\times 1.2$ and $\times 1.4$ observed probability of browsing, using Table S21). The base condition represents the observed proportion of plants browsed and nonbrowsed, by population. We used a mega-matrix approach (Pascarella & Horvitz, 1998) and defined a matrix of transition between submatrices of browsing and no browsing using models predicting probabilities for plants becoming browsed. All surviving browsed plants transitioned to a year post-browsing phase and then went to the nonbrowsing stage (Figure 1).

We projected the same model structure of the base simulation but adding the effects of prescribed fire every 10 years with two states, represented with matrices for the year of fire and the year after fire. During the fire year we assumed that all individuals were burned.

We also projected the potential effect of the change in number of individuals either by poaching or

augmentation. For augmentation or poaching, we increased or decreased the number of individuals in the vector in each simulated year by factors of 0.6, 0.8 (for poaching), 1.0 (observed), and 1.2 and 1.4 (for augmented). During the simulation for each scenario, we multiplied the chosen factor by the number of individuals between 17 and 42 cm in diameter (the size of those that probably will be poached or augmented in reality) in the corresponding population vector. This method assumed optimistically (but see above) that augmented individuals behave similarly compared to those naturally recruited in the field. We calculated the expected probability of extinction after 50 years for each of these scenarios.

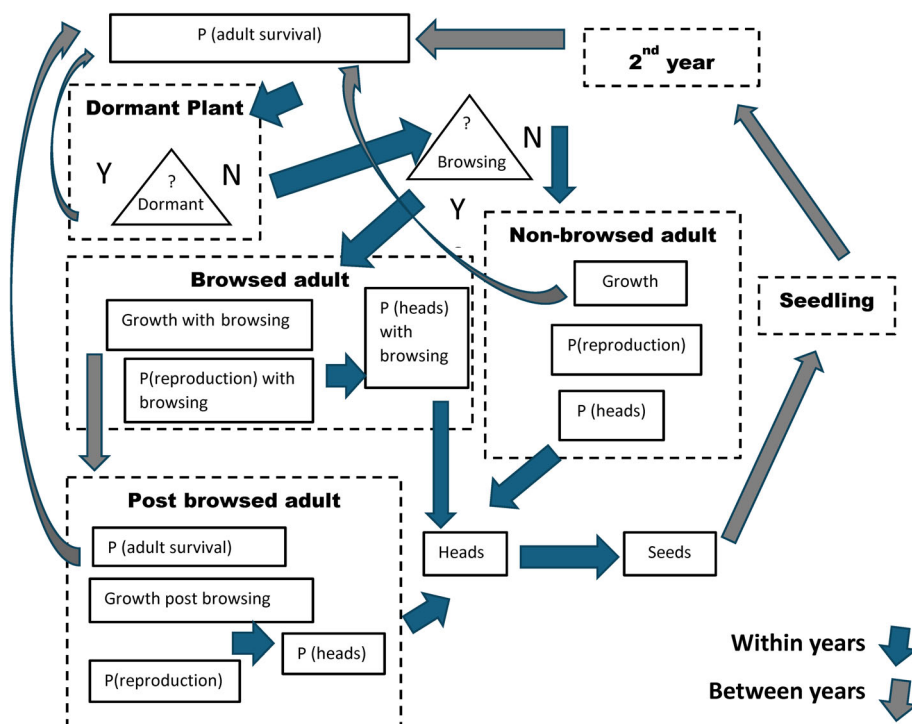
3 | RESULTS

3.1 | Observed population trends with browsing, trampling, burning, poaching and augmentation

Between 2003 and 2019, 982 individuals were censused with 15,697 cases recorded (Figure S1). Populations exhibited stable, variable, or decreasing trends during the 16 years of the study (Figure 2). Some population increases and decreases were associated with browsing, fire, poaching, and augmentation (Figure 2).

Browsing was occasionally observed on *L. helleri*, about 5% overall (Table S1). Browsing varied among populations, being highest at population E (9.7%–18.5% among years) and lowest at population A (0.9%). Year-

FIGURE 1 Diagram illustrating the mega-matrix algorithm for the base scenario including submatrices for plants with no browsing, browsing, and postbrowsing. ? = alternative direction for the state indicated in the triangle; options = Y (yes) or N (no). Plants can be browsed or not browsed and dormant or not dormant. P, probability.



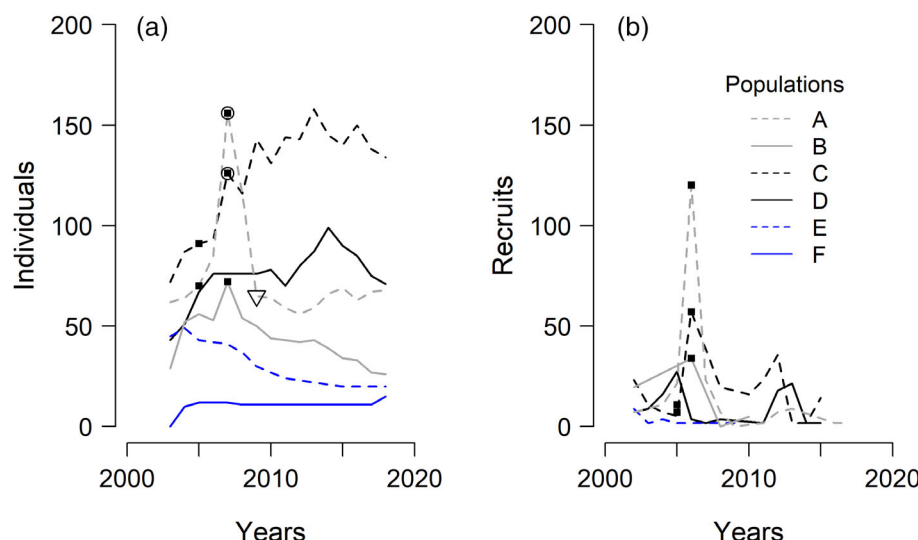


FIGURE 2 Number of observed (a) living adult and (b) new plants (first- and second-year recruits) by year and population. Shown are treated populations and years when prescribed burns (squares), augmentations (rings), or poaching (triangles) occurred. All burns happened in the previous winter or early spring (January–April) of the year shown.

to-year variation was noticeable, with high browsing rates seen in 2004 and 2017 (Table S1). Survival after browsing was high; over 90% of browsed plants survived in each population (Table S2). Browsing generally reduced plant diameter, the probability of reproduction, and the number of heads per plant, but these effects were highly variable among populations (Figure S2) and years. There was evidence that browsing triggered overcompensation in some plants (Figure S3); we observed higher growth among plants that were browsed in the previous year (postbrowsed) compared to nonaffected plants (references), all censused in the same years.

