Oecologia (2021) 196:679–691
https://doi.org/10.1007/s00442-021-04955-2

POPULATION ECOLOGY – ORIGINAL RESEARCH

Fires slow population declines of a long-lived prairie plant through multiple vital rates

Scott W. Nordstrom[1,2,3] · **Amy B. Dykstra**[4] · **Stuart Wagenius**[1]

Received: 11 December 2020 / Accepted: 26 May 2021 / Published online: 2 June 2021

Abstract

In grasslands worldwide, modified fire cycles are accelerating herbaceous species extinctions. Fire may avert population declines by increasing survival, reproduction, or both. Survival and growth after fires may be promoted by removal of competitors or biomass and increasing resource availability. Fire-stimulated reproduction may also contribute to population growth through bolstered recruitment. We quantified these influences of fire on population dynamics in *Echinacea angustifolia*, a perennial forb in North American tallgrass prairie. We first used four datasets, 7–21 years long, to estimate fire's influences on survival, flowering, and recruitment. We then used matrix projection models to estimate growth rates across several burn frequencies in five populations, each with one to four burns over 15 years. Finally, we estimated the contribution of fire-induced changes in each vital rate to changes in population growth. Population growth rates generally increased with burning. The demographic process underpinning these increases depended on juvenile survival. In populations with high juvenile survival, fire-induced increases in seedling recruitment and juvenile survival enhanced population growth. However, in populations with low juvenile survival, small changes in adult survival drove growth rate changes. Regardless of burn frequencies, our models suggest populations are declining and that recruitment and juvenile survival critically influence population response to fire. However, crucially, increased seedling recruitment only increases population growth rates when enough new recruits reach reproductive maturity. The importance of recruitment and juvenile survival is especially relevant for small populations in fragmented habitats subject to mate-limiting Allee effects and inbreeding depression, which reduce recruitment and survival, respectively.

Keywords Bayesian modeling · Fire-stimulated flowering · Fire-stimulated recruitment · Matrix models · Population dynamics

Communicated by Brian J. Wilsey.

This manuscript uses sophisticated quantitative techniques to highlight context dependence in which demographic processes contribute to population growth of a grassland forb after fires.

✉ Scott W. Nordstrom
scottwatsonnordstrom@gmail.com

1 Negaunee Institute for Plant Conservation Science and Action, Chicago Botanic Garden, 1000 Lake Cook Rd, Glencoe, IL 60022, USA

2 BioFrontiers Institute, University of Colorado Boulder, 3145 Colorado Avenue, Boulder, CO 80303, USA

3 Department of Ecology and Evolutionary Biology, University of Colorado Boulder, 1900 Pleasant Street, 334 UCB, Boulder, CO 80309, USA

4 Department of Biological Sciences, Bethel University, 3900 Bethel Drive, St. Paul, MN 55112, USA

Introduction

Disturbance is crucial for maintaining biodiversity and slowing extinctions in many ecosystems. Brief, localized events alter population and community dynamics by modifying demographic processes (Dornelas 2010), strongly influencing abundances of resident species (Supp and Ernest 2014). With increasing anthropogenic influences disrupting natural cycles of disturbance in ecosystems worldwide, species heavily reliant on certain disturbance regimes face increased threat of extinction.

One prominent example of an ecosystem dependent on disturbance is temperate grasslands, which burn frequently and contain resident species that respond positively to fire (Veldman et al. 2015). Grasslands covering approximately 40% of global terrestrial landmass (White et al. 2000) are undergoing destruction and degradation (Hoekstra et al.

2005; Gage et al. 2016). This degradation has been associated with widespread changes in biodiversity including the loss of native species (Alstad et al. 2016). Local extinctions are occurring more rapidly in grasslands where fire is rare or suppressed (Leach and Givnish 1996; Alstad et al. 2016). Consequently, understanding the mechanisms through which fire specifically and disturbance more generally forestall extinction is critical for conserving species in areas with changing disturbance regimes.

Many grassland plants are long-lived and herbaceous (Veldman et al. 2015) potentially benefitting from fire through two demographic pathways—a pathway maintaining or bolstering adult cohorts after fires (e.g., survival and growth), and a pathway increasing recruitment into the population (e.g., flowering and recruitment). Population growth in long-lived species is often highly sensitive to small changes in individual survival and growth, particularly in adults (García et al. 2008). As a consequence, one hypothesis for fire suppression's negative effect on subdominant resident species is that competition (Leach and Givnish 1996) or lack of nutrients (Hulbert 1988) impede survival and growth. Fire would thus improve survival and growth by removing standing vegetation and litter (Knapp and Seastedt 1986; Hulbert 1988) or competitors (Menges and Kimmich 1996), increasing the availability of light, a diversity-limiting resource (Borer et al. 2014). However, heightened reproduction and recruitment after burns can also contribute to population responses to fire. Fire-stimulated or fire-obligate flowering is common in many grassland species (Lunt 1994; Lamont and Downes 2011; Wagenius et al. 2020). Recruitment is typically sporadic in long-lived grassland plants but is generally enhanced by fires (Menges and Dolan 1998; Morgan 1998), and seed germination and establishment are higher after burns (Morgan 2001). Recruitment can be limited by lack of microsites (Goldberg and Gross 1988; Münzbergová and Herben 2005) or light (Goldberg and Werner 1983; Jutila and Grace 2002); fire can alleviate this limitation by creating canopy gaps and exposing soil (Morgan 1998). Quantifying and understanding the relative impacts of these two demographic pathways can inform conservation efforts for targeted action and generate predictions about which species are likely to be at heightened extinction risk as disturbance regimes change.

Quantifying the relative impacts of these demographic pathways requires a wholistic approach. Estimating fire-induced changes only in vital rates does not necessarily predict population response because vital rates differ in how much their variation affects population dynamics (de Kroon et al. 1986). Studies of population dynamics with matrix projection models have demonstrated that fire increases population growth rates in several grassland systems (e.g., Menges and Dolan 1998; Caswell and Kaye 2001; Kaye et al. 2001; Bowles et al. 2015). Yet, an increase in growth rates does not necessarily provide insight into the demographic mechanisms underpinning population dynamics. A mechanistic understanding of how fire influences population growth requires simultaneously estimating fire's effects on population growth and also how these vital rates combine to influence population growth rates.

We focus on demography and population growth in five populations of *Echinacea angustifolia* (Asteraceae), an herbaceous perennial native to the North American plains and tallgrass prairie. Prior to Euro-American settlement, when fires were managed by indigenous peoples and started by lightning (Kimmerer and Lake 2001), mean inter-fire intervals in tallgrass prairie ranged from two to three years, yet current fire intervals are 10–25 years or longer (Umbanhower 1996). As in other grassland systems, less frequent fires are associated with losses of native species and colonization by non-natives (Alstad et al. 2016). The demographic mechanisms causing species loss have not been widely studied, as examinations of fire's effects on all stages of tallgrass prairie plant life cycles and population growth are rare (but see Menges and Dolan 1998; Bowles et al. 2015). Because it is widespread and long-lived (Hurlbut 1999), *E. angustifolia* is a good model organism for understanding fire's role in species persistence. Prior work has shown increased seedling establishment (Wagenius et al. 2012) and flowering (Wagenius et al. 2020) after dormant-season burns. Matrix models suggest that populations of *E. angustifolia* in Minnesota prairie remnants are in decline (Dykstra 2013, but see Hurlbut 1999 for evidence of population stability in Kansas). The demographic pathways through which fire influences population dynamics in *E. angustifolia* have not been studied.

