

CONTRIBUTED PAPER

Prescribed burning has limited effects on the population dynamics of rare plants

Logan Novak  | Joshua P. Scholl | Gretel Kiefer | Amy M. Iler

Chicago Botanic Garden, The Negaunee Institute for Plant Conservation Science and Action, Glencoe, Illinois, USA

Correspondence

Logan Novak, Chicago Botanic Garden, The Negaunee Institute for Plant Conservation Science and Action, Glencoe, IL 60622, USA.
 Email: logannovak2021@u.northwestern.edu

Funding information

Anonymous Foundation; Forest Preserves of Cook County; Chicago Wilderness, Illinois Wildlife Preservation Fund; The Nature Conservancy-Volunteer Stewardship Network; U.S. Forest Service at Midewin National Tallgrass Prairie; Openlands; Chicago Botanic Garden

Abstract

Rare species serve important ecosystem functions, including community resilience to global change. Yet rare species are disappearing globally because of anthropogenic activities such as fire suppression. Prescribed burning is a widespread management approach that can reduce invasive plant presence, recycle nutrients, and restore species diversity. However, the effects of prescribed burning on rare plants are not well understood. We analyzed the population dynamics of 67 rare, native plant species in response to prescribed burning using the Chicago botanic garden's Plants of Concern dataset. This dataset includes rare plant populations concentrated in the northeast part of Illinois, and a few populations in Indiana and Wisconsin, United States. We evaluated the effects of burning by comparing the percent change in population size in the short-term (1–2 years) and long-term (3–4 years) after prescribed burning, to the percent change in population size not following burns. In a global model with all species, we did not detect the effects of burning on percent change in population size. In species-level analyses, we detected burn effects for most species for which we had the statistical power to detect possible burn responses, although the direction of their responses was mixed. Five species responded consistently between short- and long-term datasets, and four species had mixed responses, with most responding positively over the short-term and negatively over the long-term. We complemented this analysis with a literature review of fire responses for available species. Our literature review revealed more responses to burning than what we found from our analyses; however, most of this evidence does not compare burned and unburned populations directly and should be treated cautiously. Through community science monitoring efforts, we were able to compile one of the largest studies of burn effects on rare plants to date, but continued monitoring is necessary to fully evaluate how prescribed burning impacts rare plant species.

KEYWORDS

conservation, fire, management, population dynamics, population growth

Logan Novak and Joshua P. Scholl contributed equally and were listed alphabetically.

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1 | INTRODUCTION

Rare species are those that have very few populations, very few individuals within populations, or both within a given area. Rare species provide a variety of ecosystem functions, many of which are not replicable by other species (Mouillot et al., 2013). These species improve ecosystem productivity and bolster stability and resilience in the face of disturbance and global change (Jain et al., 2014; Leitão et al., 2016; Lyons et al., 2005; Tilman & Downing, 1994). For example, a study in an Australian grassland found that when dominant plant species were removed, rare species replaced them, and no ecosystem function was lost (Walker et al., 1999). Similarly, Ge et al. (2019) showed that climate shifts over three decades caused a loss of dominant species, which were replaced by rare species more adapted to warmer and drier conditions, while species diversity remained the same. However, due to their small population size and/or few populations, rare species face unique threats such as illegal harvesting and loss of genetic diversity through inbreeding and hybridization (Godt et al., 1996; Levin et al., 1996). The combination of functional significance and heightened risk of extinction in rare species highlights the need for increased study of processes impacting their conservation.

Fires promote spatial and temporal species diversity (He et al., 2019; Turner, 2010) and thus may be particularly important for the maintenance of rare species. Fire removes plant litter, assists with the cycling of nutrients, increases light and water availability by thinning vegetation, and can either reduce or increase the prevalence of invasive species (Bond & Keeley, 2005; Turner, 2010; Turner et al., 1997; Vander Yacht et al., 2020; Willms et al., 2017). One study monitored vegetation across 60 years of seasonal fires and found significant increases in understory diversity, abundance, richness, and evenness as compared to non-burned control plots (Knapp et al., 2015). Similarly, Alstad et al. (2016) demonstrated that extinctions decreased in burned compared to unburned prairie remnants. Additionally, it has been shown that fire in prairie habitats increases mate availability and plant reproductive success (Wagenius et al., 2020).

Fire has a much longer history of ecological management throughout North America than current prescribed burning practices. For thousands of years pre-settlement, Indigenous people ignited fires to manage game populations, cultivate certain plants, and make areas easier to traverse (Ryan et al., 2013). Following European colonization, displacement of Indigenous people and broad-scale fire suppression resulted in a loss of ecosystem services, as increased canopy cover and lack of disturbance for fire-prone species led to reduced species

diversity (Ryan et al., 2013). After decades of fire suppression, managers are working to restore historic fire regimes and improve ecosystem function by integrating prescribed burning in a variety of habitats across a wide range of temporal and spatial scales (Schwartz & Hermann, 1997). Burning is also widely employed to conserve and promote the population growth of rare species (Diamond & Heinen, 2016; Kelly et al., 2015). However, the broad application of burning as a management tool often only considers whether a particular habitat type or region was historically exposed to fire regimes. Such broad application fails to consider whether prescribed burning actually achieves the desired ecological effects or management goals for individual, rare species (Johnson & Miyanishi, 1995). Thus, although the benefits of fire on plant communities are widely documented, the impacts of burning on rare plant species are much less understood than for common plant species.

