

# Monitoring Demography of Resurrected Populations of Locally Extinct and Extant Species to Investigate Drivers of Species Loss

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**ABSTRACT:** Extinctions are predicted to rise by an order of magnitude over the next century. Although contemporary documented extinctions are uncommon, local extirpations likely provide hints about global extinction risks. Comparing responses to global change of locally extinct versus extant species pairs in a phylogenetic framework could highlight why certain species are more vulnerable to extinction than others and which anthropogenic changes are most relevant to their decline. As anthropogenic changes likely interact to affect population declines, demographic studies partitioning the effects of multifactorial stressors are needed but remain rare. I examine demographic responses to nitrogen addition and deer herbivory, two major drivers of species losses in grasslands, in experimental reintroductions of 14 locally extinct and extant confamilial native plants from Michigan prairies. Nitrogen consistently reduces survival, especially in locally extinct species, and growth of locally extinct species benefits less from nitrogen than growth of extant species. Nitrogen reduces population growth rates, largely via reductions in survival. Deer herbivory, meanwhile, had inconsistent effects on vital rates among species and did not affect population growth. Nitrogen and herbivory rarely interacted to affect vital rates. These results link community-level patterns of species loss under nitrogen addition to the population-level processes underlying those losses.

**Keywords:** demography, extirpation, herbivory, integral projection model, nitrogen, prairie.

## Introduction

Contemporary rates of extinction are threefold higher than extinctions recorded in the fossil record (Barnosky et al. 2011; Cronk 2016). Accurately predicting local species de-

clines and ultimately extinction depends on understanding demographic responses to environmental anthropogenic change. How anthropogenic factors impact the demography of plant populations across their life cycles determines whether a population will persist under anthropogenic change (Campbell 2019). However, most work on anthropogenic stressors has focused on how targeted vital rates (e.g., germination, survival, growth, or reproduction) respond to change, but different vital rates can respond differently to environmental conditions (Stearns 1989; Villelas et al. 2015), making analyses of the net fitness effects of anthropogenic change on threatened species critical. Analyzing cumulative demographic processes rather than coarse metrics (e.g., targeted vital rates or abundance) is particularly important for long-lived native plants experiencing long periods of population decline following environmental change, potentially leading to eventual extinction (Kuussaari et al. 2009; Bialic-Murphy et al. 2019).

We still have limited insight into the population dynamics of local extinction (i.e., extirpation), which is ultimately the result of a series of reductions in vital rates leading to reduced population growth rates (Doak and Morris 1999; Collen et al. 2010). Monitoring the population demography of reintroduced extirpated species will help us understand mechanisms underlying contemporary local extinction events. Moreover, comparing the responses of locally extinct versus still-extant congeneric species could help reveal whether locally extinct or rare species have generally lower vital rates or respond differently to anthropogenic change than their more successful counterparts, independently of differences in phylogeny (Bevill and Louda 2001; Murray et al. 2014). Although this method is common in community ecology, it has rarely been applied to

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demographic studies. This approach has three key benefits. First, local population declines likely reflect global extinction risks, making population decline and local extinction events indicators of at-risk species (Menges 2000; Maschinski et al. 2005; Collen et al. 2010; Davies 2019). Second, locally extinct species represent realized, local-scale extinctions following contemporary rates of habitat loss and environmental change (Hanski and Ovaskainen 2002). Therefore, they potentially provide a more relevant picture of recent extinctions than the fossil record. Finally, examining differences between already extinct versus extant species could provide novel tests of the traits, ecological processes, and demographic mechanisms underlying recent extinctions. This approach is similar to comparisons of native versus nonnative species in that it identifies traits and responses associated with shifts in abundance, in this case, decline and eventual extirpation (van Kleunen and Richardson 2007). Comparative methods could help us understand threats to recently extirpated species and mitigate that threat for either similarly imperiled species or those same extirpated species being reintroduced to their native habitat (Caughlin et al. 2019; Williams et al. 2020). They could also determine whether some of the threats commonly correlated with species losses manifest as declines in survivorship or recruitment in areas once occupied by threatened plant species (Castro et al. 2015), potentially leading to the development of optimal conservation strategies for at-risk species (Bernardo et al. 2019).

As humans continue to alter multiple facets of the environment simultaneously, anthropogenic changes might interact to influence demography. Demographic studies that experimentally manipulate multiple variables can partition the individual and nonadditive effects of co-occurring anthropogenic factors, allowing for more accurate estimations of population viability (Tye et al. 2016; Bialic-Murphy et al. 2019; Morris et al. 2020). In one of the few demographic studies examining multiple drivers of population decline, climate warming threatens *Eurybia furcata* but only when woody encroachment and deer herbivory are high (Bernardo et al. 2018). Interactions among threats can complicate conservation for threatened species (e.g., extirpated species) because it becomes difficult to disentangle which anthropogenic factor(s) might have the greatest impact (Bernardo et al. 2019).

Nitrogen addition and deer herbivory are two anthropogenic factors likely to nonadditively influence prairie plant population declines in temperate North America. In addition to causing habitat loss, changes in land use have increased both nutrient levels and herbivore populations in remaining prairie habitat (Borer et al. 2014; Payne et al. 2017; Laurent et al. 2021). Nitrogen is a leading driver of biodiversity loss in grasslands (Suding et al. 2005; Clark et al. 2007; Clark and Tilman 2008; Borer et al. 2014; Hodapp

et al. 2018), and high nitrogen levels can depress population growth rates (e.g., *Sphagnum* spp. [Press et al. 1986], *Calluna* spp. [Heil and Diemont 1983], and *Sarreccenia purpurea* [Gotelli and Ellison 2002]; note that these are unique taxa that are susceptible to nitrogen). Conversion of land for agriculture, extirpation of large predators, and hunting regulations also result in increased populations of white-tailed deer (*Odocoileus virginianus*); the subsequent herbivory can cause population declines (Knight et al. 2009; Kalisz et al. 2014; Bialic-Murphy et al. 2019), especially for rare and threatened species (Phillips and Maun 1996; Pruszenski and Hernández 2020). These two drivers may interact via several potential mechanisms. First, herbivores might consume more fast-growing, high-nutrient species under nitrogen-enriched conditions, exacerbating species loss under nitrogen addition. Alternatively, herbivores can theoretically maintain local plant diversity (Holt et al. 1994). Herbivores can alleviate some of the negative effects of nitrogen by consuming plant biomass, increasing ground-level light availability, and preventing competitive exclusion of inferior competitors (e.g., short-statured plants or those earlier in their life cycles) by dominant species (Hautier et al. 2009; Borer et al. 2014). Finally, nitrogen and herbivory can have both positive effects and negative effects across plant ontogeny. For example, nitrogen might affect plants at different stages, including growth, reproduction, and seed set (Munoz et al. 2005; Burkle and Irwin 2010), while deer herbivory can increase survival but decrease growth and reproduction (Bialic-Murphy et al. 2019). Understanding demographic responses to nitrogen and herbivory across a plant's entire life cycle could thus inform which life stages are most susceptible to each factor and provide a comprehensive assessment of extinction risk under interacting anthropogenic changes.

I experimentally manipulated nitrogen and deer access in the field to test how two major anthropogenic stressors affect the population demography of nine confamilial (often congeneric) pairs of still extant versus locally extinct prairie species once found in Michigan prairies and savannas. I ask the following questions. First, how do vital rates (survival, growth, reproduction, and recruitment) respond to nitrogen addition and deer herbivory, and do these responses differ between locally extinct and extant species? Second, I use integral projection models (IPMs) and life table response experiment (LTRE) analyses to ask how nitrogen addition and deer herbivory affect population growth rates ( $\lambda$ ) for a subset of species with sufficient vital rate data. The LTREs also allow me to estimate how each vital rate contributes to the effects of nitrogen and herbivory on  $\lambda$ . The nitrogen  $\times$  herbivory experiment includes high (agronomic) levels of fertilization, but the environmental and demographic effects of lower rates of nitrogen addition that characterize most habitats are less well studied (Clark

and Tilman 2008; Pardo et al. 2011), even though many grassland species disappear at lower levels of nitrogen addition (Simkin et al. 2016). Third, to test how even low rates of nitrogen deposition affect demography, I conducted a second nitrogen gradient experiment to tease apart locally extinct versus extant prairie species' vital rate responses to increasing levels of nitrogen deposition, asking how vital rates respond to a gradient of nitrogen addition. I predicted that nitrogen would benefit plant growth and reproduction, given that plants are often nitrogen limited, but decrease survival owing to increased biomass of background vegetation and that herbivory would decrease survival, growth, and reproduction through direct consumption. I also predicted that nitrogen and herbivory would have negative effects on plant population growth rates via reduced survival. However, the combination of nitrogen and deer presence might alleviate reductions in population growth rates for these short forb species if herbivory releases individuals from competition. Finally, I expected that locally extinct species would experience more pronounced declines under each treatment if nitrogen or herbivory contributed to their loss.