We address the following questions for five populations of *E. angustifolia* in a fragmented landscape: (1) How does fire affect each vital rate in *E. angustifolia* individuals? (2) How does fire affect population growth rates in *E. angustifolia?* (3) Which vital rate changes contribute to fire-induced changes in population growth rates? We address our first question using Bayesian mixed effects modeling and a multistage mark-recapture model (Caswell and Fujiwara 2004). We address questions two and three using matrix projection models (Caswell 2001). To fit these models, we combine 21 years of demographic surveys of adult populations and seven years of recruitment observations with two separate multi-year censuses of juvenile survival. We performed an analysis with each of our juvenile survival datasets; this allowed inference and comparison of population growth and demographic pathways under two different sets of conditions for juvenile plants. Directly estimating fire's effects on vital rates and incorporating those effects into projections of population growth, supported by the considerable temporal extent of our data, provides valuable insight into the demographic pathways through which burning promotes persistence in fire-prone ecosystems. These results are relevant to conservation biology and the protection of species threatened by changing disturbance regimes.

Materials and methods

Study species and site

E. angustifolia is a widespread and long-lived tap-rooted forb. Recruitment occurs solely by seed with no known dispersing agent. Seedling establishment is enhanced after prescribed fires (Wagenius et al. 2012). Plants typically require eight or more years to reach reproductive maturity in natural settings (Wagenius et al. 2012). Adult *E. angustifolia* plants do not flower every year (Waananen et al. 2018). In a year when a plant flowers, it usually produces only one flowering head, although more are often produced in years following fires (Wagenius et al. 2020). Plants produce basal leaves in years they do not flower; we have not observed dormancy in adult *E. angustifolia* plants. We refer to any plant with an elongated stem as flowering and non-flowering adults as basal. *E. angustifolia* is an obligate outcrosser with a sporophytic self-incompatibility system that induces a component Allee effect where reproduction in individuals is limited by the availability of mates, which occurs in small populations (Wagenius et al. 2007). Mate-limited reproduction also occurs in years when few plants flower (Wagenius et al. 2020).

We focus on five populations of *Echinacea angustifolia* in agricultural areas of Douglas and Grant Counties in western Minnesota that underwent spring burns between 1999 and 2010 (Table 1): LCW and YOH are on roadsides and oldfields that burned in 2003, RDC is in a railroad right-of-way that burned by a rail spark in 2005, ETH is on the site of a US Fish and Wildlife Service Waterfowl Production Area (WPA) experiencing a wildfire in 2003, and NNW is in a roadside by a WPA experiencing controlled burns in 1999, 2000, 2002, and 2010. These five remnant populations were typical of remnants in our study area. Apparent differences within and among sites include the past history of agricultural and roadside disturbances, including mowing, grazing, and spraying, which are reflected in difference in plant community composition and depth of litter. In spite of the differences, they all have *E. angustifolia* and all are dominated by the perennial non-native grass *Bromus inermis*, and native grasses such as *Andropogon gerardii* and *Bouteloua curtipendula.*

We define a “burn year” as a year with a spring burn. Usually burns occur in April or May around the time that cotyledons emerge from achenes. Burns typically consume all aboveground biomass in almost all of each prairie remnant. In burn years, plants and seeds may be directly affected by heat and fire, including damage to the tops of dormant roots and emerging leaf tissue in juvenile and adult plants. Seeds sired the year before a burn would be present on or near the surface of the soil during the burn. Seedlings emerging right before the burn could be killed by flames. Plants and seeds are also indirectly affected by post-fire conditions, such as less litter and more light. We also distinguished in our analyses between plants observed one year after a burn year (henceforth, one year post-burn), two years after a burn year (two years post-burn), and three or more years after a burn year (non-burn year, sensu Caswell and Kaye 2001). One and two years post-burn, plants are subject to post-fire conditions without direct physical effects of fire.

Life history stages and matrix model

We defined six stage classes for *E. angustifolia*: age-zero seedlings (S), one-year-old plants (J_1), early-stage juveniles between ages two and seven (J_2), late-stage juveniles age eight or older that have not yet flowered (J_3), flowering adult plants (F), and basal adult plants (B) (Fig. 1a). We did not measure adults in every year, precluding size-based or integral projection modeling approaches. We chose age designations based on initial models of juvenile survival suggesting substantial variation in survival among seedlings,

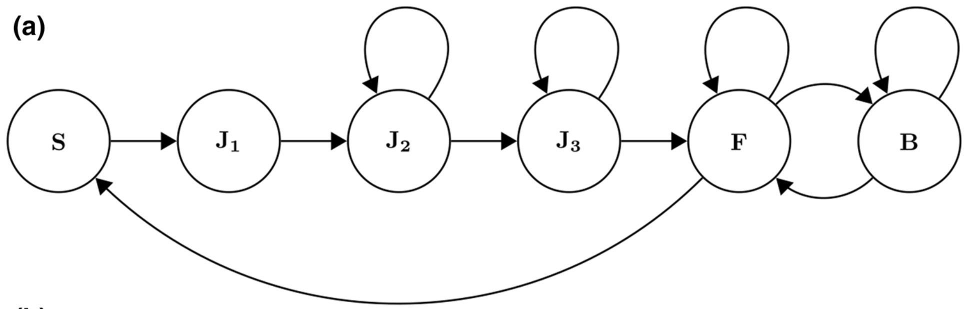
Table 1 Attributes of five focal populations of *Echinacea angustifolia*

Population	Individuals observed	Recruitment/juv. survival data	Burn events	Land use
ETH	31	Y/Y	2003	W/P
LCW	367	Y/Y	2003	R/P
NNW	71	Y/N	1999, 2000, 2002, 2010	R/P/W
RDC	64	N/N	2005	R/RR
YOH	141	N/N	2003	R/P

Individuals observed includes the number of unique individual plants observed in flower at least once during the time period 1996–2016. Recruitment/juv. survival data denotes whether the population was included in the recruitment census and/or the low juvenile survival census. Burn events denote the years in which populations experienced spring (March–June) burns. Land use codes: *R* road right of way; *RR* railroad right of way; *P* privately owned oldfield; *W* managed waterfowl protection area

Fig. 1 Diagram representing the **a** life cycle diagram of *E. angustifolia* and **b** transition matrix. In **b**, vital rates are s: annual survival, f: annual flowering, and r: annual seedling recruitment

(a)



(b)

$$
\begin{array}{cc}
 & \begin{array}{cccccc} S & J_1 & J_2 & J_3 & B & F \end{array} \\
\begin{array}{c} S \\ J_1 \\ J_2 \\ J_3 \\ B \\ F \end{array} &
\begin{pmatrix}
0 & 0 & 0 & 0 & 0 & s_F r_F \\
s_S & 0 & 0 & 0 & 0 & 0 \\
0 & s_{J_1} & \frac{s_{J_2} - s_{J_2}^{\alpha-3}}{1 - s_{J_2}^{\alpha-3}} & 0 & 0 & 0 \\
0 & 0 & \frac{s_{J_2}^{\alpha-3} - s_{J_2}^{\alpha-2}}{1 - s_{J_2}^{\alpha-3}} & s_{J_3}(1 - f_{J_3}) & 0 & 0 \\
0 & 0 & 0 & 0 & s_B(1 - f_B) & s_F(1 - f_F) \\
0 & 0 & 0 & s_{J_3} f_{J_3} & s_B f_B & s_F f_F
\end{pmatrix}
\end{array}
$$

one-year-old plants, and plants aged two years or older. We defined a variable, α, for minimum observed reproductive age (i.e., earliest age at which we observe a plant flowering in natural conditions; Levin et al. 1996), setting $\alpha = 8$ in all models (Wagenius et al. 2012). We then defined a matrix projection model (Fig. 1b). Matrix entries for early-stage juvenile plants (column J_2) were calculated using the fixed-duration stage method (Caswell 2001, Sect. 6.4, p. 159).