Many factors beyond historical prevalence influence the effects of prescribed burns on species diversity and abundance, thus making it difficult to generalize outcomes. For example, patch size burned during the 1988 Yellowstone National Park wildfire influenced individual herbaceous species differently, with some species being found in greater abundance in large burned patches and others in small burned patches (Turner et al., 1997). Specifically, smaller burned patches resulted in higher biodiversity and more weedy species as opposed to larger burned areas, which were abundant in pine and shrubs. In the Australian desert, Pastro et al. (2011) studied prescribed burns of varying spatial scales and found that responses one-year post-burn differed among species, thus making it difficult to generalize outcomes about ideal spatial scales for burning. Furthermore, prescribed burning can have vastly different results across ecosystems by removing woody plants and altering nutrient cycles, which could result in especially large changes in forested and nutrient-poor areas (Boerner, 1982; Van Mantgem et al., 2011). Thus, it is useful to evaluate the effects of prescribed burning locally, in the context of individual species and areas burned.

Moreover, the effectiveness of prescribed burning may require longer-term (≥ 3 years) evaluations of its impact on the population dynamics of target plant species (Bunting et al., 1980; Van Mantgem et al., 2011). Very few studies have focused on the longer-term effects of prescribed burning for several plant species, and we are not aware of any studies that have done so for a multitude of rare and endangered species (Patykowski et al., 2018; Young et al., 2015). This knowledge gap is especially relevant because studies that do examine species-specific effects of burning are biased toward common species.

Here we explore the effects of prescribed burns on changes in population sizes of 67 rare and endangered plant species surrounding a metropolitan area. We employ a 20-year dataset of relatively small management areas comprising woodland, wetland, urban, dune, and prairie habitats that have experienced burns. We ask: (1) Are short- and long-term post-burn population size changes different for species exposed to prescribed burning than those that were not? (2) Within species, do burn effects vary among distinct habitats? (3) How do our results for rare species compare to other findings for the same species?

2 | METHODS

2.1 | Plants of Concern program

Plants of Concern (POC) is a community science program that monitors rare plant populations in and around Chicago, Illinois, United States (Havens et al., 2012). Founded in 2001, POC comprises two decades of rare plant survey data. All POC participants undergo training in plant identification, transect methods, and data recording and reporting. Together with POC staff, community scientists have amassed data on 247 species across 2323 populations. Species are selected for monitoring based on the list of endangered and threatened species compiled by the Illinois Endangered Species Protection Board (ESPB, 2020). As of 2020, ESPB lists 266 endangered and 67 threatened plant species in Illinois of which the POC dataset comprises 100 endangered species and 29 threatened species. The remaining 118 species are either no longer listed or were never listed by the ESPB but remain regionally rare.

We did not attempt to compose a uniform definition of a rarity across the studied species. For defining rarity, we used the designations supplied by POC and thus indirectly by the Illinois ESPB. The Illinois ESPB definitions rely largely on population sizes but also sometimes on the geographic extent to define rarity (ESPB, 2020). In addition, because the ESPB listings are specific to Illinois, some of our species are only locally rare.

2.2 | POC data collection

We included element occurrence records from the Illinois Natural Heritage Database (INHD, 2020), land manager records, and newly identified locations of rare plants in monitoring efforts. An element occurrence record represents spatial location data and metadata for the plant species of interest. Once located, a plant population is

monitored annually, though some populations are monitored on a rotating basis if they are large or have remained stable for many years. Monitoring includes determining population size in terms of the number of individuals and is completed by POC staff and community scientists (hereafter referred to as monitors). Monitors determine population size by counting plants as number of stems, clumps, or rosettes, depending on the growth form of the species. In cases where populations are too large to count all individuals, individuals are counted in a subset of the population, and population size is estimated based on total area.

While the primary goal of POC is to monitor rare plant population size, monitors also evaluate habitat management activities (Bernardo et al., 2019). During plant surveys, monitors record any management efforts or evidence of such efforts that may have occurred within the last 12 months. With respect to evidence of recent burns, monitors look for burn scars, ashes, or lack of leaf litter. Where possible, monitors communicate with site managers regarding recent management activities to confirm their observations.

2.3 | POC data preparation for analyses

We conducted spatial analysis in R (R Core Team, 2020). To assign POC populations to a habitat type, we used the land cover classification dataset from the Illinois Gap Analysis Program (IGAP, 2000). We first assigned every population in our dataset to one of eight broad vegetation classes: forest, prairie, savanna, dune, wetland, agriculture, urban, or other. They were distributed across forest (45%), prairie (28%), savanna (20%), dune (3%), wetland (3%), agriculture (1%), urban (1%), and other sites (<1%). We next visually verified and corrected the habitat type assignment for each plant population using Google Earth. Different populations of a single species could be assigned different habitats. Habitat assignments remained consistent across all years of monitoring data.