Trampled individuals were noted rarely (79 trampled/9849 untrampled plants, fewer than 1% of observations; Table S1). Trampling was most pronounced at population C (58 plants) and never was observed at population E. Trampling was most common in 2017 and 2019. Trampling across the study was more than five times higher in areas with higher rock cover (12/53 plants compared to 6/171 plants in areas with less rock cover) and twice as high in areas more exposed (6/50 compared to those with 12/174 in more shrub cover; Table S3). Because trampling has the potential to remove both plants and tags, plants lost from the dataset may have also been trampled.

A prescribed burn affected *L. helleri* populations in 2005. The burn occurred in population A and affected 32 plants (40% of the plants at this site). In 2007, prescribed burns were accomplished at three sites (A, B, and C; overall 35% of plants burned; Table S4).

Between 2008 and 2009 in population A, 11 individuals (12% of 95 total plants in the site) were poached. The size of these plants ranged between 17 and 42 cm in diameter ($\bar{x}$ = 28.5 cm).

In 2007, 85 plants were augmented to existing populations, 24 individuals to population C, 19 to population B,

and 42 to population A. Their average diameter at the time of transplant was 24 cm.

3.2 | Vital rate functions of adult plants

The most likely model for survival of adult plants among the set proposed included the effect of $\ln$ (plant diameter), population, browsing and the interaction between diameter and browsing (Tables 1 and S5A). Probabilities of survival were 0.3–0.6 for small plants and increased with plant diameter, reaching more than 0.90 for plants >20 cm diameter (Figure 3). Survival was higher at populations C, D, and F and lower in populations A, B, and E. Browsing in general decreased survival (Figure 3). Burning did not have a clear effect on survival in population C but decreased survival in populations A and B (Tables 1 and S5B). Although survival of introduced plants (0.45) was lower than for naturally established plants (0.79) during year of augmentation (2007), we used the survival of naturally established plants for all plants in the simulations as an optimistic and more computationally tractable scenario.

The most likely model of growth (data logarithmically transformed) in plant diameter included previous plant diameter, as a quadratic function, and population (Tables 1 and S6). Growth was positive and faster for plants <15 cm than for larger plants (Figure 4). Growth was higher in population F, and lower in C and D (Table 1 and Figure 4). We found evidence of growth overcompensation after fire and browsing (Table S7 and Figure S4). These plants had higher growth than nonaffected reference plants censused in the same year. We did not find evidence of clear differences in annual growth in diameter between introduced plants (augmented) and

TABLE 1 Summary table of a generalized mixed linear model of P(survival), Growth, change in diameter, and P(reproduction) as a function of plant diameter (logarithmically transformed), population, and browsing.

Fixed effect Intercept: Population 1	P(survival)		Growth		P(reproduction)	
	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	0.23	0.27	1.14	0.01	−7.00	0.25
ln(diameter)	1.31	0.08	−0.01	0.004	1.99	0.08
ln(diameter) ²	−	−	0.20	0.001	−	−
Population A	−1.28	0.19	0.02	0.01	0.54	0.10
Population B	−1.06	0.22	0.01	0.01	−0.49	0.13
Population C	−0.15	0.19	0.03	0.006	0.34	0.09
Population E	−1.19	0.26	−0.02	0.01	−0.41	0.14
Population F	0.20	0.73	−0.06	0.01	1.92	0.23
Browsing	0.74	0.42	−	−	1.66	0.12
ln(diameter)*browsing	−0.44	0.18	−	−	−	−

Note: Population D was used as a reference. Random effects for survival by year had a standard deviation of 0.68 and were based on 5335 observations. Random effects for change of size by year had a standard deviation of 0.03 which is low compared to the residual standard deviation = 0.15 and were based on 4839 observations. Random effects for P(reproduction) by year had a standard deviation of 0.23 and were based on 5859 observations.