Field experiments and observations

Demographic census of adults

Annual survival and flowering probabilities in adult plants are based on demographic censuses in five remnant populations spanning 21 years (Table 2). These data result from an ongoing study in which individual flowering *E. angustifolia* plants in 30 remnants have been tagged and surveyed since 1996 as described by Wagenius et al. (2020). These censuses provided a complete count of flowering individuals in each population in each year. To assess survival of basal plants, in certain years, we performed a partial or complete census of plants observed in prior years, recording whether each plant was observed alive or not found. We performed a complete census in each population in 2016 to determine survival at the end of the study.

Census of seedling recruitment

Seedling recruitment was assessed between 2007 and 2013 in 17 remnant populations. This census was designed independently of the demographic surveys; seedlings and adults were both censused in only three populations (Table 2). The 14 populations with only seedling censuses are in oldfields,

Table 2 Summary of data sources used to estimate vital rates

Data source	Duration	Populations	Vital rates measured
Adult census	1996–2016	ETH, LCW, NNW, RDC, YOH	s_B, s_F, f_B, f_F
Recruitment census	2007–2013	ETH, LCW, NNW, + 14 others	r_F
Recruit juvenile census (low juvenile survival)	2008–2017	ETH, LCW, + 14 others	s_S, s_{J1}, s_{J2}, s_{J3}
Seedling recruitment experiment (high juvenile survival)	2000–2014	Experimental plots	s_S, s_{J1}, s_{J2}, s_{J3}, f_{J3}

The recruit juvenile census results from the continued census of seedlings observed in the recruitment census. A list of additional populations used in the recruitment and juvenile censuses are included in Online Resource 1. The sites used in the seedling recruitment experiment are oldfields within our study area with no pre-existing *E. angustifolia* plants as explained in Online Resource 2 and Wagenius et al. (2012)

on roadsides, or a preserve managed by the Nature Conservancy (Online Resource 1). Five burns at three sites occurred during our observation period. To assess seedling recruitment, we randomly sampled up to 18 plants that had flowered the previous year per population (total 1224 plants). Around each focal plant, we circumscribed a circle with radius either 41 or 50 cm. In 2007, we used a radius of 32 cm in two populations due to the close proximity of focal plants. Within each circle, we mapped and counted *E. angustifolia* seedlings in late May or early June while cotyledons were still mostly green. Seedling density could increase due to higher seed production by the focal plant, less dispersal outside the circle, or higher seed germination. In some cases, seedlings may have emerged after the census.

Censuses of juvenile plants

We used two different data sources to assess survival of pre-reproductive (juvenile) plants (Table 2). One is annual censuses of seedlings observed in the abovementioned recruitment censuses. This dataset includes 687 seedlings tracked in 16 populations (one population, NNW, produced no seedlings) from their establishment until 2017 or the plant's death, whichever occurred first. Due to low overall survival (only 99 of 687 plants survived to the end of this study), we refer to this as the "low juvenile survival" dataset. The other data source comprises annual survival records through 2014 from an experiment established in 2000. Wagenius et al. (2012) provide details and report results through 2009. More details are in Online Resource 2. Briefly, seeds were collected from nearby populations with > 100 flowering plants. Three cohorts of individuals were established by broadcasting seed into grassland plots lacking *E. angustifolia.* This experiment was conducted within the study area but at sites separate from the adult demographic and seedling recruitment observational studies. Each experimental unit was burned between zero and four times. Due to high survival in this experiment (481 of 1165 plants survived to the end of the experiment), we refer to this as the "high juvenile survival" dataset. Sixty-nine plants flowered during this experiment.

Vital rate estimation

We estimated all vital rates with Bayesian modeling. We used *tan* (Stan Development Team 2018) to estimate adult vital rates (s_F, s_B, f_F, and f_B) and Bayesian generalized linear mixed effects models (GLMMs) in *brms* (Bürkner 2017) to estimate all others. All analyses were performed in R version 3.4.2 (R Core Team 2018). Prior choices for all models are explained in Online Resource 3. We compared models using leave-one-out cross-validation (LOOIC, Vehtari et al. 2017). All model selection details and comparisons are available in Online Resource 3. All final models featured Rhat less than or equal to 1.01 for both fixed and random effects, suggesting model convergence. To incorporate uncertainty in parameter estimates into our matrix analyses, for each vital rate, we sampled 100 estimates from the parameter's posterior distribution for each population in each year. Seedlings recruited per flowering plant, survival, and flowering had integer-supported posterior distributions; we estimated population means by taking 100 bootstrapped means from 4000 posterior samples. When estimating vital rates for populations not included in either the seedling recruitment or juvenile survival datasets (Table 2), we assumed the population mean was the same as the mean of the populations used to fit the model (Gelman and Hill 2007, Sect. 12.8, p. 274).

Models for each vital rate

We estimated adult survival and flowering (s_B, s_F, f_B, and f_F) for each population-year combination using 2790 demographic records of 674 adult plants (see Table 1 for individual population sizes). These records include all instances of flowering, but we did not observe each adult basal plant in every year. To account for the incomplete sampling, we implemented a multi-stage mark-recapture model (Caswell and Fujiwara 2004). This model features transition probabilities between multiple stages (in our case, flowering plants, basal plants, and dead plants) as well as a detection probability for each stage. For each plant with missing observations, the model likelihood term for that plant's detection history includes all possible transition histories within the period of missing observations (Caswell and Fujiwara 2004). For details, see Online Resource 5. We fit models for each population separately. Although we fit models using data from all years between 1996 and 2016, we incorporated posterior estimates only for transitions between 1999 and 2014 into our matrix models. We assessed differences in s_B, s_F, f_B, and f_F among the four time-since-fire categories using permutation testing, as described in Online Resource 6. The *p* value associated with the test is the probability of observing a permuted difference in medians as large as or larger than the observed difference in medians if there were no differences among times-since-fire.

We estimated recruitment (r_F) using Bayesian GLMMs; the final model featured categorical covariates for burning one year and burning two years prior to seedling establishment and a population random effect. Model selection revealed no evidence of a seed bank (i.e., ungerminated seeds surviving more than one year), based on testing a term for head count two years prior to the seedling searches (Online Resource 3). This finding corroborates empirical results from seed addition experiments in *E. angustifolia* where 1–2% of all germinants emerged in the second year and none emerged thereafter (Dykstra 2013). Because all 37 focal plants observed in burn years had zero seedlings, our models could not estimate uncertainty in the effects of burn years on recruitment. Accordingly, we set seedling recruitment to zero in all matrices for burn years and excluded observations from burn years from our recruitment models. This assumes that seeds experience damage and high mortality with exposure to fire, consistent with results of Wagenius et al. (2012) who found only 1–2% of *E. angustifolia* seeds survived controlled burns occurring after sowing.

To estimate juvenile survival (s_S, s_{J1}, s_{J2}, and s_{J3}), we fit GLMMs with each juvenile survival dataset. The final model fit with the high juvenile survival dataset included age (0, 1, and 2 +), a predictor for whether the census took place in a burn year, and an interaction between age class and burn, and included three nested random effects to account for spatial blocking (experimental design details are in Online Resource 2). The final model fit with the low juvenile survival dataset included age class as a fixed effect and two spatially nested random effects. We estimated effects of burning only in the high juvenile survival dataset because the low-survival dataset included only 30 plants primarily in only two populations, which confounded potential burn and population effects.