Next, we assigned every population size reported in the original dataset to a burn category of either not-burned, short-term burn, or long-term burn. Populations that had never experienced a burn were assigned a category of not burned under the assumption that fire was not used as a management tool for these populations. Data collected ≤ 2 years after a burn was considered a short-term burn response, while data collected ≥ 3 years was considered a long-term response. Very few data points (2%) were in the ≥ 5 years post-burn category, so most of our long-term burn data represent 3- and 4-years post-burn data. Furthermore, the majority of our data fell into the not-burned category and the short-term category,

as most of our sites were either burned relatively frequently (i.e., once every other year or more) or not at all. The exact timing of prescribed burns within the year between count surveys is not available in our dataset; we know only if a burn occurred between growing seasons when surveys were conducted. Burns may have occurred in the fall prior to or in the spring of the monitoring year. Thus, for a fall burn, our data capture responses 4–10 months post-burn, but for a spring burn, the time-frame could be as small as a week to 6 months post-burn.

Once categorized into burn categories, we then calculated the percent change in population size ($(\text{number of plants post-burn} - \text{number of plants pre-burn}) \times 100 / \text{number of plants pre-burn}$) for each plant population in each year. We used percent change in population size instead of raw count data to standardize comparisons across populations of vastly different sizes. For the post-burn categories, we calculated the percent change in population size from just before the most recent burn to that associated with the category. For example, one of our *Hepatica americana* populations was burned before the 2008 survey and was last surveyed in 2006 (Figure 1a). Thus, we calculated the percent change in population size between 2006 and 2008 for 2 years post-burn, 2006

and 2009 for 3 years post-burn, and 2006 and 2012 for 6 years post-burn (Figure 1a). The 2-year post-burn category was then placed in the short-term category for analysis, while the 3+ years post-burn categories were placed in the long-term category for analysis. For the no-burn category (which included only sites that had never burned), we calculated the percent change in population size between the previous year and the given year (Figure 1b). For every species, we computed the percent change calculations for each monitored population separately. For populations that burned at least once during POC surveying, we assumed that they may have been burned prior to POC surveying. Thus, if the second and third surveys in the time series did not include a prescribed burn, then those were also not used because it was unknown whether the population had experienced a burn just before POC surveying began. For populations that never burned during POC surveying, we assumed that burning was not used as a management tool and thus discarded only the first data point in these cases (Figure 1b). Finally, we normalized the resulting data by log transforming the percent changes; we first added 101 to all percent changes to remove negative numbers (Figures 2 and 3).

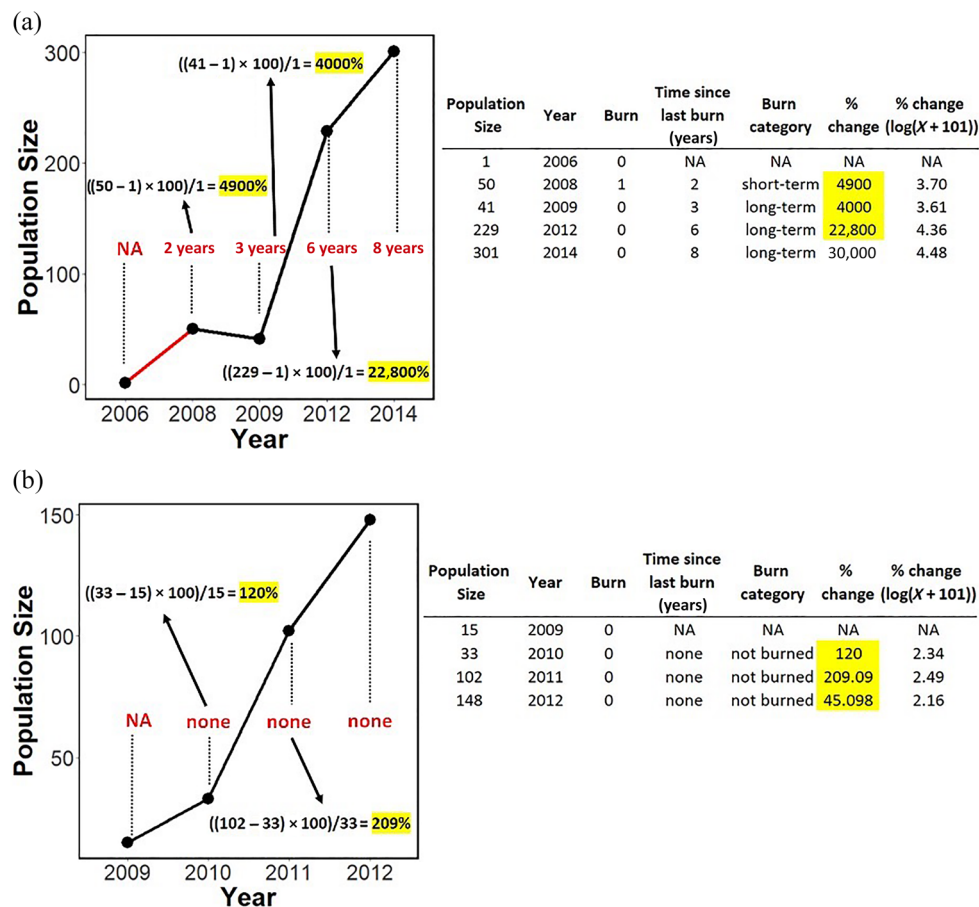


FIGURE 1 (a) Line graph and corresponding table of population size across POC survey years, post-burn categories and their associated percent population changes for one population of *Hepatica americana* in which (a) burning was used as a management tool and (b) in which burning was not used as a management tool. Red lines in the line graphs signify the occurrence of a burn between the two population surveys they connect while black lines signify the absence of a burn. Dotted lines link each survey point to a post-burn category in red which is equivalent to the “Time since last burn (years)” column in the table. These categories can include unknown (NA), none (no-burn), short-term burns (1 year or 2 years post-burn), or long-term burns (3+ years post burn)