## Material and Methods

### Study System

Kalamazoo County, covering 1,492 km<sup>2</sup> in southwestern Michigan has lost 99% of its native prairie habitat from 1800 to 2004, with only 130 of its original 21,500 acres remaining (Chapman and Brewer 2008; Zettlemoyer and Srodes 2019). The county has lost 14.01% of its native prairie species during a similar time frame (1890–2004), mostly rare perennial forbs that are prairie specialists (Hanes and Hanes 1947; McKenna 2004; Zettlemoyer et al. 2019). Although habitat loss is certainly a significant driver of species loss in the area, more species have been lost than predicted (i.e., according to the species-area relationship, 164 prairie species should remain, but only 141 do; Zettlemoyer and Srodes 2019). This suggests that other anthropogenic factors beyond habitat loss, such as nitrogen addition and deer herbivory, may play a role in plant extinctions in this area. Soil nitrogen levels in Michigan are high owing to nitrogen deposition and agricultural fertilization. Nitrogen deposition in Michigan is higher than the US average (MI: 0.5–0.7 g N m<sup>-2</sup> year<sup>-1</sup> [Pardo et al. 2010]; US: 0.1–0.4 g N m<sup>-2</sup> year<sup>-1</sup> [Fenn et al. 2003]). Agricultural nitrogen fertilization recommendations range from 0.67 to 20 g N m<sup>-2</sup> year<sup>-1</sup> (Warncke et al. 2009). Grassland species are more susceptible to nitrogen-induced declines and disappear at lower levels of nitrogen deposition relative to species from other habitat types (Simkin et al. 2016). Simultaneously, white-tailed deer populations in Michigan began

increasing in the 1890s following hunting regulations, rising to 1.5 million statewide in the late 1940s and peaking at 2.2 million in 1995 (MI DNR 2016), matching the period of species decline examined here (1890–2004).

Studies were conducted in restored prairies at the Boudeman Conservation Farm (BCF; Richland, MI) and the Kalamazoo Nature Center's Kal-Haven Prairie (KHP; Kalamazoo, MI). Both prairies were burned for management in fall 2016, just before the start of this experiment. BCF is ~20 years old, dominated by *Andropogon gerardii*; KHP is ~10 years old, dominated by *Sorghastrum nutans*.

### Nitrogen Addition × Deer Herbivory Experiment

In 2017 I set up a 2 × 2 split-plot experiment manipulating deer herbivory and nitrogen addition. To exclude deer, I constructed 10-ft-high deer fencing around the perimeter of five randomly selected 9 × 9-m whole plots at each site. Five additional 9 × 9-m whole plots per site served as herbivore present controls ( $n = 10$  whole plots/site [5 fenced and 5 unfenced] × 2 sites = 20 whole plots). I applied nitrogen (44% time-release urea) at 10 g m<sup>-2</sup> year<sup>-1</sup> (elemental mass: 22.73 g m<sup>-2</sup> year<sup>-1</sup>) to a randomly selected 4.5 × 9-m subplot within each whole plot ( $n = 40$  subplots; Nutrient Network). Nitrogen addition significantly increased productivity (total aboveground biomass) and decreased light availability (fig. S1).

To test how locally extinct versus extant species' vital rates respond to nitrogen and deer herbivory, I selected eight confamilial pairs and one triplet of native, perennial, prairie specialist forbs in which one (two for the triplet) species is “locally extinct” (defined here as species that have disappeared from a particular county; Pimm et al. 2014), while the other persists (“extant”; supplement S1, table S1.1). The species selected represent all possible locally extinct species that are native, perennial, prairie specialist forbs. I selected prairie specialists because they are at higher risk of loss than species that can persist in other habitat types (Zettlemoyer et al. 2019) and so that differences in habitat affinity (i.e., the ability to persist in different habitat types) are not confounded with extinction. I selected perennial species because they are more likely to demonstrate delayed extinctions following environmental change (Vellend et al. 2006) and delayed responses to nitrogen addition (Monaco et al. 2003) and because annuals are rare in older prairies. For each locally extinct species, I then selected the most closely related extant species that was also a native, perennial, prairie specialist forb. Seeds were sourced from nurseries as locally to Michigan as possible and always from a midwestern seed source (nurseries in order of selection: Michigan Wildflower Farm, Portland, MI; Naturally Native Nursery, South Bend, IN; Agrecol,

Edgerton, WI; Prairie Moon, Winona, MN). I chose to use nurse-propagated seeds because they would not be locally adapted to experimental sites, which could influence plant responses to environmental conditions (Ehrlén et al. 2016). In spring 2017 I sowed all 17 species in low-nutrient potting media (Sunshine Mix LP5) in the greenhouse. Fourteen species successfully germinated. I transplanted 6-week-old seedlings of those species into randomly selected field locations (planted 40 cm apart) within each subplot ( $n = 10$  seedlings/species/subplot  $\times$  40 subplots  $\times$  14 species = 5,600 seedlings). I included a 40-cm buffer area from the fences to control for edge and shading effects.

I monitored vital rates of all individuals from spring 2017 to fall 2019. Vital rates included survival, growth, reproductive status, flower production, seed production, and recruitment. Seedlings were considered dead if they were not found in two subsequent yearly surveys. Plant size was measured as height (cm) to the highest photosynthetic leaf. A plant was considered reproductive if it produced any flowers during a given year. Flower production was measured as the total number of flowers produced by an individual over a single growing season. Seed production was measured two ways: (i) number of seeds produced per fruit, estimated by sampling one fruit from each reproductive plant, and (ii) total number of seeds produced per plant, estimated as number of seeds/fruit  $\times$  number of flowers produced. Seed production may be overestimated because I did not estimate how many flowers matured into fruits.

To determine recruitment (germination), I established a seed addition experiment in October 2019 at BCF. I sowed 100 seeds/species into a circular ring (0.5 m in diameter  $\times$  8 cm deep) surrounded with aluminum flashing into each subplot ( $n = 100$  seeds/species/ring  $\times$  1 ring/subplot  $\times$  20 subplots = 2,000 seeds/species  $\times$  17 species = 34,000 seeds). I left 4 cm of flashing above the soil to prevent seeds from washing away. I marked germinated seedlings weekly in May 2020 ( $n = 4$  surveys) to estimate germination (“recruits” = number of seeds germinated/100 seeds sown) and germinant mortality (number of dead recruits/total recruits over the month) under each nitrogen  $\times$  herbivory treatment combination.

#### *Nitrogen Gradient Experiment*

To examine whether nitrogen levels from natural deposition (0 g N added) to agricultural fertilization (12 g N m<sup>-2</sup> year<sup>-1</sup>) influence vital rates, I set up a nitrogen gradient experiment at BCF in unfenced plots. Nitrogen was applied to 3-m<sup>2</sup> plots (all separated by 3 m) at six levels: 0, 1, 2, 4, 8, and 12 g m<sup>-2</sup> year<sup>-1</sup>. Nitrogen decreased light availability (fig. S2). A subset of species, the three confamilial pairs and one triplet ( $n = 9$  species) with high survival in the

nitrogen  $\times$  herbivory experiment, were included in this experiment (table S1). Seedlings were germinated in the greenhouse (see above) and transplanted into random locations within each field plot ( $n = 10$  seedlings/species/plot  $\times$  6 N levels  $\times$  3 plots/N level  $\times$  9 species = 1,620 seedlings). Vital rates were determined as described previously from 2018 to 2020.

#### *Data Analysis*

*Vital Rates of Locally Extinct versus Extant Species.* I used census data to fit statistical models for six vital rates that together influence population dynamics: (1) survival (1 = alive, 0 = dead), (2) growth (height in year  $t + 1$ ), (3) probability of flowering (1 = flowered, 0 = did not flower), (4) flower production (number of flowers/plant), (5) seed production (see below), and (6) recruitment (proportion of seeds germinated). I fitted all generalized linear mixed models (GLMMs) using the lme4 package in R version 4.0.4 (Bates et al. 2015; R Core Team 2021), using orthogonal, ordered contrasts for a factorial design. Because of low survival at KHP, potentially due to seedlings rotting under large amounts of white clover (*Trifolium repens*) at KHP in 2018 (subsequently limiting sample size and affecting growth and reproduction estimates), I present vital rate models using data only from BCF in the article; models including KHP are included in table S1.2.