We estimated annual flowering probabilities for late-stage juveniles (f_{J3}) using the high juvenile survival dataset. The juvenile flowering model featured a categorical variable for observations in a burn year to capture the effects of fire and a site-level random effect. We did not model juvenile flowering with the low juvenile survival dataset because it included only one flowering plant. See Online Resource 3 for all model selection details.

Population growth rates

Because we had two sets of estimates of juvenile survival, we estimated population growth rates separately with each dataset. This allowed us to assess the robustness of our results to different conditions of juvenile survival (high- versus low-survival conditions). Using 100 posterior estimates for each vital rate, we compiled 200 transition matrices (100 with each juvenile survival model) for each of 75 population-year combinations (five populations with 15 annual transitions from 1999 to 2014). When presenting high juvenile survival and low juvenile survival matrices for the same population-year combination, all vital rate estimates except for s_S, s_{J1}, s_{J2}, and s_{J3} are identical. We classified each matrix as one of four time-since-fire categories: burn year, one year post-burn, two years post-burn, and three or more years post-burn.

To assess the effects of burn frequency on population growth, we calculated mean stochastic population growth rates ($\overline{\lambda}_s$) for each population at six annual burn probabilities evenly spaced between 0 and 50%. For each population at each burn frequency, we generated a random burn sequence of 1500 time-steps (i.e., 1500 years), randomly sampled matrices from that population corresponding to the burn sequence and left-multiplied a population vector by the product of these matrices. The current stage distributions of the populations we modeled are unknown; we used the first 500 time-steps in the sequence as a “burn-in” ensuring that growth rates were calculated with an equilibrium initial stage distribution based on observed transition matrices. We defined the annual stochastic growth rate as $\lambda_s = (N_{1500}/N_{501})^{1/1000}$, where N_{501} and N_{1500} are the total population sizes in time-steps 501 and 1500, respectively. We calculated mean stochastic growth rate ($\overline{\lambda}_s$) by averaging λ_s over 500 independent trials. A growth rate of $\overline{\lambda}_s > 1$ implies a population is growing on average. Notably, this procedure models the effects of burning as additive and independent of the frequency of burning, a common feature of models estimating growth rates at varying frequencies of disturbance (e.g., Kaye et al. 2001). This procedure is not meant to forecast a thousand years of population dynamics; rather, it is a procedure using bootstrapping to estimate mean population growth rates and their uncertainties given temporal variation in vital rates (Caswell 2001, p. 415).

Decomposition of vital rates

To quantify the effects of fire-induced changes in vital rates on population growth, we decomposed the effect of burning on $\overline{\lambda}_s$ into contributions from each vital rate using an approach similar to the “Relative Interactive Effects” approach of Louthan et al. (2018). For vital rate *i*, we defined $\lambda_{s,i}$ as the stochastic growth rate where each burn or post-burn matrix is substituted for a randomly drawn non-burn matrix with only vital rate *i* set to a randomly drawn burn- or post-burn value. In these matrices, instead of all vital rates being affected by fire, only vital rate *i* is. We then calculated the stochastic population growth rate for the same sequence of matrices but with vital rate *i* set to non-burn values; we define this growth rate in the absence of fire as $\lambda_{s,0}$. The difference $r_i = \log\left(\lambda_{s,i}\right) - \log(\lambda_{s,0})$ is a first-order approximation of the contribution of vital rate *i* to λ_s's response to burning. We ran this procedure 500 times for each vital rate in each population at annual burn probabilities of 10% and 50%; the average over these 500 trials we called $\overline{r}_i$. If $\overline{r}_i$ is positive, then vital rate *i*'s response to fire makes a positive contribution to the population growth rate; the opposite is true if $\overline{r}_i$ is negative. We estimated the contributions of post-burn juvenile survival only with the high juvenile survival dataset.

The approach we used to decompose vital rates allowed us to isolate effects of fire on individual vital rates while incorporating annual variation where available. We did not use a stochastic life table response experiment (Davison et al. 2010) for two reasons. First, we did not have year- and population-specific estimates of each vital rate in each year within each population and thus were unable to accurately estimate all variances and covariances in vital rates. Second, we were not interested in annual vital rate variation per se, but the effects of fire acting through vital rates.

Results

Vital rates

Flowering in adults was about twice as likely in a burn year, i.e., a summer with a spring burn, compared to all post-burn or non-burn years (Fig. 2). Median flowering probabilities were 0.33 for basal plants and 0.45 for flowering plants when pooling posterior estimates across all burn years ($n = 700$). All other times-since-fire had median flowering probabilities less than 0.2, with the exception of one year post-burn f_F (median probability 0.21). For both basal and flowering plants, flowering was higher in burn years than in all other times-since-fire (all $p < 0.03$). All p values associated with adult flowering are presented in Online Resource 6. Fire also increased the flowering in late-stage juveniles (f_{J3}) (log odds ratio increase of 1.01, 95% Credible Interval 0.37–1.63). Without fire, late-stage juvenile flowering was rare, with only 0.7% probability of flowering per year (CI 0.02–9.8%). This probability nearly quadrupled to 2.7% (CI 0.07–25.5%) in a burn year.

Flowering *E. angustifolia* plants recruited more offspring in the two years following a burn. In non-burn years, recruitment was poor (mean seedlings per plant 0.37, 95% CI 0.18–0.64), but increased both one year (mean 2.06, CI 0.77–6.01) and two years post-burn (mean 1.69, CI 0.48–6.86).

Fire effects on adult survival were negligible to slightly positive (Fig. 2). Little evidence supported the hypothesis that time-since-fire consistently influences survival probabilities of basal plants (all $p > 0.10$). In burn years and one year post-burn, survival of flowering plants was 2–4% higher than two or more years post-burn. Median survival probabilities (s_F and s_B) for all times-since-fire were between 0.87 and 0.94. p values associated with adult survival and time-since-fire are reported in Online Resource 6.

Patterns of survival and response to fire differed between our two juvenile survival models. In the high juvenile survival dataset, survival increased with age such that plants older than age two had mean survival exceeding 94% (Fig. 3). In this experiment, burning had negative impacts on seedlings and plants at age one and a positive effect on plants age 2+ (Fig. 3). In the low juvenile survival dataset, mean seedling survival was 84.7% (CI