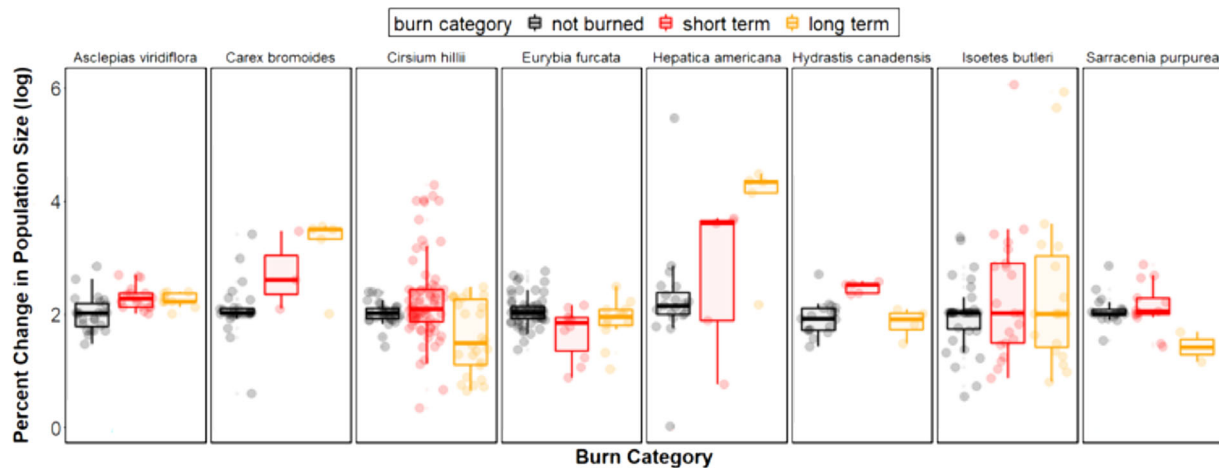


FIGURE 2 Percent change in population size for different post-burn categories for the eight species whose best model incorporated only burning as a significant predictor accounting for differences in population changes as compared to population changes between years of no burns

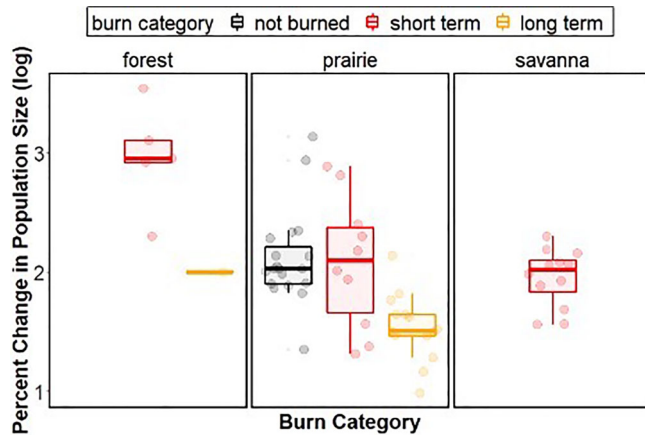


FIGURE 3 Percent change in *Ranunculus rhomboideus* population size across the three post-burn categories and different vegetation types. This species' best model incorporated burning and habitat as predictors ($p < .001$ and $R^2_m = 0.46$). No data were available for the non-burn category in either forest or savanna habitats, thus for this species, we were unable to test for an interaction between burning and habitat. Only one data point was available for the long-term burn category for savanna and forest habitats and therefore interactions could not be explored

We next removed any single population with less than 3 years of survey data. Subsequently, we removed any species that, across all its populations, had less than five data points in the unburned category (0) or less than five data points across all burned categories (short- and long-term). This resulted in a dataset of 67 species. Several of these species are subspecies but will be referred to as species throughout this paper. These species were composed of 61 herbaceous plants, 2 shrubs, 3 trees, and 1 vine. Of these species, 62 (93%) were perennials and 5 (7%) were annuals.

2.4 | Data analysis

We analyzed burn responses at two scales: across all species and within species. For our global model including all species, we examined how our dependent variable, percent change in population size, was predicted by the independent variable of burn category and its interactions with species growth form (shrub, tree, vine, or herbaceous), population habitat (forest, prairie, savanna, wetland, dune, or other) and life-cycle duration (annual or perennial). In other words, we wanted to determine whether the short- and long-term effects of fire on population size changes depend on growth form, habitat, or life-cycle duration. For our global analysis across all species, we compared a candidate set of models using Akaike information criterion (AIC) values (Table S1). Our full model included an interaction between our burn categories, species growth form, population habitat, and species duration to determine if the effect of burning depended on interactions with these other factors. We included all possible reduced models that included our post-burn categories (Table S1). In each model, we set species, population, and year as random intercept terms to control for the non-independence of repeat measurements within species and across populations and years, respectively (Harrison et al., 2018).

For our within-species analyses we examined how our dependent variable, percent change in population size, was predicted by the independent variable of post-burn category and its interaction with population habitat (forest, prairie, savanna, wetland, dune, or other). It was not always possible to include interactions because we did not always have sufficient data for the burn and no-burn categories in different habitats. Our full model

included an interaction between our post-burn categories and population habitat to determine if the effect of burning depended on interactions with habitat. We also included reduced models without population habitat. In each model, we set species, population, and year as random intercept terms to control for the non-independence of repeat measurements within species and across populations and years, respectively (Harrison et al., 2018).