To test treatment effects on survival, I included survival as a binomial response variable and height (cm) in year  $t$  (height <sub>$t$</sub> ; ln transformed to meet assumptions of normality here and in all models hereafter), nitrogen (nitrogen vs. control), herbivory (herbivory vs. fenced), local extinction status (locally extinct vs. extant), and their interactions as predictor variables. Year (2017–2019) was included as a fixed factor to control for temporal variation. However, because of the cohort design of this study, year may account for variation in environmental conditions or changes in plant size and ontogeny. I included species (nested within phylogenetic pair [family or genus], nested within status; pair is included to ensure comparisons are within each phylogenetic contrast) and subplot (nested within nitrogen [treatment at the split-plot level], nested within plot, nested within herbivory [treatment at the whole-plot level]) as random intercepts. I included species-specific random slopes for height <sub>$t$</sub>  (i.e., height <sub>$t$</sub> |species) to control for species-specific differences in changes in vital rates with height. To test treatment effects on growth, I used a linear mixed model with the same predictors and random effects described. I also conducted all models excluding the three extra extant species (table S1.1); results are qualitatively similar (table S1.3). I tested treatment effects on reproduction using four metrics: (1) probability of flowering (binomial

distribution), (2) flower production (number of flowers produced; beta distribution), (3) seed production (number of seeds produced/fruit and number of seeds produced/plant), and (4) recruitment (Poisson distribution). Reproductive models included only species that flowered (*Monarda fistulosa*, *Pycnanthemum tenuifolium*, *Penstemon digitalis*). For probability of flowering and recruitment, I used the same fixed effects and random intercepts described above. For flower and seed production, because of low sample sizes within species, I normalized the data using feature scaling (Legendre and Legendre 2012), resulting in values between zero and one (wherein plants with a value close to one had high reproduction, and plants with a value close to zero had low reproduction). Because the data were left skewed with a long tail, I used a beta distribution (Damgaard and Irvine 2019). I included flower or seed production as separate response variables; height, nitrogen, herbivory, status, and their interactions as predictor variables; and subplot (nested in plot) as a random factor.

In the nitrogen gradient experiment, I again analyzed vital rates using separate GLMMs. I included height, nitrogen (continuous, 0–12 g N m<sup>-2</sup> year<sup>-1</sup>), status, and their interactions as predictor variables; year (2018–2020) as a fixed factor; species (nested in pair, nested in status) and plot (nested in nitrogen treatment) as random intercepts; and species-specific random slopes for height. I hypothesized that vital rates would demonstrate a unimodal response to nitrogen addition and so included a quadratic term (nitrogen<sup>2</sup>) in all models. In this experiment, five species flowered (*M. fistulosa*, *P. tenuifolium*, *P. digitalis*, *Penstemon hirsutus*, *Penstemon pallidus*) and were included in reproductive models. Data for this study have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.xwdbrv1dd>; Zettlemoyer 2022).

**Population Modeling.** To build species-specific IPMs from all data sources, I examined the vital rates described above for each species separately using models similar to those described above. I used these size-dependent, species-specific vital rate models (supplement S2) to parameterize IPMs for the species that had sufficient survival, growth, and reproductive data (three in the nitrogen × herbivory experiment [ $n = 2$  extant, 1 locally extinct]; five in the nitrogen gradient [ $n = 2$  extant, 3 locally extinct]). Because IPMs were conducted only on the subset of species that flowered, I did not have sufficient statistical power to statistically compare population growth rates between locally extinct versus extant species. Therefore, these IPMs test how nitrogen addition and deer herbivory affect population growth rates ( $\lambda$ ) for a subset of species and how each vital rate contributes to the effects of nitrogen and herbivory on  $\lambda$ .

IPMs integrate contributions from vital rates across a continuous range of plant sizes (here, height) to predict population growth in discrete time steps (year  $t$  to  $t + 1$ ; Easterling et al. 2000; Ellner and Rees 2006). By integrating across a survival-growth kernel and a reproductive kernel, IPMs produce a projection kernel that describes all possible combinations of size-dependent demographic parameters. Briefly, I included the probability that an  $x$ -sized plant survives from year  $t$  to  $t + 1$  and grows from size  $x$  to size  $y$  in the survival-growth kernel. In the reproductive kernel, I included the probability of an  $x$ -sized individual producing flowers, flower and seed production of an  $x$ -sized plant conditional on flowering, and recruitment (from the seed addition experiment). For recruitment, I included new recruits (number of seeds germinated/100 seeds sown), probability of germinant mortality (dead recruits/total recruits), and an estimate of seed predation (i.e., proportion of seeds removed by small mammals and arthropods) from a separate seed predation study (Johnson and Zettlemoyer 2022; tables S2.2, 2.4). I included seed predation because plots were fenced but not trenched, allowing small mammals and arthropods to consume seeds. Because recruitment did not differ across experimental treatments, I used species means for recruitment terms (tables S2.2, 2.4). The size distribution of new seedlings was the mean and standard deviation of first-year seedlings. The 95% confidence intervals were estimated using parametric bootstrapping ( $n = 1,000$  iterations). See supplement S3 for details on IPM construction. Deterministic estimates of  $\lambda$  can be adequately estimated with a 3-year study (Jonjégans et al. 2011; Crone et al. 2013). However, because results are from two small experimental founder populations, I focus on differences in  $\lambda$  between treatments, not absolute values of  $\lambda$ , in “Results.”

To test for consistent effects of nitrogen and herbivory on  $\lambda$ , I used a linear mixed model with  $\lambda$  as the response variable; nitrogen, herbivory, and their interactions as predictor variables; and species as a random effect. For the nitrogen gradient experiment, I conducted similar IPMs and examined  $\lambda$  as a function of nitrogen and nitrogen<sup>2</sup>, with species included as a random effect.

Finally, I used a LTRE to quantify the contributions of each vital rate to observed differences in  $\lambda$  (Horvitz et al. 1996; Caswell 2001). The difference in  $\lambda$  between the control experiment and a treatment was calculated as the difference in a vital rate between the treatment and control matrices times the sensitivity of  $\lambda$  to changes in that vital rate (here, a perturbation of 0.01). A negative LTRE contribution indicates that the value of that vital rate under that experimental treatment is lower than the control (i.e., a negative contribution of nitrogen to survival means that the probability of survival from year  $t$  to  $t + 1$  is lower under nitrogen addition).

**Results**

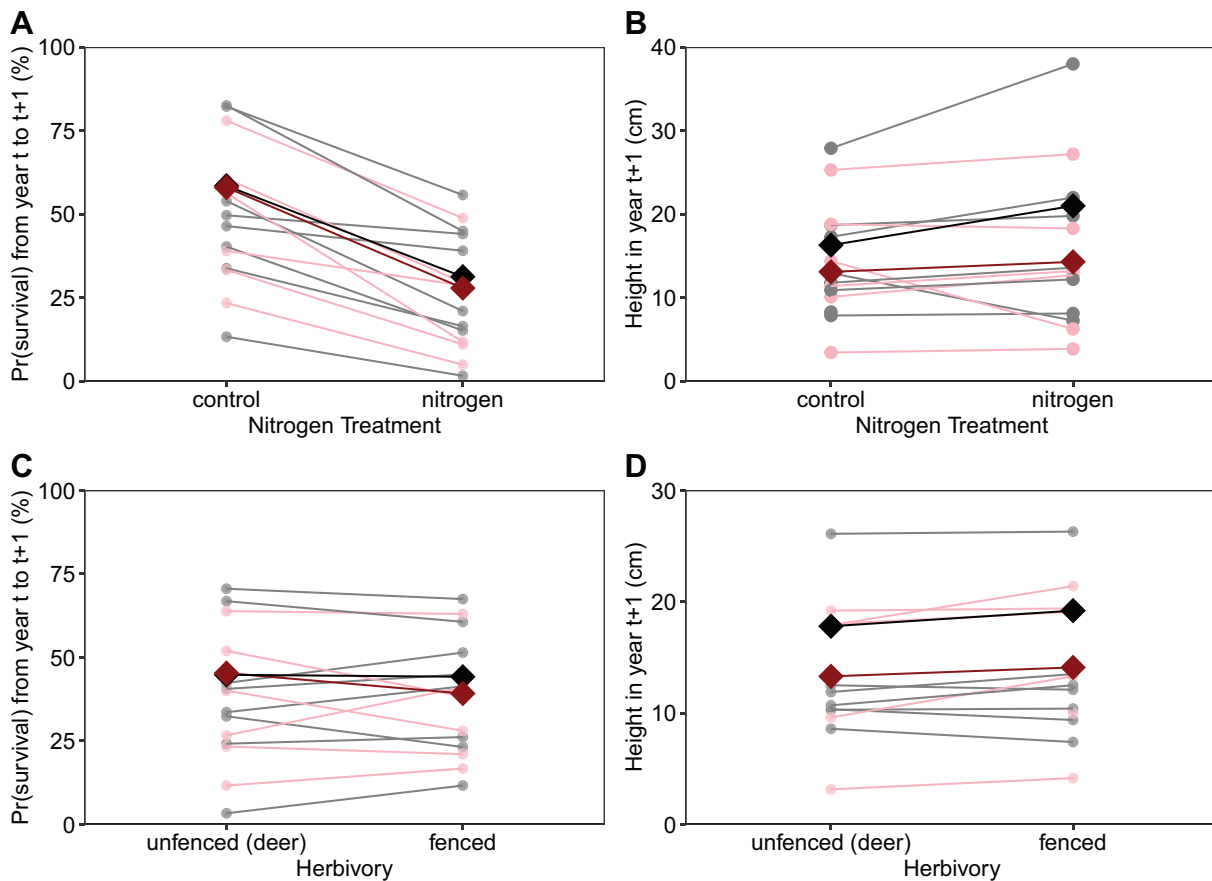
*Effects of Nitrogen on Locally Extinct versus Extant Species' Vital Rates*