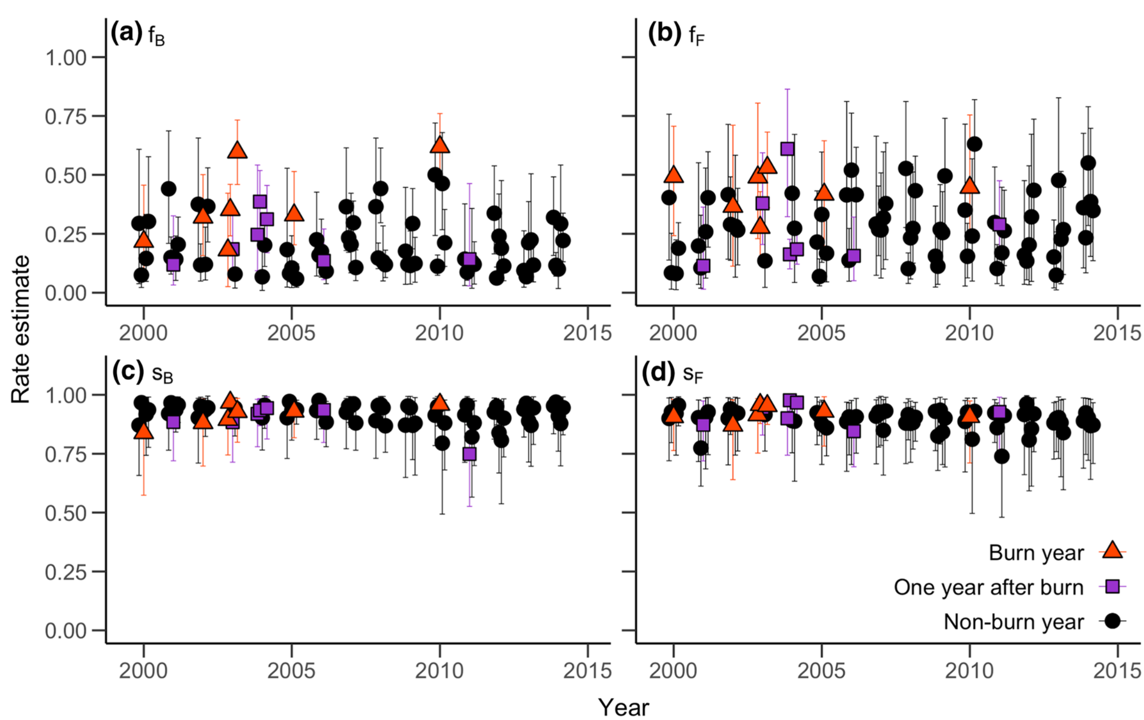


Fig. 2 Estimates of four vital rates (with 95% credible intervals) for five adult *E. angustifolia* populations between 2000 and 2014. Vital rates include: flowering probabilities of **a** basal (f_B) and **b** flowering plants (f_F), respectively and survival probabilities of basal (s_B) and flowering plants (s_F), respectively

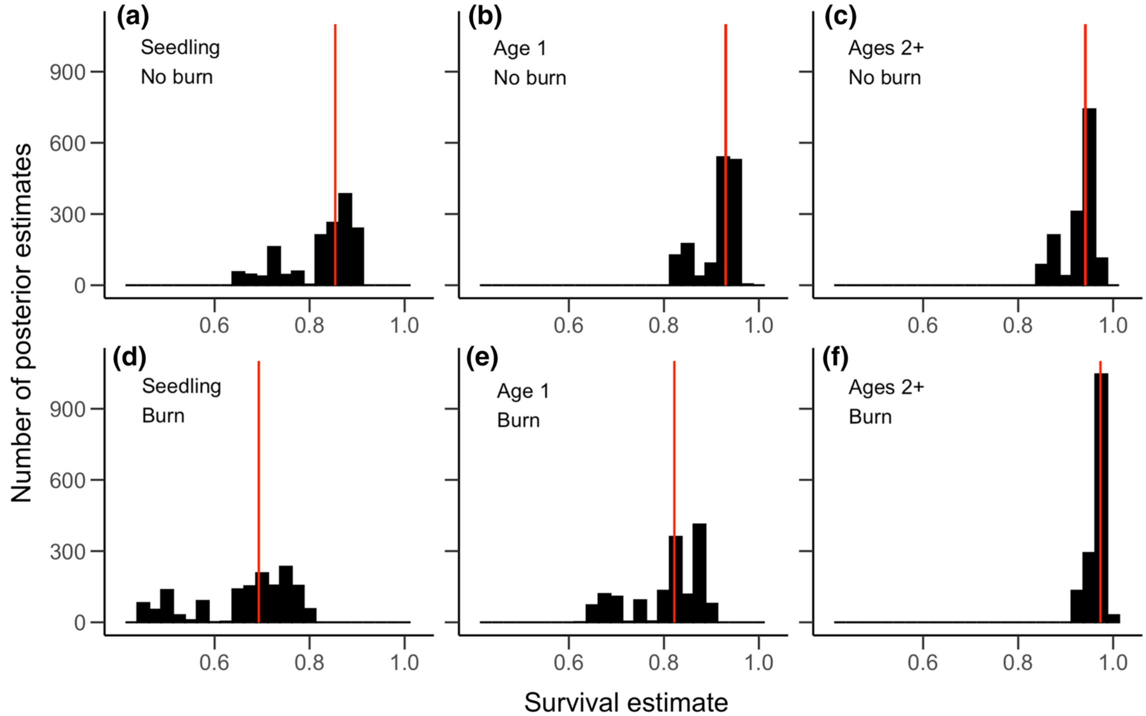


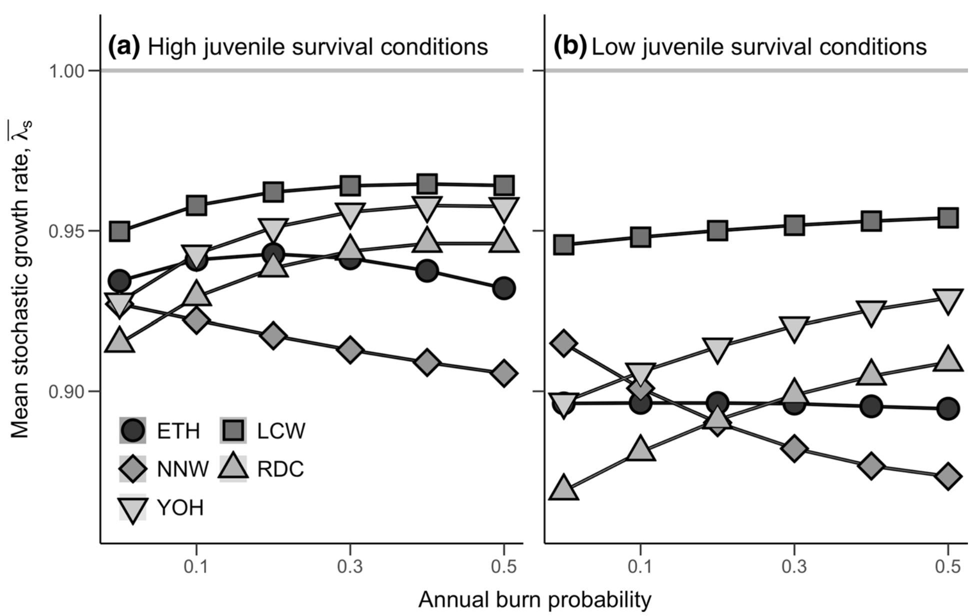
Fig. 3 Survival rates of juvenile *E. angustifolia* in years **a**–**c** without and **d**–**f** with burns. Each histogram contains 100 posterior estimates of juvenile survival for each of 15 years. *Red* lines are the median survival estimate, pooled across all years, for each age-burn status combination

71.4–92.8%) and mean survival of all other juveniles was 63.3% (CI 40.1–81.9%). Spatial variation, i.e., the magnitude of the random effects of population and blocks, and population-level random effects for all GLMMs are provided in Online Resource 3.

Stochastic population growth rates

Populations are predicted to decline (i.e., $\overline{\lambda}_s < 1$) regardless of burn frequency (Fig. 4). However, growth rates generally increase ($\overline{\lambda}_s$ closer to 1) with more frequent burning. The consistency of this effect depends on juvenile survival. With high juvenile survival, growth rates in the absence of

Fig. 4 Mean stochastic growth rate ($\overline{\lambda}_s$) with varying burn frequency for five remnant populations of *E. angustifolia,* estimated using **a** high and **b** low juvenile survival conditions. Each point is the mean of 500 simulations of a 1000-year burn sequence at the given burn frequency. $\overline{\lambda}_s < 1$ predicts populations are in decline. Bands around mean represent twice the standard error of $\overline{\lambda}_s$ estimates



fire ranged from $\overline{\lambda}_s = 0.91$ to $\overline{\lambda}_s = 0.95$ (Fig. 4a). Population growth increased with burning frequency in four of five populations, although one population (ETH) had its highest growth rate at intermediate burn rates. Stochastic growth rates with low juvenile survival were low without fire ($\overline{\lambda}_s$ ranging from 0.87 to 0.95, Fig. 4b), and had mixed response to burning; with more frequent burning, $\overline{\lambda}_s$ increased in two populations, remained nearly constant in two populations, and decreased in one population (Fig. 4b).