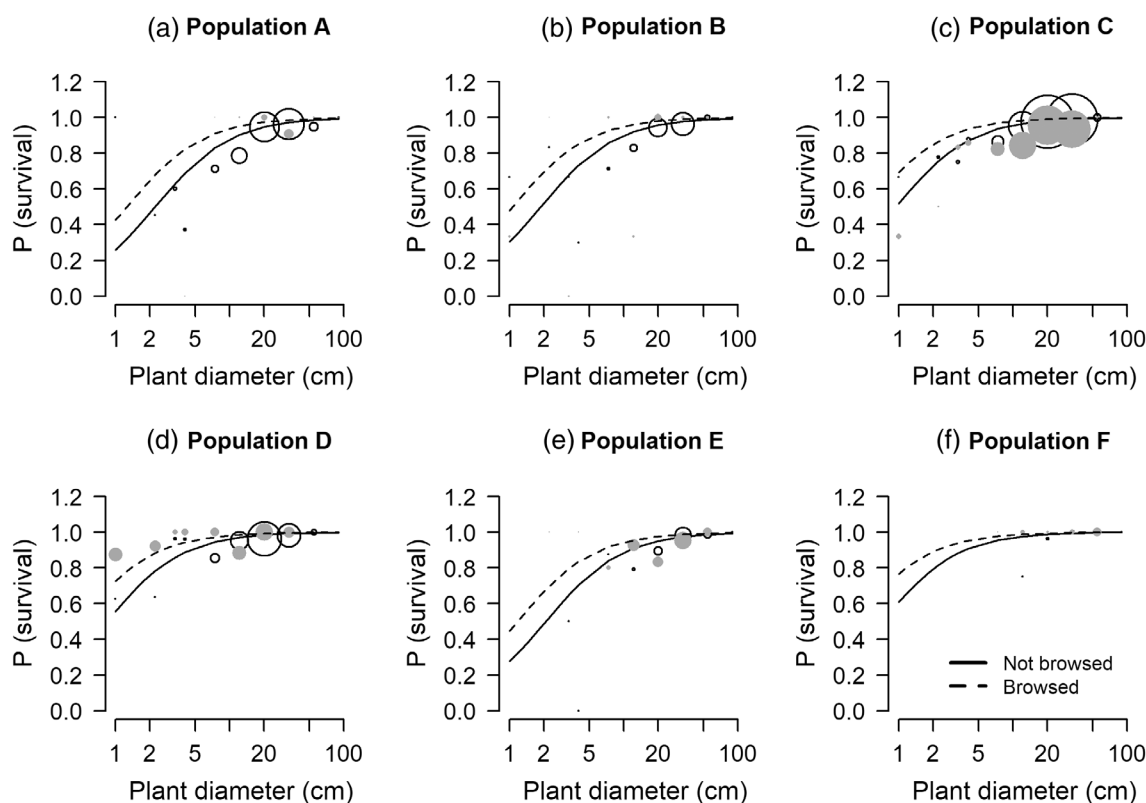


FIGURE 3 GLMM models for survival of adult *Liatris helleri* plants as a function of ln (plant diameter (t)) and browsing per population (A–F). Symbols indicate the relative number of observed plants surviving binned evenly by plant diameter. The size of the circle represents the relative number of plants per bin (number $\times$ 0.011 for not browsed, and number $\times$ 0.1 for browsed plants to fit in the plot). Open circles are for nonbrowsed plants and gray circles are for browsed plants. (a)–(f) Population A–F.

naturally established plants (Figure S5; difference between these groups evaluated only during the introduction year).

Probability of reproduction was most likely predicted by ln (plant diameter), browsing and population (Figure 5, and Tables 1 and S8). Probability of

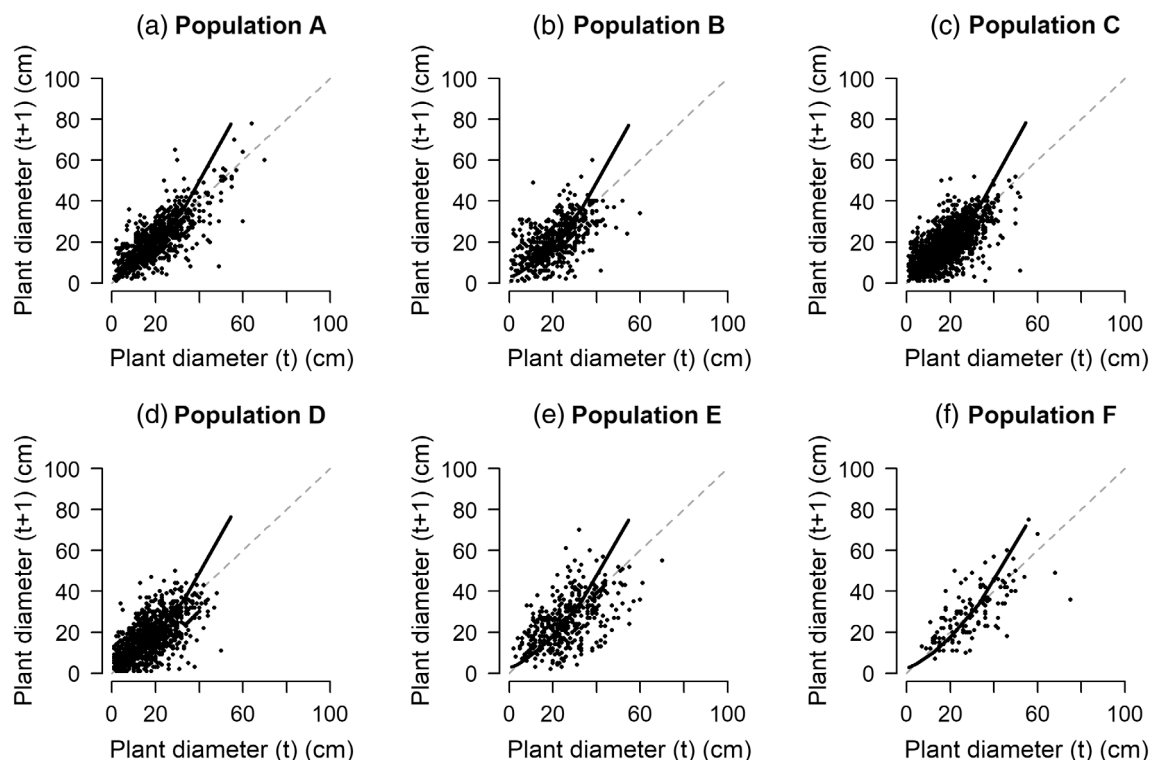


FIGURE 4 GLMM models for change in plant diameter of adult *Liatris helleri* plants as a function of $\ln(\text{plant diameter}(t))$ and population (A–F). Dots indicate data for observed plants and the discontinuous line no change. The dark line is the average model and the broken line represents no change in diameter, and it is used as reference. (a)–(f) Population A–F.

reproduction increased with height to reach 0.6–0.9 among the largest plants. Predicted probability of reproduction was greater among previously browsed plants but parameter uncertainty was much higher in the model for these plants. Plants at population F had higher probabilities of flowering than in any of the other populations (Figure 5 and Table 1).

Among plants with flowering stems, some did not produce flowering heads (4%), mostly plants <20 cm (Table S9). The probability of having heads was higher among nonbrowsed plants (Table S10). The number of flowering heads per plant increased with plant diameter and varied among populations (Figure 6 and Tables S11 and S12). A sample of 60 heads collected from plants at population A during 2005 yielded a mean of 10.4 (7–23) total seeds and 2.72 (0–11; mean 26%) viable seeds per head (Table S13).

3.3 | Seedlings and recruits

We observed a total of 15 seedlings and 55 second-year recruits during summer censuses. Additional information on 58 seedlings was collected in April 2005. Using seedlings' and recruits' survival and the amount of observed putative new plants (new censused plants with ≤ 10 cm

diameter and no flowering stems; 60% of the total new plants after 2003) in the census, we calculated an estimate of the numbers of seedlings and recruits per population and year (Figure S6). We calculated an average of 0.56 annual survivals for recruits and 0.26 for seedlings (Table S14). When dividing the number of “new plants” by the survival estimate of seedlings and recruits, we could estimate the number of seedlings that germinated 2 years ago. For example: there were nine “new plants” in 2005 in population D, then $9/0.56 = 16$ estimated recruits in 2004, and $16/0.26 = 62$ estimated seedlings in 2003. If there were recruits or seedlings observed in a year, they were added to the estimated seedlings and recruits (Table S15). Increases in seedling numbers were most likely predicted by the positive effect of postfire conditions (Figure S7, and Tables S16 and S17).