*Nitrogen × herbivory experiment.* Nitrogen decreased survival, especially for locally extinct species ( $N \times \text{status}$ :  $\chi^2_{1,4,873} = 4.9$ ,  $P = .03$ ; table S1.4; fig. 1A). While locally extinct and extant species both had approximately 57% survival under the control treatment, locally extinct species had only 23.7% survival compared with 31.3% survival of extant species under nitrogen addition. Tall plants had higher survival under nitrogen addition but not in control plots ( $N \times \text{height}$ :  $\chi^2_{1,4,648} = 33.58$ ,  $P < .0001$ ; table S1.4; fig. 2A). Within species (i.e., species-specific models), nitrogen significantly decreased survival in four of six locally extinct species and in four of eight extant species (significant nitrogen × height or nitrogen terms; table S2.1),

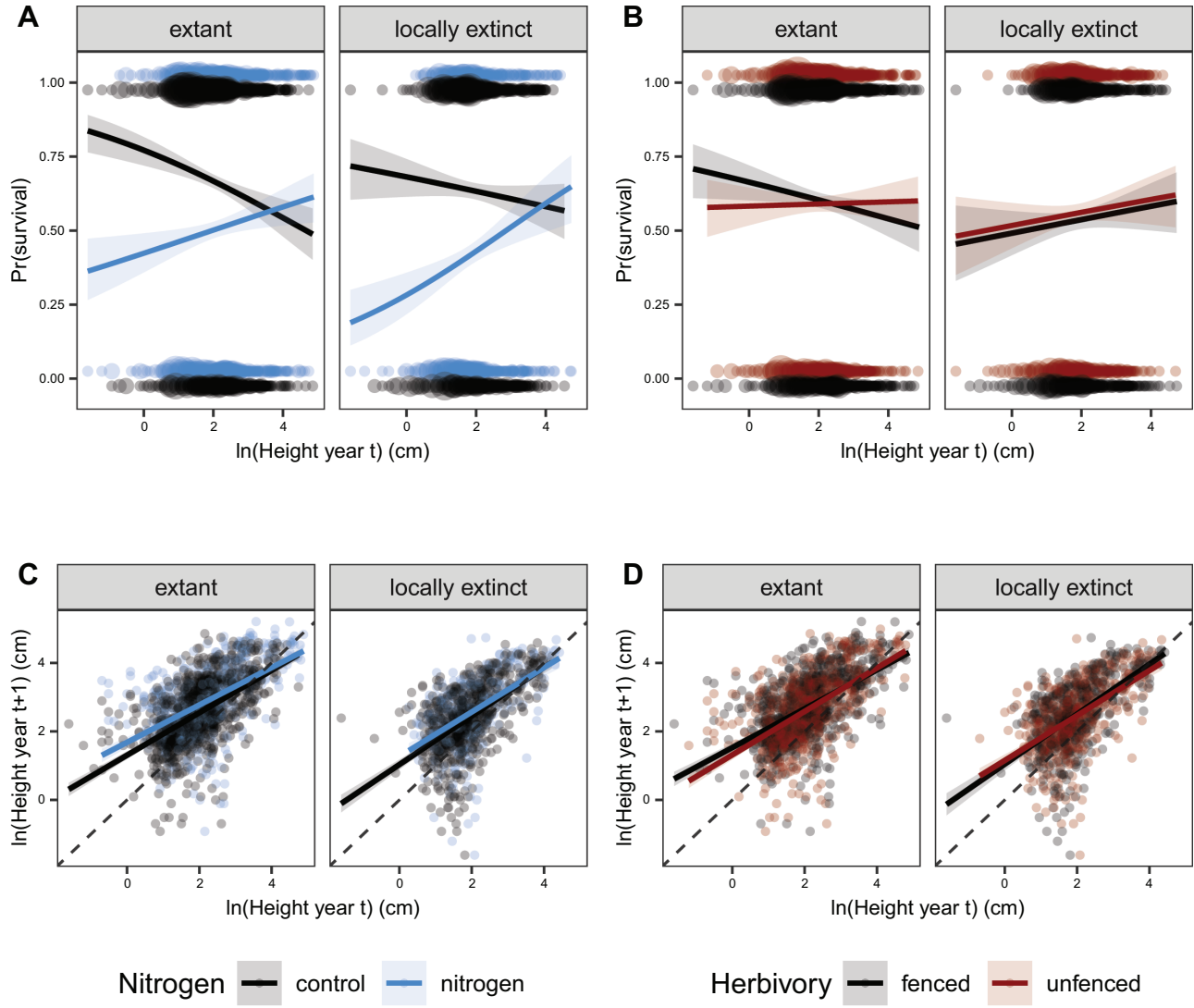
and all remaining species exhibited nonsignificant trends toward lower survival under nitrogen addition (fig. S3).

Nitrogen increased size-dependent growth rates in both locally extinct and extant species ( $\chi^2_{1,2,645} = 13.45$ ,  $P = .0002$ ; table S1.4; fig. 2B). However, extant species' growth benefited more from nitrogen than locally extinct species' growth ( $N \times \text{status}$ :  $\chi^2_{1,2,811} = 7.47$ ,  $P = .006$ ; table S1.4; fig. 1B). Extant species grew 48% larger under nitrogen addition relative to control plots, while locally extinct species grew only 34% larger under nitrogen addition. Within species, four of eight extant species and one of six locally extinct species' growth significantly benefited from nitrogen, and nitrogen generally increased growth in all other species except *Baptisia* (fig. S4; table S2.1).

Nitrogen increased the probability of flower production in tall extant species, whereas tall locally extinct species were less likely to flower under nitrogen addition than in control



**Figure 1:** Locally extinct and extant species differ in their survival and growth responses to nitrogen (*top*) and deer herbivory (*bottom*; nitrogen × herbivory experiment). A and C show probability of survival (Pr[survival]; %), and B and D show growth (change in height from year  $t$  to  $t + 1$ , averaged across years; cm) for locally extinct (pink) and extant (gray) species in control versus nitrogen addition (A, B) or unfenced (deer herbivory) versus fenced plots (C, D). Values are least squares means after adjusting for random effects. Each connected line represents a confamilial pair. Large red and black diamonds represent overall means for locally extinct and extant species, respectively. The two species that respond negatively to nitrogen in B are the two *Baptisia* (Fabaceae) species.