For all analyses, we compared a candidate set of models using AIC values. A model was accepted as the best model if it had the lowest AIC score. Except for the null model, which was an intercept-only model, we did not include reduced models without post-burn categories, because the goal of our analysis was to evaluate the effect of burning on population size. We ran all models using the lmer function from the lme4 package in R (Bates et al., 2015). Our best models did not include interactions. Therefore, we summarized them by chi-squared (X^2), degrees of freedom (df) and p -value (p) obtained from a Type II Wald X^2 test for models without interactions. In addition, we calculated a marginal and conditional R^2 after Nakagawa and Schielzeth (2013) to represent the explanatory power of the predictor variables and the predictive power of the model as a whole, respectively.

For both modeling scales, within and across all species, we conducted post hoc power analyses using the powerSim function with 1000 simulations from the simr package in R (Green & MacLeod, 2016). For these analyses, we report the probability of committing a type II error, or falsely accepting the null hypothesis. For the broadscale analysis across all species, this power analysis was based on the mixed effect model including only the burn category as a fixed effect and population identity, species, and year as random effects. For the within-species analysis, this power analysis was based on each species mixed effect model including only the burn category as a fixed effect and population and year as random effects. We considered probabilities $\geq .80$ as sufficient statistical power.

2.5 | Literature review of burn effects

To supplement and contrast our POC data analyses, we performed a literature review of fire ecology data for POC species. We conducted Google scholar searches for each of the 67 POC species using the species' scientific name and synonyms combined with the terms "prescribed burning," "burning," and "fire." We categorized the effects of burning (positive, negative, mixed response, no effect) for each species based on the literature that we found. We also categorized the strength of the evidence. For example, if a species was directly and quantitatively studied and

determined to increase post-burn, we termed this as strong evidence. If a species was anecdotally observed to increase post-burn, or if it was known to prefer shaded habitats and thus assumed to be affected negatively by burns, we deemed it weak evidence.

3 | RESULTS

3.1 | Effects of burning on percent change of rare plant populations

In our global model, there was no detectable effect of post-burn category, species growth-form, population habitat, and life-cycle duration on percent change in population size across all species included in this study (the best model was the null model, with the next best model 6 AIC units away; Table S1). The power analysis for our global model gave a 76% chance of correctly rejecting the null hypothesis. In our within-species analysis, there was no detectable effect of burning on changes in population size for 58 species, or 87% of the rare plants in our dataset (Table 1). For the remaining nine species (13%), burning was included in the best model (Table 1; Figure 2). All nine species for which we detected significant effects of burning had an associated statistical power $>80\%$ (Table S1). Only three of the species for which we did not detect burn effects had $>80\%$ power (Table S1). Of the nine species with detectable burn responses, four species responded positively to burning and one responded negatively to burning in both short- and long-term datasets; the remaining four species responded both positively and negatively to burning depending on whether the response occurred over the short- or long-term (Table 1). Overall, in short-term responses, eight species responded positively, and one species responded negatively to burning. Whereas in long-term responses, four species responded positively, and five species responded negatively to burning.

Habitat was included as an additive predictor in only one model. Percent change in population size varied across habitats for *Ranunculus rhomboideus* (Ranunculaceae; Figure 3). In all other species, habitat was not included as an additive or interactive predictor in the best-fit model.

3.2 | Literature review of POC species

In a literature review, we found responses to burning for 44 out of the 67 species we analyzed (Database S1). Of these, four species were reported as unaffected by burning, 27 as positive responders, 6 as negative responders, and 7 with mixed responses to burning. Of all the species

TABLE 1 Statistical summary table for species whose best models incorporated burning as a significant predictor accounting for differences in population changes in the short- (1–2 years) or long-term (3+ years) post-burn as compared to population changes between years of no burns

This study burn effect		Lit. review burn effect	Species	Family	Primary POC habitat	# Pops	Avg. years per Pop.	Predictor	X ²	df	p	R ² m	R ² c	AIC diff. from null
Short-term	Long-term													
+	+	ND	<i>Carex bromoides</i>	Cyperaceae	Forest	9	4.2 ± 2.8	Burn	25.71	2	<.001	0.40	0.46	6.6
+	–	–	<i>Cirsium hillii</i>	Asteraceae	Prairie	13	10.2 ± 3.9	Burn	19.63	2	<.001	0.13	0.15	9.9
–	–	(+)	<i>Eurybia furcata</i>	Asteraceae	Forest	11	7.7 ± 5.4	Burn	15.05	2	<.001	0.15	0.15	2.0
+	+	(+)	<i>Isoetes butleri</i>	Isoetaceae	Prairie	9	8.3 ± 2.9	Burn	21.29	2	<.001	0.17	0.58	3.2
(+)	–	No effect	<i>Ranunculus rhomboideus</i>	Ranunculaceae	Prairie	9	6.8 ± 2.6	Burn Habitat	23.82 27.17	2 2	<.001 <.001	0.46	0.50	10.2
+	–	(+)	<i>Sarracenia purpurea</i>	Sarraceniaceae	Prairie	5	7 ± 2.4	Burn	14.555	2	<.001	0.24	0.60	0.4
+	–	+	<i>Hydrastis canadensis</i>	Ranunculaceae	Savanna	6	4.3 ± 2.5	Burn	15.931	2	<.001	0.38	0.46	1.3
+	+	(+)	<i>Hepatica americana</i>	Ranunculaceae	Forest	8	3.8 ± 1.2	Burn	11.32	2	.003	0.15	0.92	0.7
+	+	ND	<i>Asclepias viridiflora</i>	Apocynaceae	Prairie	9	5.6 ± 3.2	Burn	14.99	2	<.001	0.23	0.27	1.8