3.4 | Dormant plants

Approximately 2% of the plants in any year become dormant (Table S18). Of those dormant, 71% left dormancy after a year and a similar proportion left dormancy from the second to the third year ($13/28 = 68\%$). The probability of becoming dormant was higher for smaller plants (Figure S8 and Tables S19 and S20). Long-term dormant

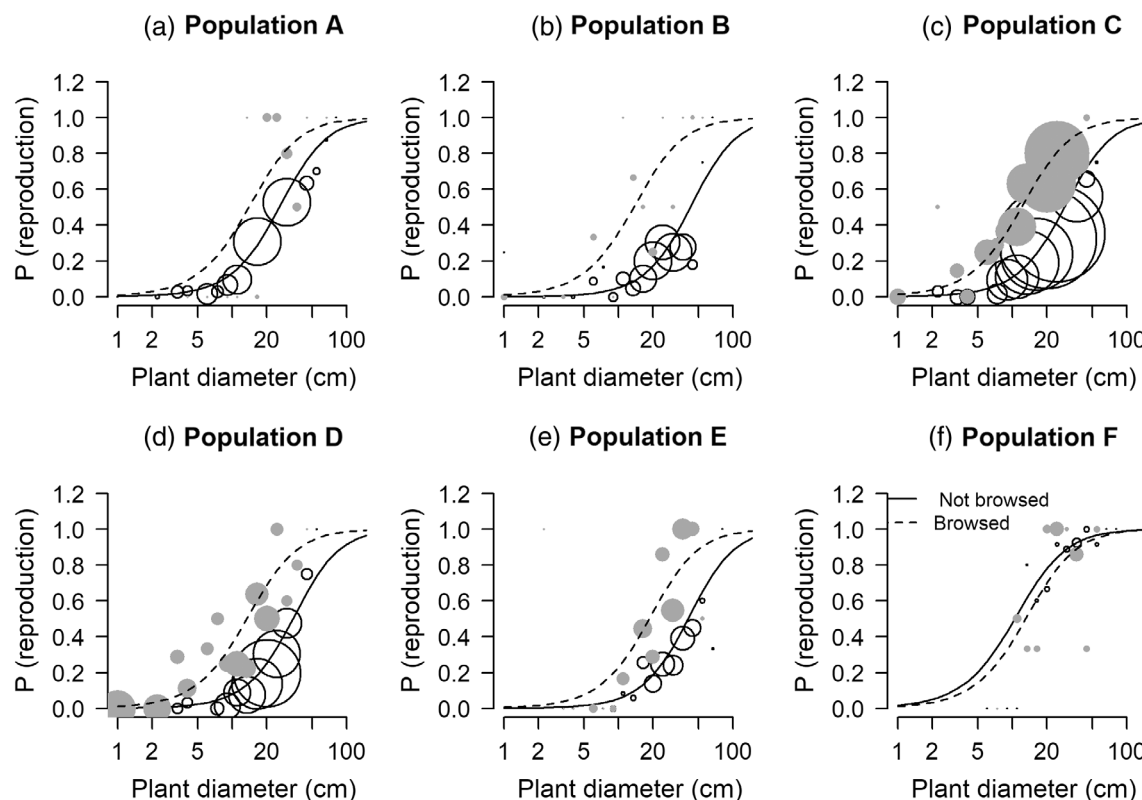


FIGURE 5 GLMM models for probability of reproduction of adult *Liatris helleri* plants as a function of $\ln(\text{plant diameter } (t))$, browsing, and population (A–F). Symbols indicate the relative number of observed reproductive plants binned evenly by plant diameter. The size of the circle represents the relative number of plants per bin (number $\times 0.04$ for not browsed, and $\times 0.25$ for browsed plants to fit in plot). Open circles are for nonbrowsed plants and gray circles are for browsed plants. (a)–(f) Population A–F.

plants becoming active were smaller ($\ln(\text{plant diameter}) = 2.54$, $\text{SE} = 0.56$) than first year dormant becoming active (2.61 , $\text{SE} = 0.68$) and these were smaller than non-dormant plants after the same interval (2.85 , $\text{SE} = 0.65$) (Figure S8).

3.5 | Projecting population growth and extinction

The IPM representing the annual life cycle of *L. helleri* included five stages (Figure 7). Seedlings (1) grew into second-year recruits (2) which in turn reached the adult stage (4). Adults could become dormant plants (3), which could return as adults (4), or could remain dormant (7), these long-term dormant plants could remain dormant (6) or return as adults (5). Nondormant surviving adults transitioned to the next year (8) and produced seeds that became seedlings (9) in the next census after seed production. In this life cycle, seeds were implicit in the fecundity transition (9).

Predicted average stochastic lambdas for the base model per population without fire and with observed browsing indicated slow growing or relative stable

populations ($\lambda_s = 0.99$ – 1.07 except $\lambda_s = 1.26$ at population F; Figure S9), consistent with observed population trajectories (Figure 2). Only population B had predicted average stochastic lambda lower than one (0.99) indicating a possible slow decline. Predicted stochastic lambdas of models with simulated reduced browsing were higher ($\lambda_s = 1.0$ – 1.3) than with models with observed browsing and indicated potentially growing populations (Figure S9).