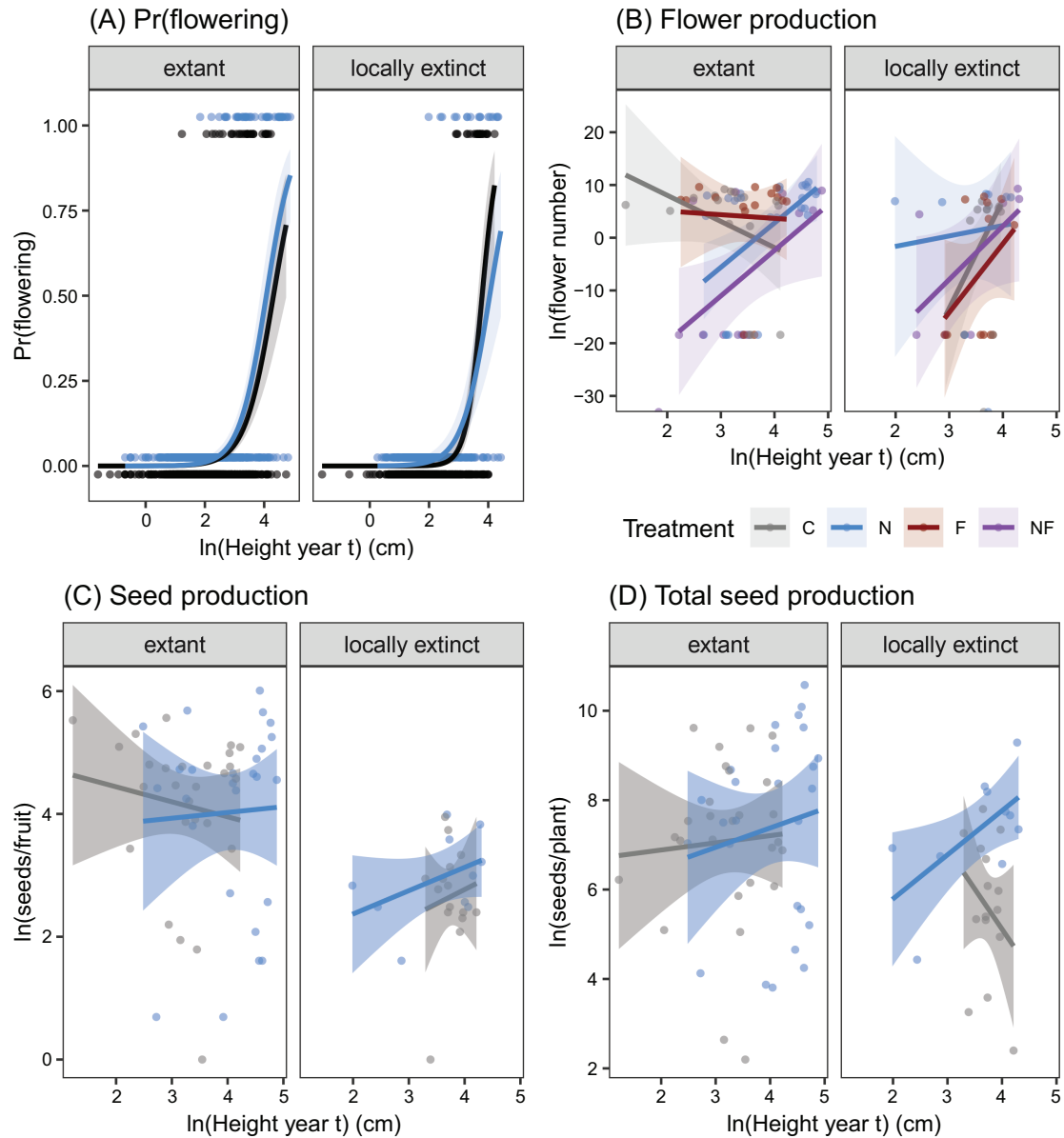


**Figure 2:** Effect of nitrogen addition ( $10 \text{ g N m}^{-2} \text{ year}^{-1}$ ; A, C) and deer herbivory (B, D) on size-dependent probability of survival ( $\text{Pr}[\text{survival}]$ ; A, B) and growth ( $\ln[\text{height in year } t + 1]$ ; cm; C, D) in extant versus locally extinct species. Size is height in year  $t$  (cm;  $\ln$  transformed). Shaded areas represent 95% confidence intervals. Dot sizes in A and B are scaled by the number of individuals of that height. The dashed lines in C and D represent 1:1 growth.

conditions (height  $\times$  N  $\times$  status:  $\chi^2_{1,1657} = 5.59, P = .02$ ; tables S1.5, S2.2; figs. S5, 3A). Reproductive effort depended on a complex interaction between height, status, nitrogen, and herbivory (height  $\times$  N  $\times$  herbivory  $\times$  status:  $\chi^2_{1,96} = 5.55, P = .02$ ; table S1.5, S2.2; figs. S6, 3B). Nitrogen addition increased size-dependent flower production in both locally extinct and extant species. In locally extinct species, nitrogen increased flower production, while fencing decreased flower production relative to the control treatment. Nitrogen increased size-dependent seed production (seeds/fruit and seeds/plant), especially in locally extinct species (height  $\times$  N  $\times$  status: for seeds/fruit,  $\chi^2_{1,94} =$

$7.55, P = .006$ ; for seeds/plant,  $\chi^2_{1,94} = 4.14, P = .04$ ; tables S1.5, S2.2; figs. S7, S8, 3C, 3D).

*Nitrogen gradient experiment.* Nitrogen increased survival of tall plants until about  $6 \text{ g N m}^{-2}$ , after which point survival declined (height  $\times$  N<sup>2</sup>:  $\chi^2_{1,3854} = 12.19, P = .0005$ ; table S1.6; fig. 4A). Within species, this relationship was statistically supported in three of four locally extinct and two of three extant species, but all species tended to demonstrate this pattern (table S2.3; fig. S9A). Nitrogen addition also decreased survival of small plants, especially in locally extinct species (N  $\times$  status  $\times$  height:  $\chi^2_{1,3852} = 25.3, P < .0001$ ). Growth increased with nitrogen addition



**Figure 3:** Effects of nitrogen and herbivory on size-dependent reproduction in extant versus locally extinct species. *A*, Nitrogen increases probability of flowering ( $\text{Pr}[\text{flowering}]$ ) in tall extant, but not locally extinct, species. *B*, Differences in flower production ( $\ln[\text{number of flowers}]$ ) across all treatments (gray indicates control [C; no nitrogen, deer present]; blue indicates nitrogen addition [N;  $10 \text{ g N m}^{-2} \text{ year}^{-1}$ ]; red indicates fenced [F]; purple indicates nitrogen addition and fenced [NF]). Nitrogen addition increases seed production, especially in locally extinct species (*C* shows number of seeds/fruit; *D* shows number of seeds/plant; both  $\ln$  transformed). Size is plant height (cm) in year  $t$  ( $\ln$  transformed). Shaded areas represent 95% confidence intervals.

until about  $6 \text{ g N m}^{-2}$ , after which growth benefits tapered off ( $N^2: \chi^2_{1,298.9} = 3.97, P = .04$ ; table S1.6; fig. 4B). This relationship was supported in only two extant species: *Monarda fistulosa* and *Penstemon digitalis* ( $N^2$ : for *M. fistulosa*,  $\chi^2_{1,161.66} = 4.34, P = .04$ ;  $N^2 \times \text{height}$ : for *P. digitalis*,  $\chi^2_{1,471.17} = 5.44, P = .02$ ; table S2.3; fig. S9B).