Note: The effect (correlation) of burning on a species' rate of population change in this study is indicated by the + (positive) and – (negative) symbols, at the beginning of each row, in the first two columns of the table. Literature review-based burn responses for species are given in the third column (ND = no data, ± = evidence for positive/negative response). Responses with weak evidence are denoted in parentheses and responses with strong evidence are without parentheses. The primary POC habitat for each species represents the habitat in which most of that species' POC populations are found. All species in this table were herbaceous perennials with respect to duration and growth form. The number of populations (# of Pops) and average years per population (Avg. years per Pop.) and standard deviation (±) represent the data used in the analysis for that row's species. The chi-squared (X²), degrees of freedom (df), and p-value (p) stem from Type II Wald X² tests for models without interactions. Only one species showed an additive effect of habitat. The partial R² was calculated after Nakagawa and Schielzeth (2013) and represents the effect size of its corresponding predictor in the linear mixed effects model. Burn was a categorical predictor (not burned, short-term burn, or long-term burn) as were population and habitat (i.e., land cover). Subpopulation and year were random effects in all models.

Abbreviations: AIC, Akaike information criterion; ND, no data; POC, Plants of Concern.

documented in the literature, only six overlapped with the nine species that showed a response in our analyses. Of the literature findings for these six species, five agreed with our burn response findings in either the short- or long-term datasets, and one disagreed (Table 1). Three of these species had mixed responses to burning in short- and long-term datasets and therefore only agreed with the literature in either the short- or long-term. We did not find any published burn responses for the remaining 25 of our species. Additionally, 21 species had weak evidence, 17 had strong evidence, and 6 had a combination of weak and strong evidence depending on habitat type (Database S1).

4 | DISCUSSION

In this study, we address the broad question of whether burning influences rare species population size by evaluating relationships between burning and percent changes in population size across a unique long-term, rare plant dataset. Broadly our results suggest that burning may be an important management tool for several species in the short term with mixed long-term responses, although our statistical power for detecting burn effects was limited. When we compared the effects of burning across 67 rare species in a global model, we found no support for the effects of burn category (short- or long-term response) on percent change in population size, nor any interactions with population habitat, species growth-form, or life-cycle duration, though this analysis had borderline statistical power. When we evaluated individual species responses to burns, 9 out of 12 species for which we had sufficient statistical power showed burn responses. Of these nine species that experienced changes in population size following burns, responses to burning depended on post-burn categories in five species, with different responses in short- and long-term datasets. Overall, however, the power available across species varied widely, and 55 species (87%) lacked sufficient power to detect potential fire effects.

4.1 | Species-specific responses to burning

Of the nine species that had noticeable changes to population size following burns, eight species responded positively to burning in short- and/or long-term datasets. Populations increasing in size after burning could be the result of fewer competitors, particularly woody plants that prevent light from reaching understory species. Burning could also benefit rare species via other mechanisms such

as synchronizing flowering years to increase seed production (Richardson & Wagenius, 2022; Wagenius et al., 2020) and nutrient deposition (Boerner, 1982; Christensen, 1973, 1977). Synchronized flowering has been shown to be a particularly important mechanism for prairie species (Richardson & Wagenius, 2022; Wagenius et al., 2020) and thus might be important for *Asclepias viridiflora*, *Cirsium hillii*, *Isoetes butleri*, and *Sarracenia purpurea*, which all responded positively to burns in short- and/or long-term datasets. Similarly, burning releases nutrients from leaf litter into the soil, which could benefit herbaceous species (Glasgow & Matlack, 2007). Another possible mechanism for the positive responses to burning in our study is variation in the detectability of plants in the presence versus the absence of prescribed burns. Burning removes leaf litter, ground cover, and opens the canopy, all of which might improve the ability of monitors to detect rare individuals. These and other hypotheses based on our results and posited throughout the discussion could be tested in the future with additional data.

In contrast, five species had decreased population size following burns in short- and/or long-term datasets. Negative burn responses could be explained by burning too frequently and preventing adequate recovery or burning plants during their growing season (Brockway et al., 2002; Valkó et al., 2014). Similarly, negative burn responses could be the result of more severe burns in areas with higher fuel availability (Johnson & Miyanishi, 1995; Richter et al., 2019). Severe burns could damage individuals—particularly since all species negatively affected by burns were perennials—or change moisture dynamics that could negatively impact mesic species (Richter et al., 2019). If rare species grow more successfully in shaded areas, burning could preferentially select shade-intolerant plants that can outcompete their rare counterparts.