Using simulations starting with a predicted stable stage distribution per population (Figure S10) and densities consistent with initial observed data, models with no fire and observed browsing projected low extinction (0.10) after 50 years for populations A, C, D, and F, but extinction proportions close to 0.81 for B and 0.74 for E (Figure 8). In general, increased rates of browsing increased extinction probability while decreased rates reduced it (Figure 8). Scenarios with increasing browsing increased extinction probabilities or kept similar extinction probabilities after 50 years (B: 0.82 and E: 0.79) (Figure 8). Decreasing browsing reduced extinction probabilities in population B (0.60) and E (0.40). Browsing combined with fire either did not change the chances of extinction compared to absence of fire in populations with low effects of

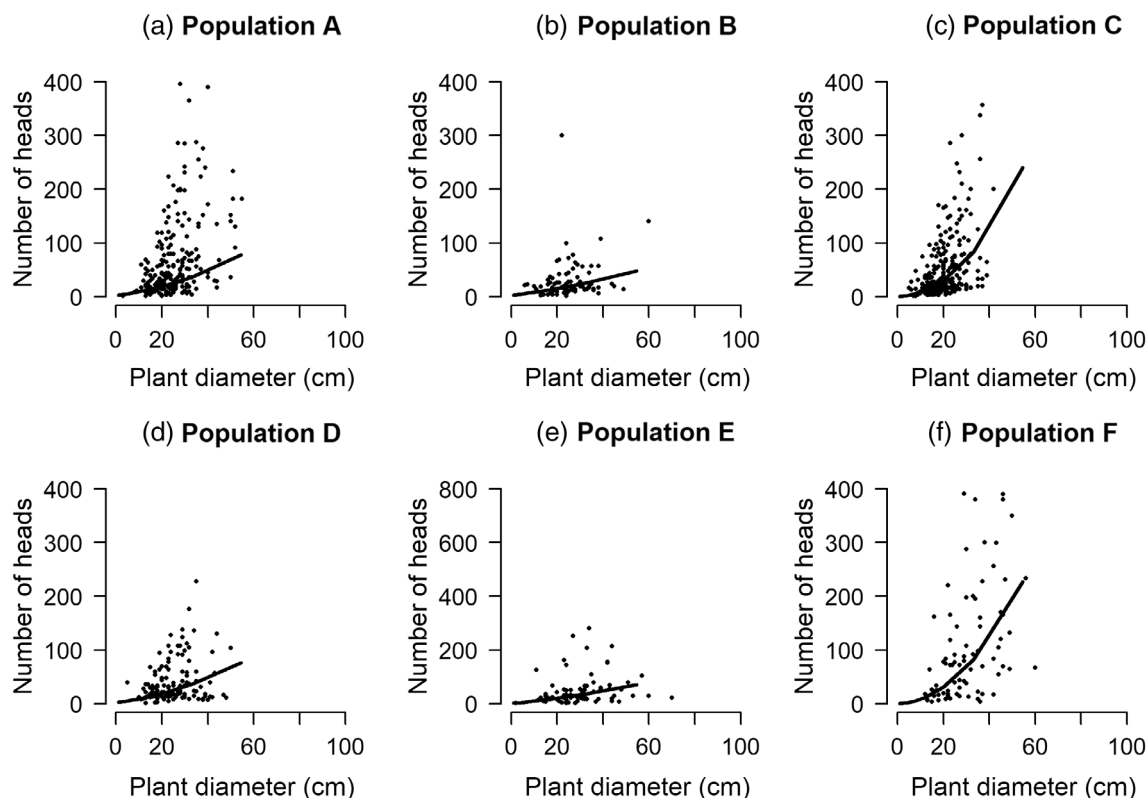


FIGURE 6 GLMM models for number of heads by adult *Liatris helleri* plants as a function of $\ln(\text{plant diameter}(t))$ and population (A–F). Dots indicate data for observed plants. (a)–(f) Population A–F.

browsing or showed a complex interaction of the effect of browsing with a net increase of extinction probability. Projections with simulated poaching and augmentation generated minimal changes of extinction risk after 50 years for all populations (Figure 8).

Examples of simulated trajectories are provided in Figures S11–S13.

4 | DISCUSSION

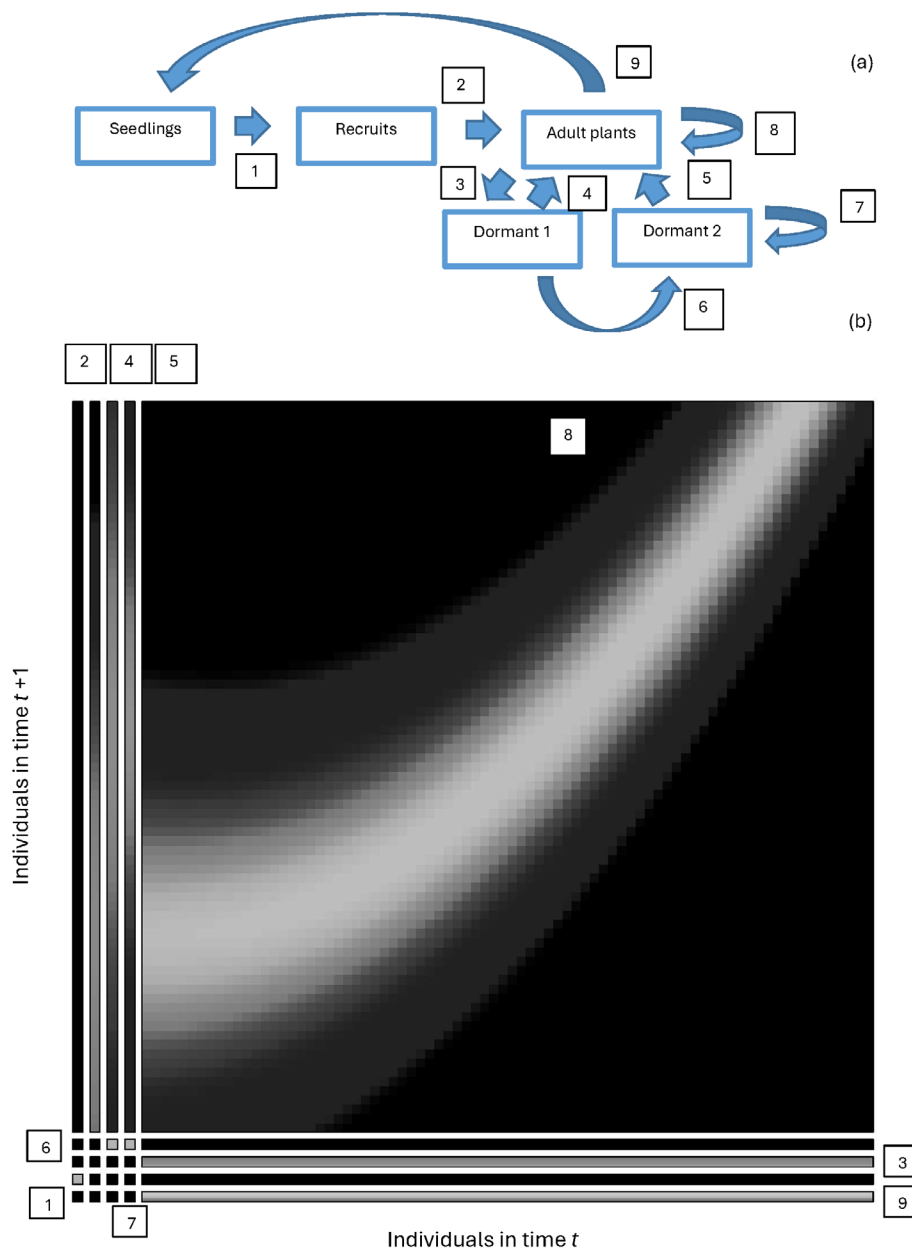
Our ability to identify management opportunities to address current environmental threats depends, among other matters, on a clear understanding of the response of population dynamics of the focal organisms to environmental drivers of demography (Crone et al., 2013; Ehrlén & Morris, 2015; Quintana-Ascencio et al., 2021). Although circumstances determining population viability and dynamics are mostly species and location specific, demographic studies convey valuable general lessons for management and conservation. Our study on *L. helleri* demography confirmed the widespread importance of disturbances and species interactions for the persistence of populations. We also verified the perverse effect of some anthropogenic actions and their combined effects