Vital rate decomposition

Which vital rates contributed most to post-fire population growth depended on juvenile survival conditions and burn frequency (Fig. 5). In conditions with high juvenile survival, several rates contributed to population growth after fires. At low burn probabilities (10%), increased seedling recruitment (r_F) made the largest contribution to population growth in four of five populations (Fig. 5a). Increased survival of late-stage juveniles (s_{J3}) also contributed to population growth. Increased flowering of basal (f_B) and late-stage juvenile plants (f_{J3}) made contributions modest in magnitude and mixed in sign while all other vital rates had negligible contributions. With more frequent burning (annual burn probability 50%), s_{J3} contributed most to population growth in all populations, while r_F also contributed significantly to growth rate increases (Fig. 5c). In conditions with lower juvenile survival, basal plant survival (s_B) made the largest contributions to post-fire population growth in four populations (Fig. 5b,d). However, the sign of this contribution varied by population. In all populations, increased recruitment and flowering made positive but negligible contributions to population growth, with the exception of a large negative contribution of f_B at LCW. In conditions with low juvenile survival, burn frequency did not affect which vital rate had the largest contributions to population growth, only the magnitudes of the contributions.

Discussion

Growth rates of remnant populations of *Echinacea angustifolia* change with fire (Fig. 4), and the demographic mechanism promoting change hinges on juvenile survival. Increased seedling recruitment is important for fostering population growth when juvenile survival is high enough for

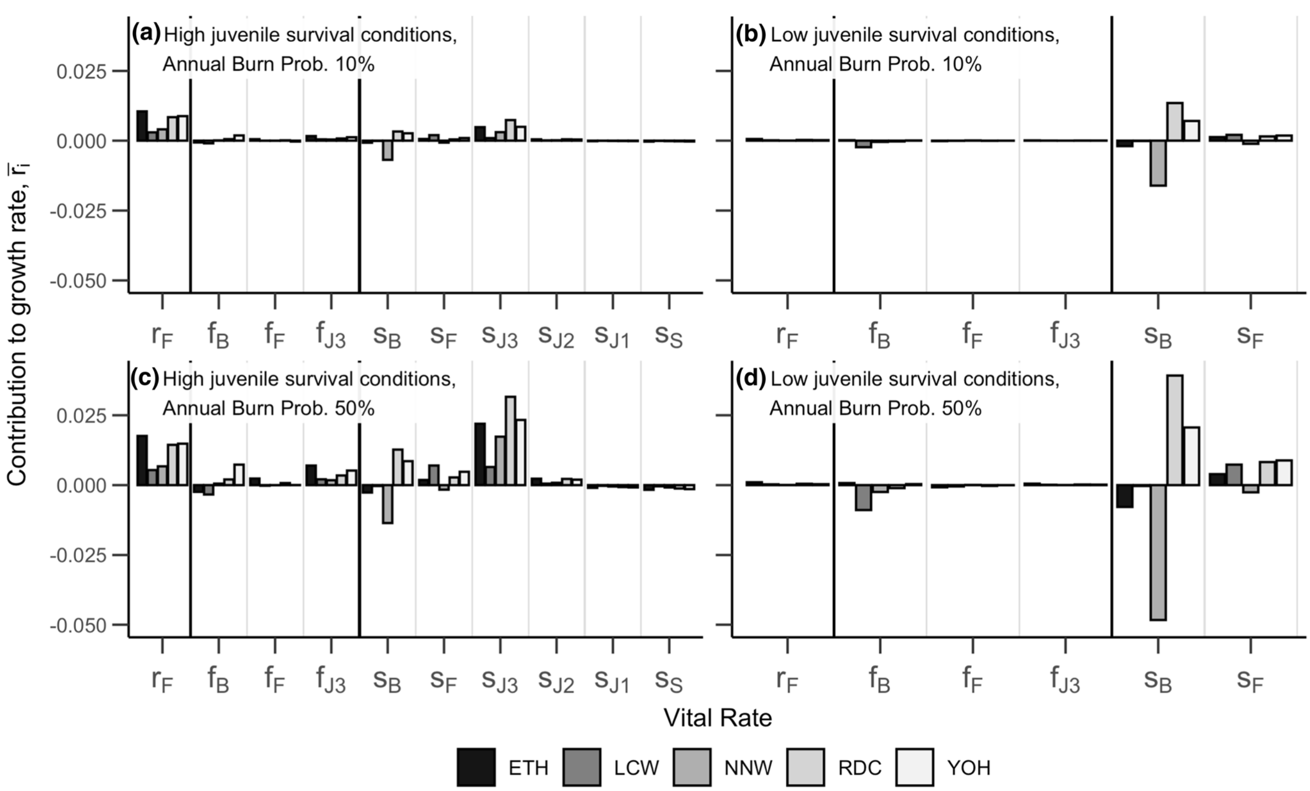


Fig. 5 Mean contribution ($\overline{r}_i$) of each vital rate to the population growth rate response to fire at **a**, **b** 10% and **c**, **d** 50% annual burn probability using two separate datasets of juvenile survival. Positive $\overline{r}_i$ implies that the effect of fire on vital rate *i* has a positive effect on population growth rates. Contributions of fire-induced changes in seedling and juvenile survival (s_S, s_{J1}, s_{J2}, and s_{J3}) were estimated only with the high juvenile survival dataset because fire's influence on these vital rates was estimated only with that dataset

new recruits to reach reproductive age (Fig. 5a,c). When few juveniles survive to reproductive age, increases in seedling recruitment have minimal effects on population growth and instead population dynamics respond more to small changes in adult survival (Fig. 5b,d).

Post-fire recruitment is important for population growth after fires

Increased seedling recruitment could result from alleviated microsite limitation, alleviated seed limitation, or both. Wagenius et al. (2020) attributed doubling of fecundity in *E. angustifolia* after fires to likely increased pollination resulting from decreased spatial isolation of plants. This demonstrates that fire alleviates seed limitation in *E. angustifolia* populations. However, the present study provides evidence of alleviated microsite limitation. We saw increased flowering in a burn year (Fig. 2), followed the next year by increased seedling recruitment. However, we saw only weak evidence of enhanced flowering one year post-burn, yet these years were also followed by years of higher seedling recruitment than non-burn years. A prior experiment showed that *E. angustifolia* seeds scattered by hand have higher establishment on recently burned sites than unburned ones (Wagenius et al. 2012), and in many grasslands, favorable post-fire recruitment conditions can persist for several years as vegetation regenerates (Morgan 1998). Thus, we expect that at least some of our observed increase in recruitment is due to multiple years of improved ground conditions for seedling recruitment, including increased sunlight (Goldberg and Werner 1983; Morgan 1998; Jutila and Grace 2002) or heat (Hulbert 1988), or alleviated competition for microsites (Münzbergová and Herben 2005). If *E. angustifolia* seeds compete for microsites, it is unlikely to be competition from conspecifics, as baseline seedling recruitment is low and we observed few cases of high-density clusters of *E. angustifolia* seedlings. Instead, limitation likely results from standing vegetation or litter from dominant grasses such as *Andropogon gerardii*, *Bouteloua curtipendula, Sorghastrum nutans,* and the non-native *Bromus inermis* in our tallgrass prairie remnants. Thus, while fire's removal of competitors, standing biomass, or litter may increase plant survival and growth (Knapp and Seastedt 1986), it also benefits plants by providing more sites for recruitment.