The nine species that had significant changes in population size following burns are all herbaceous species. Herbaceous plants could be more sensitive to burning than woody species as the removal of woody and large herbaceous plant competitors could have greater impacts on smaller, light-deprived species (Bond & Keeley, 2005; Turner et al., 1997; Vander Yacht et al., 2020). Many herbaceous species growing in forested habitats thrive on disturbance events that open canopies and provide favorable short-term growing conditions (Vander Yacht et al., 2020). Because herbaceous plants do not maintain their aboveground biomass throughout the year and may have underground structures such as rhizomes or bulbs, they can grow quickly and respond more rapidly than woody species to disturbances such as burning (DiTomaso et al., 2006). Woody species may be damaged initially by burns and recover over several years, whereas perennial herbaceous species are usually able to regrow

within a year of burns. This suggests that any effects of burns may take several more years to be fully noticeable in woody species and therefore may not have been detectable in our study (Diotte & Bergeron, 1989; Overlease, 1987). However, several of the herbaceous species in our study were negatively affected by burning, so recovery time after burns is not the only mechanism influencing changes in rare plant population size.

4.2 | Short- and long-term responses to burning

Out of the nine species that had significant changes in population size following burns, only five species responded consistently to burning in both short- and long-term datasets. Within these five species, burning increased population size in four species and decreased population size for one species. For the four species that had consistent positive responses to burning in the short- and long-term (*A. viridiflora*, *Carex bromoides*, *H. americana*, and *I. butleri*), burning on a semi-annual basis may be a good management practice to increase population size.

The only species that was consistently negatively impacted by burning in both short- and long-term datasets is *Eurybia furcata*. Previous research on *E. furcata* shows that woody plant encroachment and heavy deer browse in combination with climate change pose threats to this species (Bernardo et al., 2019). Since burning typically reduces woody encroachment, it is unclear why this species responds negatively to burning. It is possible that plants were already stressed from the impacts of climate change and deer browse and the additional disturbance from burning resulted in increased plant mortality. Furthermore, *E. furcata* flowers and produces seeds during the fall (August–October) and fall burns could negatively impact reproductive output (WDNR, 2021). Similarly, mate limitation is a documented issue affecting *E. furcata* reproduction, and any loss of individuals as a result of burning could compound that issue (Gavin-Smyth et al., 2021). When possible, managers should avoid burning populations of *E. furcata*, but may need to employ other methods to remove woody competitors and address other threats, such as mate limitation (Gavin-Smyth et al., 2021).

The remaining four species had mixed responses to burning with increased population size in the short-term and decreased population size in the long-term. Three of these four species predominately grow in prairies, with the remaining species growing predominately in savannas. Both prairies and savannas are characterized by largely herbaceous understories and few mid-story trees and shrubs. Removal of woody species could have

immediate positive impacts on rare plant populations by increasing light availability, so the negative impacts of burning may take several years to detect (Weir & Scasta, 2017). Negative responses to prescribed burns that manifest 3 or more years after burning could be explained if rare species are shade-tolerant or burning increases the abundance of invasive species, as the bare ground resulting from burning can encourage invasive plant colonization (Willms et al., 2017). In *Cirsium hillii*, negative long-term impacts of burning are hypothesized to be unrelated to burning itself, but to the absence of other management practices that were commonplace before burning was used (Dornbush, 2004). Overall, there are likely multiple factors influencing rare plants' short- and long-term responses to burning, such as burn severity, burn season, changes in climate, and interacting effects of management and environment, among others (Brockway et al., 2002; Patykowski et al., 2018).

4.3 | No responses to burning

The three species with sufficient data to detect burn responses that were unaffected by burning are *Asclepias exaltata*, *Toxicodendron vernix*, and *Trillium erectum*. Therefore, burning does not appear to be a useful management tool for these species, but also should not have any unintended consequences when burning habitats. All three species were previously reported to benefit from burning (weak evidence for *T. erectum* and *A. exaltata* and both strong and weak evidence for *T. vernix*). However, the unique conditions of each population could influence species' responses to burning. For example, *T. vernix* is believed to benefit from burning when woody plant encroachment causes canopy enclosure, but populations in our dataset occurred predominately in prairies where burns may be less beneficial if woody species encroachment is not an issue (Overlease, 1987). *A. exaltata*'s seeds are believed to remain viable in the seedbank for many years, so older populations with more extensive seedbanks may recover more quickly after burns (Wilbur, 1976). Previous literature on *T. erectum*'s response to burning comes from a single population that may not reflect a broader species-level response (Apfelbaum et al., 2000). Therefore, burning could benefit some populations of these species as has been previously reported in the literature, but the populations in our analyses were not detectably affected by burns.

In addition to a lack of statistical power at the species-level, our global model had borderline statistical power (76% with a threshold of 80%) but provided some evidence that burning had no effect on population size across all species in our study. As shown through our

power analysis, many individual species did not have sufficient data to detect burn effects, so this result should be approached cautiously. Aside from insufficient power, our lack of finding burn effects for the majority of our species could be attributable to our sites being burned relatively frequently (i.e., once every other year or more) and before POC monitoring began. Sites may have been burned several times in the years leading up to monitoring, but we do not have complete site history data for our populations. Some of the primary benefits of burning such as woody species and litter removal would be most notable in previously unburned populations. Thus, our study might not capture the dramatic increase populations might incur when a degraded, largely overgrown habitat is burned for the first time in decades. Similarly, perennial species may require several years to recover from burns, and frequent burning could eliminate any benefits of burns before they are detected. Therefore, it is possible that some species reported to be unaffected by burning could react strongly in the absence of burning leading up to monitoring.