with other drivers. Here, we take advantage of long-term data (16 years), including many individuals (nearly 1000 plants and 16,000 cases) and consistent records of the responses of their vital rates to major drivers. We used demographic data on *L. helleri* to assess the potential future impact of various drivers on its population viability. We built models predicting each vital rate (survival, growth, probability of flowering, number of flowering heads, seedling recruitment) as a function of population variation, plant size, fire, and browsing. Vital rate models were then combined into integral projection models (with plant diameter as the size variable and with five stages: seedling, second-year recruit, adult, first year dormant, and later year dormant) to project population dynamics for 50 years for each population, to predict chances of extinction and of recruitment of new individuals.

Overall, these models indicated that *L. helleri* populations are likely to persist in the near term under current conditions. For simulations without fire, most values of stochastic lambda were close to one, indicating populations were generally stable. It appears that fire results in a generational replacement. Although survival, growth, and reproduction were reduced immediately after fire, growth and reproduction were overcompensated the

FIGURE 7 Example of Integral projection model matrix for *Liatris helleri*. (a) Life history diagram.

Seedlings (1) grew into second-year recruits (2) which in turn reached the adult stage (4). Adults could become dormant plants (3), which could return as adults (4), or could remain dormant (7), these long-term dormant plants could remain dormant (6) or return as adults (5). Nondormant surviving adults transited to the next year (8) and produced seeds that became seedlings (9) in the next census after seed production. In this life cycle, seeds were implicit in the fecundity transition (9). (b) Projection matrix decomposed by the main transitions indicated in the diagram. Some numbered transitions also relate to distributions in Figure S8. Every IPM consisted of a rectangular matrix for adults (of 80×80 cells), five vectors, one for the transition of recruits to adults, two for the transitions of dormant plants to adults, one vector for recently produced seedlings (80×1 cells each), and another vector for adults transiting to dormancy, and three scalars describing seedling survival and short and long-term plant dormancy. It also included three vectors with structural zeroes and 13 zero scalars for impossible transitions.



following year. Crucially, fire had large, positive effects on recruitment. Simulations with occasional fire (every 10 years) projected similar population growth and similar extinction probabilities than unburned simulations. This is concordant with the overall stability observed in population sizes during the 16 years of this study. Although fire regimes often have dramatic effects on populations of plants that are killed by fire (Backus et al., 2023), resprouting plants like *L. helleri* often have similar demographic responses to fire versus no fire (Menges et al., 2020).

Herbivory, although currently relatively low, increased uncertainty in population growth and chances of extinction and should be closely monitored in the future. We speculate that browsing by rabbits may

increase with increased shrub cover by providing protection from aerial predators. However, browsing may also be a function of limited resources so that in years of limited browse material, rabbits may seek out *L. helleri* more than in years of abundant food. Herbivory often has strong effects on the demography of browsed plant species (e.g., Tye et al., 2016).

Augmentation (adding plants) and poaching (removing plants) should have direct effects on populations by increasing or decreasing population size. Both augmentation and poaching have occurred in populations of *L. helleri*, and we considered both types of scenarios in our modeling. Simulated augmentation, consistent with current efforts, had negligible effects on population growth and extinction probability. Because augmentation