We found that increased flowering has modest effects on population growth (Fig. 5), but this conclusion may ignore key density-driven influences that increased flowering could have on annual seed production. The rate decomposition procedure we used measured the effects of increasing the rate of flowering while holding per-plant recruitment constant. This demonstrated that an increase in the number of flowering individuals will not supplement population growth if there is no corresponding increase in mean per-plant recruitment (Fig. 5). However, our analysis did not explicitly quantify increases in mean per-plant recruitment due to the higher density of nearby flowering plants (Wagenius et al. 2020). Increased pollination due to decreased spatial isolation (Van Nuland et al. 2013; Mola and Williams 2018), increased temporal synchrony or phenophase extension (Mola and Williams 2018; Wagenius et al. 2020) or an increase in seed quality or quantity via more genetically compatible mates (Franceschinelli and Bawa 2005) could contribute to post-fire increases in seed set in flowering plants. This is especially important for populations subject to a mate-finding Allee effect, which is common in small remnant populations in fragmented or degraded habitat (Menges 1991; Morgan et al. 2013), self-incompatible species (Levin et al. 2009), or species where individuals do not flower every year (Waananen et al. 2018). We demonstrate that with high juvenile survival, seedling recruitment is a crucial aspect of population response to fire. Partitioning fire's effects on increased recruitment into alleviated recruitment limitation (increased microsite availability and quality) and alleviated seed limitation (increased seed production and quality) is the next step in uniting our understanding of disturbance, reproductive output, and population persistence.

Our results underscore the importance of the reproductive pathway in the population dynamics of this long-lived plant. Many grassland plant populations have sporadic reproduction (Menges and Dolan 1998; Morgan 2001); this is especially true in small populations with mate-finding Allee effects (Morgan et al. 2013). Lunt and Morgan (2002) posited that fire provides a brief "window of opportunity" with conditions favorable for recruitment, thus favoring seed production. Our results support this hypothesis with the caveat that populations are only bolstered under conditions with sufficient juvenile survival. These recruitment pulses after fire are reminiscent of the Storage Effect (Warner and Chesson 1985), wherein inferior competitors avoid competitive exclusion by exhibiting high fitness when resources are abundant and being buffered from population decline when resources are scarce. In our prairie remnants, light is likely a limiting resource (Knapp and Seastedt 1986); infrequent burns create conditions favorable for recruitment while high survival buffers populations from decline when litter or competitors accumulate (Fig. 2). Other disturbances that remove vegetation and increase light availability, such as mowing or grazing (Collins et al. 1998; Borer et al. 2014), may similarly create periods favorable for reproductive activity and seedling recruitment, although grazing in our study area is associated with declining native plants and increasing non-natives. Our findings broaden our understanding of how fire benefits plant population dynamics by demonstrating that the recruitment pathway can aid populations of long-lived plants after burns.

Increased survival is important when recruitment is ineffective

In contrast to the generalization that population growth rates in long-lived plants are typically most sensitive to adult survival (Franco and Silvertown 2004; García et al. 2008), we found that adult survival had the most influence on post-fire population growth only under limited circumstances (Fig. 5). Reduced efficacy of the recruitment pathway shifts sensitivity of population growth from recruitment to adult survival. We found steadily high survival (Fig. 2), consistent with observations of García et al. (2008) that adults of long-lived species have stable survival. However, we did not find strong or consistent effects of fire on adult survival across sites. Because of the high sensitivity of $\overline{\lambda}_s$ to adult survival, site-specific responses of basal plants (s_B) contributed to population growth, but with inconsistent direction (Fig. 5b,d). The inconsistency may reflect that in four of five populations, we only have data on adult survival from one burn, confounding effects of burning and year. Adult survival also may have especially large influence because our populations are in decline ($\overline{\lambda}_s < 1$, Fig. 4). Declining populations are most sensitive to adult survival (Franco and Silvertown 2004), as small changes in survival alter the rate at which populations approach extinction. These results suggest that in threatened species with fire-stimulated recruitment, survival of adults will most strongly govern population dynamics in cases of poor recruitment or juvenile survival.

Juvenile survival is critically important for determining the effectiveness of post-fire recruitment. The high juvenile survival model estimated an average 55% probability of a seedling surviving to age eight, while the low juvenile survival model estimated an average of 3.6% for the same event. The consequence of this difference is stark: increased recruitment drove increases in population growth with high juvenile survival, but the same increases in recruitment had negligible effects on population dynamics with low juvenile survival (Fig. 5). Because these censuses were performed at different sites, site-level characteristics such as soil quality, competitor community, or herbivore density may explain differences in survival. However, seed provenance likely also contributes to these differences. Plants in the high juvenile survival dataset grew from seed collected from a large nearby population (> 100 flowering plants), while plants observed in remnant populations were likely sired from intrapopulation mating (Ison et al. 2014). Many of these remnants in the low-survival dataset are small and likely suffer from inbreeding depression. Experimentally induced inbreeding in *E. angustifolia* originating from the study area resulted in 20% lower survival of plants through age seven in natural field conditions (Wagenius et al. 2010) and lower survival and fitness throughout the life cycle of inbred plants has been observed in several other species (e.g., Menges 1991; Mannouris and Byers 2013). Grasslands are subject to fragmentation (Haddad et al. 2015) and habitat loss (Hoekstra et al. 2005), making populations residing in remnants highly susceptible to inbreeding depression. This inbreeding and the resulting fitness penalty can reduce or negate the positive effects of burning in species heavily reliant on recruitment pulses after fires.

Implications for conservation of grassland plants

Despite the increases in population growth associated with fire, we predict that all populations are declining regardless of burn frequency (Fig. 4), as did Dykstra (2013). Prior studies have found widespread species loss in tallgrass prairie, noting accelerating extinctions when fires are suppressed (Leach and Givnish 1996; Alstad et al. 2016). We found a similar pattern of faster decline in the absence of fire (Fig. 4). Our findings indicate that supplemental management strategies, in addition to controlled burning, will be needed to sustain *E. angustifolia* populations. We demonstrate that reproduction and juvenile survival are critically important life-history stages in population responses to fire, although they do not necessarily drive growth rate changes in all cases. The importance of fire effects on reproduction, recruitment, and young plants is likely relevant in grasslands worldwide, as most include populations of long-lived plants adapted to fire (Veldman et al. 2015) and continue to experience destruction and degradation (Hoekstra et al. 2005).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-021-04955-2.

Acknowledgements We express gratitude to Gretel Kiefer, Amy Waananen, and Will Reed for assisting in organizing seedling and demographic data as well as members of Team Echinacea, 1999–2016, for assisting in collecting all field data. Additionally, we thank Ruth Shaw, Daniel Doak, and Jared Beck for providing feedback on modeling and early versions of the manuscript. We finally thank land owners and agency employees for granting access to sites and Troy Boschee for providing information about burns. The Echinacea project has been supported by the NSF including awards 1557075, 1355187, 1052165, 1051791, 0545072, 0544970, and 0083468. SWN was also supported by NSF IGERT award 114807.

Author contribution statement SW and ABD planned and executed data collection. SW and SWN conceived project idea. SWN and ABD organized and prepared data. SWN designed methods, analyzed data, and wrote the first draft of the manuscript. All authors contributed substantially to subsequent editing and revision of manuscript and figures.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Data archiving We have archived all data and scripts to reproduce analysis and figures on the Echinacea Project website at http://echinaceaproject.org/datasets/nordstrom-fire-demography-2020/.