Additionally, large populations of species that benefit from burns may not increase in size if they are at or near local carrying capacity. While most of our populations contain fewer than 1000 individuals, it is difficult to determine the carrying capacity for a given species, and we cannot rule out the possibility that some populations were too large to detectably benefit from burning. Importantly, our analyses should have been able to detect negative responses to burning in large populations, so the risk of prescribed burns having negative impacts on rare plant populations remains relatively low.

Our statistical models compare the percent change in population size following a recent burn to the percent change in years without a recent burn. Thus, we assessed whether burning is associated with larger or smaller changes in population size than not burning, as opposed to testing whether burning increases or decreases the number of individuals within populations. Because of this, a change in a few individuals may cause a dramatic percent change in small populations, while it takes a much larger change in individual numbers to detect a significant change in larger populations. We think the advantages of this analysis outweigh the costs, but this method may account for some inconsistencies compared to results from other studies.

Two important ecological changes occurred over the last century that our study does not directly address: the widespread prevalence of invasive species and habitat fragmentation. Nearly every natural ecosystem across the planet is now plagued by invasive plant species (Vilà et al., 2011). Some of these species are controlled by fire, but many are aided by such disturbance events (Brewer

et al., 2015) or even change the dynamics of burns and consequently, the plant community that recolonizes after a burn (McDonald & McPherson, 2011, 2013). In these cases, the physical removal of invasive species prior to burning may be necessary. Urbanization has resulted in a fragmented landscape in which natural areas are often small and isolated. This can reduce plant dispersal (Gelmi-Candusso & Hämäläinen, 2019; Richardson et al., 2000) and thus post-burn recolonization for many species. In addition, this fragmented landscape reduces gene flow, which may be particularly intense for rare plants that are likely already limited in their genetic diversity (reviewed by Hamrick & Godt, 1990; but see also Gitzendanner & Soltis, 2000). Both post-burn recolonization and low genetic diversity could be managed through seeding or transplanting following prescribed burning (Moyes et al., 2005; Young et al., 2015) or by mating individuals between populations (Gavin-Smyth et al., 2021). Overall, many populations surveyed through the POC program require multifaceted management approaches, in which burning could play a role.

4.4 | Habitat-specific responses to burning

Habitat was only included in the best model for one species, as an additive predictor (*R. rhomboideus*). This is likely attributable in large part to a lack of monitoring data for a given species across several habitats. Fuel, moisture, litter, and plant community composition, among other factors, all vary hugely between habitats and can determine the severity and spread of burns. The lack of monitoring data across habitats could have influenced our ability to capture habitat-specific burn responses in some species. Notably, most species in our analyses were predominately found in forests, where burning may be less vital in maintaining the biome than in prairies, which depend on fire to keep woody species at bay (Bond & Keeley, 2005). We expect that as the POC program continues to grow, our ability to evaluate within-habitat responses will improve and habitat-dependent burn responses will emerge.

4.5 | Literature review

There were seven POC species that responded to burning and had literature documenting the impacts of burning. However, previous literature for a given species typically only described an overall response to burning and did not consider short- versus long-term impacts. Four of these species had mixed responses to burns in our

analysis, and the literature agreed with either short- or long-term responses to burning in three of these four species. The disagreement between short- and long-term effects highlights the importance of considering the time-scale of burn responses. The only species that disagreed in both short- and long-term datasets with the literature review was *E. furcata*, where the literature reported a positive effect of burning, and our analysis detected negative short-term and long-term effects.

When we consider our findings in combination with published literature, we found fewer responses to burning than had been previously reported. Our global analysis provides evidence that fewer of the rare species than previously reported undergo increases in population size following burns. Additionally, many of the studies included in our literature review are observational, occurred in a single habitat or population, and/or occurred in regions or countries where species are not rare. While the majority of our species-level analyses were not strong enough to detect responses to burning, our study provides a direct comparison between burned and unburned populations across two timescales and added burn responses for many species that were not reported in prior literature. Additionally, our global model found no overall effects of burning on rare plant populations across species. The scarcity of existing literature available for POC species highlights the general need for long-term rare plant monitoring programs.

AUTHOR CONTRIBUTIONS

Logan Novak and Gretel Kiefer conceived the project. Joshua P. Scholl and Amy M. Iler conducted data analyses. Logan Novak and Joshua P. Scholl wrote initial drafts. All authors revised multiple versions of the manuscript.

ACKNOWLEDGMENTS

This work was funded by the Chicago Botanic Garden, Forest Preserves of Cook County, Openlands, U.S. Forest Service at Midewin National Tallgrass Prairie, The Nature Conservancy-Volunteer Stewardship Network, Chicago Wilderness, Illinois Wildlife Preservation Fund, and an Anonymous Foundation. We are grateful to our volunteer monitors, current and past Plants of Concern staff, and Susanne Masi, who founded the Plants of Concern program.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are not publicly available due to the threat of poaching rare species using location data. Data can be

requested after signing a data confidentiality form by contacting Amy Iler at ailer@chicagobotanic.org.

ORCID

Logan Novak  <https://orcid.org/0000-0002-8213-3098>

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SUPPORTING INFORMATION

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

How to cite this article: Novak, L., Scholl, J. P., Kiefer, G., & Iler, A. M. (2022). Prescribed burning has limited effects on the population dynamics of rare plants. *Conservation Science and Practice*, e12792. <https://doi.org/10.1111/csp2.12792>