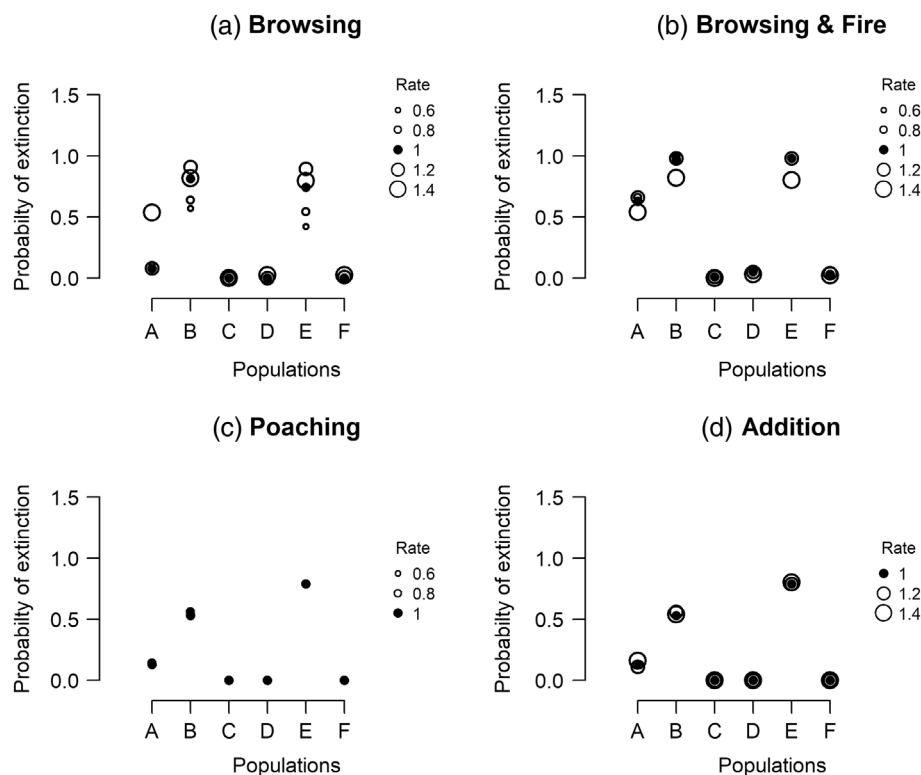


FIGURE 8 Probability of extinction for simulated *Liatris helleri* after 50 years with different levels of (a) browsing ($\times 0.6$, $\times 0.8$, $\times 1$, $\times 1.2$, and $\times 1.4$ probability of browsing, respectively), (b) browsing and fire ($\times 0.6$, $\times 0.8$, $\times 1$, $\times 1.2$, and $\times 1.4$ probability of browsing respectively and fire every 10 years), (c) observed browsing and poaching ($\times 0.6$, $\times 0.8$, and $\times 1$ observed plants), and (d) observed browsing and augmentation ($\times 1$, $\times 1.2$, and $\times 1.4$ observed plants). Simulations started with stable stage distribution for each population.

at a sufficiently high level should necessarily increase population growth and viability (Bell et al., 2003), our results suggest that higher levels of augmentation will be necessary to be effective as a conservation strategy. Likewise, simulated levels of poaching, consistent with observed levels or slightly higher and lower levels, also had slight effects on extinction probability. Higher levels could, of course, lead to population declines. Poaching or overharvesting has been shown to affect the population dynamics of some wild plants (McGraw et al., 2013).

Finally, trampling by humans, although observed rarely, may be affecting *L. helleri* plants growing in accessible and open conditions, and has the potential to reduce population growth. Visual evidence of repeated trampling was high near crowded trails at two study populations but was not evident in areas that had less visitation, higher shrub cover, or steeper slopes. Trail counters have documented increases in on and off-trail use over time (Chris Ulrey, unpublished data). For example, in 2004, at population D there were 23,465 visitors that hiked the trail between April 15 and November 15 (the effective growing season for *L. helleri*); of those, 3354 ventured off trail entering fragile areas in proximity of the *L. helleri* population (14% of visitors). At population A, which is a restricted area, we counted 2214 visitors between the same dates. More recent, in 2018, trail counting at another population in a higher elevation site estimated that 100,000–120,000 visitors hiked that trail. Although rarely studied in relation to demography, trampling has

the potential to affect critical populations of threatened species (Rossi et al., 2009).

Given *L. helleri*'s restricted distribution, quasi-stable populations (growth rates near one), low numbers of individuals, and relatively poor recruitment, any drivers that could reduce the currently high adult survival are threats to this species. We provide evidence that any increase in trampling, browsing, lack of fire, and poaching can be a concern for its viability. Detailed data on the effects and pattern of these drivers will allow more detailed simulations exploring their combined effects.

Climate changes in southern Appalachian region are likely to threaten high elevation endemic plants (Ulrey et al., 2016). It is expected to cause increases in actual evapotranspiration and water deficits (Ochocki et al., 2023) and decreases in soil moisture (Wu et al., 2014). These forecasts predict warmer and wetter climate that may alter *L. helleri* demography, increase vegetation cover, and change the frequency of prescribed fires.

In general, evaluations of species and population viability need to consider greater complexity and explicit consideration of demographic drivers. Most demographic studies do not include enough drivers (Crone et al., 2011; Ehrlén et al., 2016; Ehrlén & Morris, 2015). Without incorporating drivers, population models often do a poor job of projecting population dynamics (Crone et al., 2013). In this study, factors affecting *L. helleri* included population, year, fire, herbivory, trampling, augmentation, and

poaching. Not only do these factors (and potentially others not explicitly studied such as climate change) often have strong effects on population dynamics, but their inclusion also allows a more mechanistic approach to understanding and projecting past and future population trajectories given environmental change (Ehrlén & Morris, 2015; Gotelli & Ellison, 2006). Only with better understanding of these drivers and their effects can we expect to anticipate and deal with threats that increase extinction risks of rare species.

AUTHOR CONTRIBUTIONS

Pedro F. Quintana-Ascencio, Eric S. Menges, and Chris Ulrey participated in the conceptualization of this work. Chris Ulrey and Eric S. Menges collected and curated the data. Pedro F. Quintana-Ascencio performed the analysis. Chris Ulrey obtained the funding. Together they wrote the first draft and collaboratively edited all subsequent versions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