References

Alstad AO, Damschen EI, Givnish TJ, Harrington JA, Leach MK, Rogers DA, Waller DM (2016) The pace of plant community change is accelerating in remnant prairies. Sci Adv 2:e1500975

Borer EB et al (2014) Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520

Bowles ML, McBride JL, Bell TJ (2015) Long-term processes affecting restoration and viability of the federal threatened Mead's milkweed (*Asclepias meadii*). Ecosphere 6:1–22

Bürkner P (2017) brms: An R package for Bayesian multilevel models using Stan. J Stat Softw 80:1–28

Caswell H (2001) Matrix population models, 2nd edn. Sinauer Associates Inc, Sunderland

Caswell H, Fujiwara M (2004) Beyond survival estimation: mark-recapture, matrix population models, and population dynamics. Anim Biodivers Conserv 27:471–488

Caswell H, Kaye TN (2001) Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii*) in a dynamic fire regime. Adv Ecol Res 32:1–47

Collins SL, Knapp AK, Biggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in tallgrass prairie. Science 280(5364):745–747

Davison R, Jacquemyn H, Adriaens D, Honnay O, de Kroon H, Tuljapurkar S (2010) Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. J Ecol 98:255–267

de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431

Dornelas M (2010) Disturbance and change in biodiversity. Phil Trans R Soc B 365:3719–3727

Dykstra AB (2013) Seedling recruitment in fragmented populations of *Echinacea angustifolia*. PhD dissertation, Plant Biological Sciences, University of Minnesota, St. Paul, Minnesota, USA

Franceschinelli EV, Bawa KS (2005) The post-fire effects on the outcrossing rate of a Brazilian savannah shrub, *Helicteres sacarolha* A.St.-Hil. Braz J Bot 28:163–170

Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538

Gage AM, Olimb SK, Nelson J (2016) Plowprint: tracking cumulative cropland expansion to target grassland conservation. Gt Plains Res 26:107–116

García MB, Picó FX, Ehrlén J (2008) Life span correlates with population dynamics in perennial herbaceous plants. Am J Bot 95:258–262

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models, 1st edn. Cambridge Univ. Press, Cambridge, UK

Goldberg DE, Gross KL (1988) Disturbance regimes of midsuccessional old fields. Ecology 69:1677–1688

Goldberg DE, Werner PA (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). Oecologia 60:149–155

Haddad NM et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecol Lett 8:23–29

Hulbert LC (1988) Causes of fire effects in tallgrass prairie. Ecology 69:46–58

Hurlburt DP (1999) Population ecology and economic botany of *Echinacea angustifolia*: a native prairie medicinal plant. PhD dissertation, Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA

Ison JL, Wagenius S, Reitz D, Ashley MV (2014) Mating between *Echinacea angustifolia* (Asteraceae) individuals increases with their flowering synchrony and spatial proximity. Am J Bot 101:180–189

Jutila HM, Grace JB (2002) Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. J Ecol 90:291–302

Kaye TN, Pendergrass KL, Finley K, Kauffman JB (2001) The effect of fire on the population viability of an endangered prairie plant. Ecol Appl 11:1366–1380

Kimmerer RW, Lake F (2001) The role of indigenous burning in land management. J For 99(11):36–41

Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. Bioscience 36:662–668

Lamont BB, Downes KS (2011) Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. Plant Ecol 212:2111–2125

Leach MK, Givnish TJ (1996) Ecological determinants of species loss in remnant prairies. Science 273:1555–1558

Levin L, Caswell H, Bridges T, DiBacco C, Cabrera C, Plaia C (1996) Demographic responses of estuarine polychaetes to pollutants: life table response experiments. Ecol Appl 6:1295–1313

Levin DA, Kelley CD, Sarkar S (2009) Enhancement of allee effects in plants due to self-incompatibility alleles. J Ecol 97:518–527

Louthan AM, Pringle RM, Goheen JR, Palmer TM, Morris WF, Doak DF (2018) Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*. PNAS 115:543–548

Lunt ID (1994) Variation in flower production of nine grassland species with time since fire, and implications for grassland management and restoration. Pac Conserv Biol 1:359–366

Lunt ID, Morgan JW (2002) The role of fire regimes in temperate lowland grasslands of southeastern Australia. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambidge, UK, pp 177–191

Mannouris C, Byers DL (2013) The impact of habitat fragmentation on fitness-related traits in a native prairie plant, *Chamaecrista fasciculata* (Fabaceae). Biol J Linn Soc 108:55–67

Menges ES (1991) Seed germination percentage increases with population size in a fragmented prairie species. Conserv Biol 5:158–164

Menges ES, Dolan RW (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. J Ecol 86:63–78

Menges ES, Kimmich J (1996) Microhabitat and time-since-fire: effects on demography of *Eryngium cuneifolium (Apiaceae)*, a Florida scrub endemic plant. Am J Bot 83:185–191

Mola JM, Williams NM (2018) Fire-induced change in floral abundance, density and phenology benefits bumblebee foragers. Ecosphere 9:e02056

Morgan JW (1998) Importance of canopy gaps for recruitment of some forbs in *Themeda triandra*-dominated grasslands in south-eastern Australia. Aust J Bot 46:609–627

Morgan JW (2001) Seedling recruitment patterns over 4 years in an Australian perennial grassland community with different fire histories. J Ecol 89:908–919

Morgan JW, Meyer MJ, Young AG (2013) Severe habitat fragmentation leads to declines in genetic variation, mate availability, and reproductive success in small populations of a once-common Australian grassland daisy. Int J Plant Sci 174:1209–1218

Münzbergová Z, Herben T (2005) Seed dispersal, microsite, habitat and recruitment limitation: identification of terms and concepts in studies of limitations. Oecologia 145:1–8

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing.

Stan Development Team (2018) Rstan: the R interface to Stan. R package version 2.17.13. http://mc-stan.org

Supp SR, Ernest SKM (2014) Species-level and community-level responses to disturbance: a cross-community analysis. Ecology 95:1717–1723

Umbanhower CE (1996) Recent fire history of the northern Great Plains. Am Midl Nat 135:115–121

Van Nuland ME et al (2013) Fire promotes pollinator visitation: implications for ameliorating declines of pollinator services. PLoS ONE 8:e79853

Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat Comput 27:1413–1432

Veldman JW et al (2015) Toward an old-growth concept for grasslands, savannas, and woodlands. Front Ecol Env 13:154–162

Waananen A, Kiefer G, Ison JL, Wagenius S (2018) Mating opportunity increases synchrony of flowering among years more than synchrony within years in a nonmasting perennial. Am Nat 192:379–388

Wagenius S, Lonsdorf E, Neuhauser C (2007) Patch aging and the S-Allee effect: breeding system effects on the demographic effects of plants to habitat fragmentation. Am Nat 169(3):383–397

Wagenius S, Hangelbroek HH, Ridley CE, Shaw RG (2010) Biparental inbreeding and interremnant mating in a perennial prairie plant: fitness consequences for progeny in their first eight years. Evolution 64:761–771

Wagenius S, Dykstra AB, Ridley CE, Shaw RG (2012) Seedling recruitment in the long-lived perennial, *Echinacea angustifolia*: a 10-year experiment. Restor Ecol 20:352–359

Wagenius S, Beck J, Kiefer G (2020) Fire synchronizes flowering and boosts reproduction in a widespread but declining prairie species. PNAS 117:3000–3005

Warner RR, Chesson PL (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. Am Nat 125:769–787

White R, Murray S, Rohweder M (2000) Pilot analysis of global ecosystems: grassland systems. World Resources Institute, Washington, DC, USA