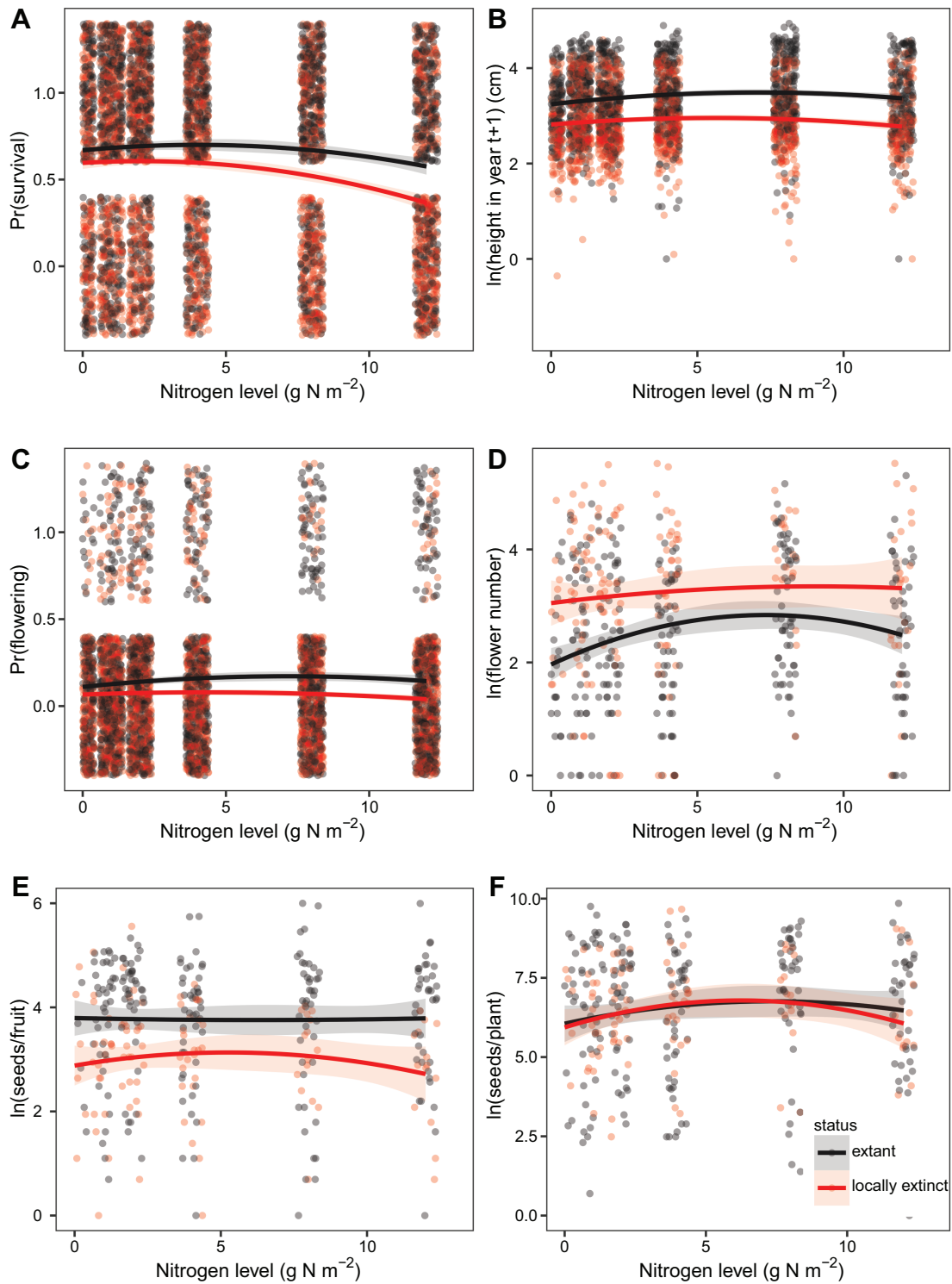
I detected no overall effects of a nitrogen gradient on reproductive vital rates (tables S1.7, S2.4; fig. S9). Extant

species tended to produce more seeds/fruit than locally extinct species ( $\chi^2_{1,467} = 2.24, P = .1$ ; fig. 4E).

#### *Effects of Deer Herbivory on Locally Extinct versus Extant Species' Vital Rates*

Deer herbivory had variable effects on survival and growth (fig. 1C, 1D). First, tall plants had higher survival





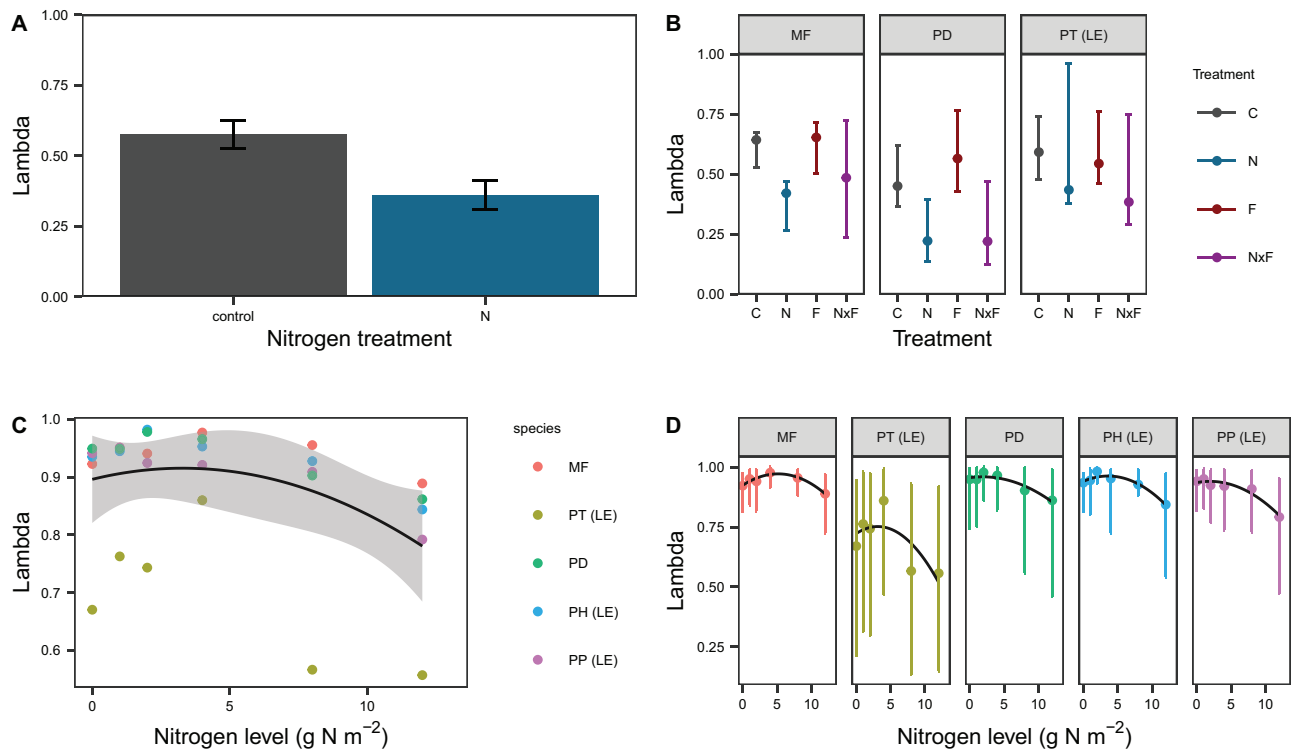
**Figure 4:** Effect of a gradient of nitrogen addition (0–12 g N m<sup>-2</sup> year<sup>-1</sup>) on probability of survival (Pr[survival]) from year  $t$  to  $t + 1$  (jittered points; A), growth from year  $t$  to  $t + 1$  (cm; ln transformed; B), probability of flowering (Pr[flowering]) in year  $t + 1$  (jittered points; C), reproductive effort in year  $t + 1$  (ln[number of flowers produced]; D), reproductive output in year  $t + 1$  (ln[number of seeds/fruit]; E), and total reproductive output in year  $t + 1$  (ln[number of seeds/plant]; F) in extant (black) versus locally extinct (red) species. Lines show quadratic model fit. Shaded areas represent 95% confidence intervals.

when deer were present (height × herbivory:  $\chi^2_{1,4865} = 4.25$ ,  $P = .04$ ; table S1.4; fig. 2C). Within species, tall individuals experienced greater survival when deer were present in locally extinct *P. digitalis* and extant *Ratibida pinnata* (height × herbivory: for *P. digitalis*,  $\chi^2_{1,694.52} = 8.64$ ,  $P = .003$ ; for *R. pinnata*,  $\chi^2_{1,531.38} = 3.95$ ,  $P = .04$ ; table S2.1; fig. S10). In extant *P. digitalis*, survival decreased with height where deer were excluded (height × herbivory:  $\chi^2_{1,902.35} = 7.75$ ,  $P = .005$ ). Herbivory decreased survival of extant *Eryngium yuccifolium* and locally extinct *Silphium terebinthinaceum* but increased survival of locally extinct *Baptisia bracteata* (herbivory: for *E. yuccifolium*,  $\chi^2_{1,122.83} = 5.60$ ,  $P = .02$ ; for *S. terebinthinaceum*,  $\chi^2_{1,87.76} = 3.43$ ,  $P = .06$ ; for *B. bracteata*,  $\chi^2_{1,500.43} = 4.88$ ,  $P = .03$ ; table S2.1; fig. S10). In *Silphium perfoliatum*, herbivory decreased survival, especially when nitrogen was added (nitrogen × herbivory:  $\chi^2_{1,668.55} = 5.61$ ,  $P = .02$ ; table S2.1; fig. S11). Second, deer exclusion increased size-dependent

growth (height × herbivory:  $\chi^2_{1,2815} = 4.14$ ,  $P = .04$ ; table S1.4; fig. 2D). Within species, deer exclusion increased growth in extant *R. pinnata* and tall *S. perfoliatum* (herbivory: for *R. pinnata*,  $\chi^2_{1,129.57} = 7.22$ ,  $P = .007$ ; height × herbivory: for *S. perfoliatum*,  $\chi^2_{1,342.05} = 5.35$ ,  $P = .02$ ; table S2.1; fig. S12). Herbivory increased growth in tall *M. fistulosa* (height × herbivory:  $\chi^2_{1,517.91} = 4.70$ ,  $P = .03$ ; table S2.1; fig. S12). Finally, tall plants were more likely to flower when deer were present (height × herbivory:  $\chi^2_{1,517.91} = 3.77$ ,  $P = .05$ ; fig. S13).