- Backus, G. A., Rose, M. B., Velazco, S. J. E., Franklin, J., Syphard, A. D., & Regan, H. M. (2023). Modeling the effects of spatially explicit patterns of climate and fire on future populations of a fire-dependent plant. *Frontiers on Ecology and Evolution*, 11, 1149509. <https://doi.org/10.3389/fevo.2023.1149509>
- Bell, T. J., Bowles, M. L., & McEachern, A. K. (2003). Projecting the success of plant population restoration with viability analysis. In C. A. Bringham & M. W. Schwartz (Eds.), *Population viability in plants. Ecological studies* (Vol. 165, pp. 313–348). Springer. https://doi.org/10.1007/978-3-662-09389-4_12
- Clark, L. C. (2019). *Development of microsatellite markers to evaluate current species boundaries between Liatris helleri porter and Liatris turgida (Gaiser) (Asteraceae)*. (Master's Thesis). Appalachian State University, 46pp.
- Crone, E., Menges, E., Ellis, M., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T., Knight, T., Lesica, P., Morris, W., Oostermeijer, G., Quintana-Ascencio, P. F., Stanley, A., Valverde, T., Ticktin, T., & Williams, J. (2011). How do plant ecologists use matrix population models? *Ecology Letters*, 14, 1–8.
- Crone, E. E., Ellis, M., Morris, W. F., Stanley, A., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T. N., Knight, T. M., Lesica, P., Oostermeijer, G., Quintana-Ascencio, P. F., Ticktin, T., Valverde, T., Williams, J. L., Doak, D. F., Ganesan, R., McEachern, K., Thorpe, A. S., & Menges, E. S. (2013). Ability of matrix models to explain the past and predict the future of plant populations. *Conservation Biology*, 27, 968–978.
- Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature*, 467, 959–962.
- Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81, 694–708.
- Eckhart, V. M., Geber, M. A., Morris, W. F., Fabio, E. S., Tiffin, P., & Moeller, D. A. (2011). The geography of demography: Long-term demographic studies and species distribution models reveal a species border limited by adaptation. *The American Naturalist*, 178, S26–S43.
- Edenius, L., & Ericsson, G. (2015). Effects of ungulate browsing on recruitment of aspen and rowan: A demographic approach. *Scandinavian Journal of Forest Research*, 30, 283–288.
- Ehrlén, J., & Morris, W. F. (2015). Prediction changes in the distribution and abundance of species under environmental change. *Ecology Letters*, 18, 303–314.
- Ehrlén, J., Morris, W. F., Von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally explicit structured population models of plants. *Journal of Ecology*, 104, 292–305.
- Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations: A practical guide to the integral projection model*. Springer Publishing.
- Ellner, S. P., & Rees, M. (2006). Integral projection models for species with complex demography. *The American Naturalist*, 167, 410–428.
- Gaoue, O. G., & Ticktin, T. (2010). Effects of harvest of nontimber forest products and ecological differences between sites on the demography of African mahogany. *Conservation Biology*, 24, 605–614.
- Godt, M. J., & Hamrick, J. L. (1995). The mating system of *Liatris helleri* (Asteraceae), a threatened plant species. *Heredity*, 75, 398–404.
- Godt, M. J., & Hamrick, J. L. (1996). Genetic diversity and morphological differentiation in *Liatris helleri* (Asteraceae), a threatened plant species. *Biodiversity and Conservation*, 5, 461–471.
- Gotelli, N. J., & Ellison, A. M. (2006). Forecasting extinction risk with non-stationary matrix models. *Ecological Applications*, 16, 51–61.
- Halsey, S. J., Cinel, S., Wilson, J., Bell, T. J., & Bowles, M. (2017). Predicting population viability of a monocarpic perennial dune thistle using individual-based models. *Ecological Modelling*, 359, 363–371.
- Maron, J. L., & Crone, E. (2006). Herbivory: Effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B*, 273, 2575–2584.
- Maschinski, J., Frye, R., & Rutman, S. (1997). Demography and population viability of an endangered plant species before and after protection from trampling. *Conservation Biology*, 11, 990–999.
- McGraw, J. B., Lubbers, A. E., Van der Voort, M., Mooney, E. H., Furedi, M. A., Southern, S., Turner, J. B., & Chandler, J. (2013). Ecology and conservation of ginseng (*Panax quinquefolius*) in a

- changing world. *Annals of the New York Academy of Sciences*, 1286, 62–91. <https://doi.org/10.1111/nyas.12032>
- Menges, E. S. (2000). Population viability analyses in plants: Challenges and opportunities. *Trends in Ecology & Evolution*, 15, 51–56.
- Menges, E. S., Quintana-Ascencio, P. F., Weekley, C. W., & Gao, O. G. (2006). Population viability analysis and fire return intervals for an endemic Florida scrub mint. *Biological Conservation*, 127, 115–127.
- Menges, E. S., Smith, S. A., Olano, J. M., Schafer, J. L., Clarke, G., & Main, K. (2020). Effects of frequent fire and mowing on resprouting shrubs of Florida scrub. *Fire Ecology*, 16, 10. <https://doi.org/10.1186/s42408-020-0069-1>
- North Carolina Natural Heritage Program (NCNHP). (2010). *Element occurrence records for Liatris helleri*. Department of Environment and Natural Resources.
- Ochocki, C., Schoenecker, R., & Thompson, M. (2023). Climate change and climate analogs for the Southern Appalachians. (Doctoral dissertation). Duke University.
- Pascarella, J. B., & Horvitz, C. C. (1998). Hurricane disturbance and the population dynamics of a tropical understory shrub: Matrix elasticity analysis. *Ecology*, 79, 547–563.
- Quintana-Ascencio, P. F., Koontz, S. M., Smith, S. A., Sclater, V., David, A. S., & Menges, E. S. (2018). Predicting landscape-level distribution and abundance: Integrating demography, fire, elevation, and landscape habitat configuration. *Journal of Ecology*, 106, 2395–2408.
- Quintana-Ascencio, P. F., Menges, E. S., Cook, G. S., Ehrlén, J., & Afkhami, M. E. (2021). Drivers for demography: Past challenges and promise for a changed future. Chapter 6. In R. Salguero-Gómez & M. Gamelon (Eds.), *Demography across the tree of life* (pp. 113–127). Oxford University Press. Oxford GB.
- Rossi, G., Parolo, G., & Ulian, T. (2009). Human trampling as a threat factor for the conservation of peripheral plant populations. *Plant Biosystems*, 143, 104–113. <https://doi.org/10.1080/11263500802633725>
- Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., ... Vaupel, J. W. (2015). The COMPADRE plant matrix database: An open online repository for plant demography. *Journal of Ecology*, 103, 202–218.
- Schemske, D. W., Husband, B. C., Ruckelshaus, M. H., Goodwillie, C., Parker, I. M., & Bishop, J. G. (1994). Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, 75, 584–606.
- Tye, M. R., Menges, E. S., Weekley, C., Quintana-Ascencio, P. F., & Salguero-Gómez, R. (2016). A demographic ménage à trois: Interactions between disturbances both amplify and dampen population dynamics of an endemic plant species. *Journal of Ecology*, 104, 1505–1528.
- Ulrey, C., Quintana-Ascencio, P. F., Kauffman, G., Smith, A. B., & Menges, E. S. (2016). Life at the top: Long-term demography, microclimatic refugia, and responses to climate change for a high-elevation southern Appalachian endemic plant. *Biological Conservation*, 200, 80–92.
- United States Fish and Wildlife Service. (2013). *Heller's blazing star (Liatris helleri) 5-year review: Summary and evaluation* (p. 28). U.S. Fish and Wildlife Service, Southeast Region, Asheville Ecological Services Field Office.
- Watanabe, S. (2013). WAIC and WBIC are information criteria for singular statistical model evaluation. In *Proceedings of the workshop on information. Theoretic Methods in science and engineering* (pp. 90–94).
- Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *Bioscience*, 48, 607–615.
- Wiser, S. K. (1994). High elevation cliffs and outcrops of the southern Appalachians: Vascular plants and biogeography. *Castanea*, 59, 85–116.
- Wu, W., Clark, J. S., & Vose, J. M. (2014). Response of hydrology to climate change in the southern Appalachian Mountains using Bayesian inference. *Hydrological Processes*, 28, 1616–1626.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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