*Integral Projection Models and Life Table Response Experiment*

Averaged across three species, nitrogen addition reduced population growth rates by 63% (N:  $\chi^2_{1,8} = 43.57$ ,  $P < .0001$ ;  $\lambda_{\text{control}} = 0.58 \pm 0.05$  vs.  $\lambda_{\text{nitrogen}} = 0.36 \pm 0.05$ ; table S1.8; fig. 5A, 5B). Reduced survival under nitrogen



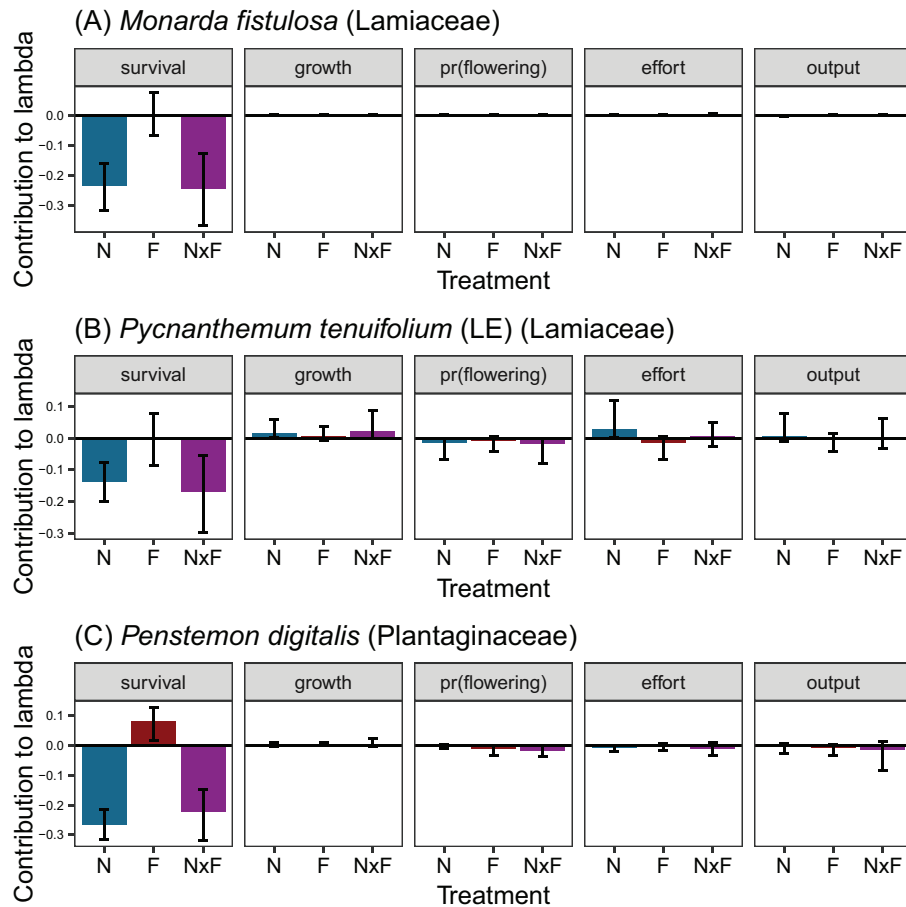
**Figure 5:** Nitrogen addition reduces population growth rates. A, Population growth rates ( $\lambda$ ) under control versus nitrogen addition (least squares means  $\pm$  SE). B, Values of  $\lambda$  for *Monarda fistulosa* (MF), *Pycnanthemum tenuifolium* (PT), and *Penstemon digitalis* (PD) under each experimental treatment (C = control [no nitrogen, deer]; N = nitrogen [nitrogen, deer]; F = fenced [no nitrogen, fenced]; N × F = nitrogen × fenced; LE = locally extinct species). Values are means, and bars indicate 95% confidence intervals. C, Values of  $\lambda$  across a nitrogen gradient (0–12 g N m<sup>-2</sup> year<sup>-1</sup>). Dots are colored by species (red indicates MF; gold indicates PT; green indicates PD; blue indicates *Penstemon hirsutus* [PH]; purple indicates *Penstemon pallidus* [PP]). The black line represents quadratic model fit, and the gray area represents the 95% confidence interval. D, Values of  $\lambda$  across the nitrogen gradient for each species. Results are from small experimental founder populations, so I discuss differences in  $\lambda$  between treatments rather than absolute values of  $\lambda$  (although populations are nearly extirpated in both experiments).

addition contributed most to differences in  $\lambda$  between nitrogen and control conditions in all species ( $\Delta\lambda^{N-C}$ ; table S1.9; fig. 6). Similarly,  $\lambda$  was lower in all three species when nitrogen was added and deer were absent owing to negative contributions of survival under nitrogen addition (figs. 5, 6). Plant growth and reproduction under nitrogen addition had a surprisingly small contribution to  $\Delta\lambda^{N-C}$  (i.e., increased growth and reproduction under nitrogen addition did not benefit  $\lambda$  in these species). In the nitrogen gradient, population growth rates decreased nonlinearly with increasing nitrogen levels for all five species ( $N^2$ :  $\chi^2_{1,28} = 8.23$ ,  $P = .004$ ; fig. 5C, 5D; tables S1.8, S1.10). Qualitatively, herbivory (unfenced plots) decreased  $\lambda$  in two of three species (*M. fistulosa* and *P. digitalis*), likely because

deer exclusion increased survival (figs. 5, 6; tables S1.8, S1.9).

Discussion

Land use has caused nitrogen deposition and deer populations to rise in remaining prairie habitat, threatening the prairie forbs that withstood habitat loss with local extinction. I assessed the role of these two common hypothesized drivers of biodiversity loss, nitrogen addition and deer herbivory, on the population demography of locally extinct and extant native species found in Michigan prairies. Nitrogen significantly decreased survival, particularly in locally extinct species. Extant species' growth also



**Figure 6:** Life table response experiment (LTRE) contributions of each vital rate (survival, growth, probability of flowering, flower production, seed production) to differences in population growth rates ( $\lambda$ ) between control conditions (no nitrogen, deer present) and treatments of nitrogen addition (N; blue), fenced/deer absent (F; red), and nitrogen addition  $\times$  fenced (N  $\times$  F; purple) in *Monarda fistulosa* (extant; A), *Pycnanthemum tenuifolium* (locally extinct [LE]; B), and *Penstemon digitalis* (extant; C). Plant family is provided in parentheses. The LTRE contribution of each vital rate  $a_{ij}$  to  $\Delta\lambda$  is estimated as the difference in  $a_{ij}$  between the treatment and control multiplied by the sensitivity of  $\lambda$  to changes in  $a_{ij}$  (here, a perturbation of 0.01). A negative LTRE contribution indicates that the value of those matrix elements is lower in the treatment than in the control. Values are means, and bars indicate 95% confidence intervals.

benefited more from nitrogen addition than locally extinct species. These results indicate that locally extinct and extant taxa differ in their vital rate responses to nitrogen addition, with nitrogen providing less detriment (or more of a benefit in terms of growth) to extant species. Nitrogen reduced lower population growth rates across species, mostly via reductions in survival. This suggests that increasing nitrogen levels influence population declines in native prairie forb species. Deer herbivory effects varied across species, but herbivory generally decreased survival and population growth rates. Below, I discuss how this study provides a novel link between species loss under nitrogen addition in grasslands and the population-level processes that cause those losses and how these results highlight the increasingly recognized need to examine cumulative vital rates across a plant's life cycle to understand processes of population decline in response to anthropogenic change.

#### *Linking Community-Level Species Losses to Population Processes*

Nitrogen decreased population growth rates across the grassland species studied here. This result reflects patterns of diversity loss under nitrogen addition in North American grasslands, wherein species losses (mostly of short, locally rare species) follow nitrogen-induced increases in total community productivity (Aerts and Chapin 2000; Suding et al. 2005; Clark et al. 2007, 2013). However, while other studies demonstrate that nitrogen causes loss of rare species, this study suggests that nitrogen might cause declines in more common grassland forbs as well. Additionally, population growth rates showed a hump-shaped relationship with nitrogen addition across a gradient, mirroring patterns of herbaceous plant species losses in grasslands varying in nitrogen deposition (Simkin et al. 2016). Specifically, population growth rates increased with low levels of nitrogen addition ( $1\text{--}4\text{ g N m}^{-2}$ ) before declining at  $8\text{--}12\text{ g N m}^{-2}$ . Altogether, these results link the commonly observed pattern of species loss under nitrogen addition (Midolo et al. 2019) to population declines, connecting community-level responses to nitrogen deposition to population dynamics.

This study also highlights the specific demographic processes underlying those declines, indicating a mechanism for biodiversity decline at the ecosystem level: reduced survival under nitrogen fertilization. Although nitrogen increased plant growth and reproduction, as found in other studies (Seastedt et al. 1991; Collins et al. 1998; Burkle and Irwin 2010), any benefits to growth and reproduction were not enough to overcome nitrogen's consistently negative effects on survival. In the nitrogen  $\times$  herbivory experiment, all 14 species demonstrated reduced survivorship under nitrogen addition. In the nitrogen gradient experiment, sur-

vival increased until  $\sim 6\text{ g N m}^{-2}$  before declining at higher levels of nitrogen addition, again across all study species (note that all species in the nitrogen gradient were also susceptible to deer herbivory). Furthermore, LTRE analyses indicate that reduced survival contributed to the significantly lower population growth rates under nitrogen addition relative to control plots. This reduction in survival could be due to competitive exclusion of inferior competitors or competition for light (Hautier et al. 2009; Bobbink et al. 2010; Bobbink and Hicks 2014; Borer et al. 2014). In this experiment, background vegetation biomass increased (mostly *Andropogon gerardii*, *Sorghastrum nutans*, and *Solidago canadensis*) and light availability decreased with N addition (fig. S1). Interestingly, tall plants sometimes had lower survival than shorter plants, particularly in control conditions. This may be due to herbivory, as tall plants were often consumed by deer by the end of the growing season (M. A. Zetlemoyer, personal observation). Ongoing work is examining differences in herbivore damage across treatments. Anecdotally, areas with dense vegetation often had patches of bare soil beneath them where small seedlings could persist. Finally, tall plants were more likely to grow taller and flower, suggesting that there could be trade-offs between survival and growth or reproduction. Future work might investigate life history trade-offs in these species, whether these small seedlings ever escape the canopy, and how competition with neighbors (especially with invasive species, given clover as a major source of mortality) versus light limitation influences survival and subsequent population dynamics in these species.

Locally extinct and extant species differed in several demographic responses to anthropogenic change, suggesting that widespread habitat loss alone did not drive these species to extirpation. Specifically, nitrogen decreased survival more and benefited growth less in locally extinct species than in extant species, potentially implicating nitrogen addition in the local extinction of these prairie forbs. Given that IPMs always demonstrated lower population growth rates under nitrogen addition owing to reduced survival, it follows that locally extinct species might have lower population growth rates under nitrogen addition than extant species. However, I was able to calculate  $\lambda$  for only a few locally extinct species (*Pycnanthemum tenuifolium*, *Penstemon hirsutus*, *Penstemon pallidus*) owing to low survivorship and reproduction in locally extinct species. While habitat destruction is still likely the main cause of prairie species loss in this region, differences in susceptibility to nitrogen suggest that additional anthropogenic changes might affect extirpations in remaining habitat patches. As the locally extinct species studied here are likely rare or declining elsewhere in their range, these differences in demographic responses to anthropogenic factors might aid in conservation and management to help mitigate their loss

elsewhere. In particular, this study demonstrates that resurrecting populations of extirpated species can help us understand drivers of population decline and potential management options for reintroductions of extirpated or imperiled species (Caughlin et al. 2019). For instance, these species are commonly seeded in tallgrass prairie restorations (Grman et al. 2015); my results suggest that reintroduction and management of these native species should prioritize nitrogen mitigation and enhancing survival. Such resurrection experiments could help maintain threatened species within their native habitat and develop conservation actions for similarly vulnerable species (Williams et al. 2020).

#### *Different Responses among Vital Rates*

The prairie species studied here all demonstrated contrasting responses to nitrogen and herbivory across their life cycles. For instance, vital rate models showed that nitrogen increased plant growth. However, nitrogen decreased  $\lambda$  overall by reducing survival across all species, an effect we would not have detected by measuring biomass or reproduction alone (although these two metrics are commonly used as estimates of plant responses to nitrogen; e.g., Burkle and Irwin 2010; Borer et al. 2014). However, the cohort design of this study could influence these findings, as planting year could influence both vital rates and their responses to treatments (Groves and Brudvig 2019; Werner et al. 2020). This result highlights the need to examine differing responses to anthropogenic change across a plant's entire life cycle, as analyses of targeted vital rates might obscure important responses to that change that ultimately influence population decline.

Also demonstrating contrasting effects across the life cycle, herbivory had variable effects on survival, growth, and reproduction across the species studied here. For instance, herbivory decreased survival in *Eryngium yuccifolium* and both *Silphium* species. In contrast, herbivory benefited growth and survival in several *Penstemon*. Anecdotally, populations of dominant *S. canadensis* (Canada goldenrod) and *Cirsium arvense* (Canada thistle) were less dense in plots where deer were able to browse, so deer browsing may increase the amount of light reaching shorter seedlings (Hautier et al. 2009). Finally, herbivory decreased survival of locally extinct species more than extant species (fig. 1C), although this pattern was not significant. Future work might investigate whether the locally extinct species are more sensitive to light limitation or competition. Ultimately, this result is consistent with previous work detecting inconsistent effects of herbivores on plant diversity in grasslands (Borer et al. 2014).

Herbivory qualitatively decreased population growth rates in two of three species examined here. Deer herbivory sim-

ilarly decreases population growth rates in forbs, such as *Trillium grandifolium*, *Polemonium vanbruntiae*, and *Eurybia furcata* (Knight et al. 2009; Birmingham 2010; Bernardo et al. 2018). Ongoing work in this system is investigating whether patterns of herbivory differ between locally extinct versus extant species, which could have contributed to lower survival among taller plants in some species. Finally, I detected very few instances where nitrogen and herbivory interacted to affect vital rates, despite the common hypothesis that deer browsing might alleviate nitrogen-mediated reductions in light. Moreover, although herbivory tended to dilute the negative effects of nitrogen on survival in the LTRE, herbivory did not ultimately reduce the effects of nitrogen on reductions in population growth rates. This suggests that herbivory's role in ameliorating light limitation in eutrophied systems could be limited (e.g., species specific) or require longer-term studies.

#### **Conclusions**

Using IPMs to compare vital and population growth rates of closely related locally extinct versus extant species under anthropogenic change provides a framework for two useful comparisons. First, we can examine drivers of contemporary, local extinction events. Modeling the demographic processes that led to decline, particularly in response to multiple and interacting anthropogenic changes, permits more mechanistic explanations of species losses (Merow et al. 2014) and will inform predictions of extinction risk and development of targeted management recommendations for today's threatened species (Davies 2019). Second, by monitoring the population demography of reintroduced, recently extinct species, we can assess demographic differences between more "successful" (i.e., still extant) and locally extinct species and contribute to our still inadequate understanding of the population dynamics of extirpation (Bevill and Louda 2001). Ultimately, such models can improve our ability to project population risk of these species in other locations and of other threatened species experiencing similar changes in local environmental conditions due to anthropogenic change.

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### Data and Code Availability

All data and code for this study are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.xwdbvr1dd>; Zettlemoyer 2022).

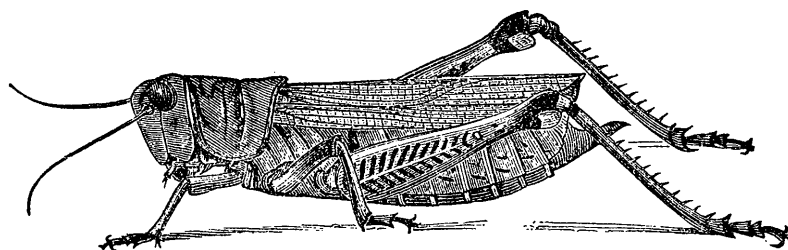
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“Careful examination of locust eggs in the vicinity of potato fields frequented by these beetles show[s] a varying proportion of the egg-pods affected, and in some locations nearly every pod of the differential locust (*Caloptenus differentialis*) [figured] will contain the *Epicauta* larva.” From “On the Transformations and Habits of the Blister-Beetles (Continued)” by Chas. V. Riley (*The American Naturalist*, 1878, 12:282–290).