

ARTICLE

Prescribed fire increases plant–pollinator network robustness to losses of rare native forbs

Susan M. Waters¹  | Rachel M. Mitchell²  | Emily R. Brown¹ | Ethan M. Taber²

¹Quamash EcoResearch, Olympia, Washington, USA

²School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA

Correspondence

Susan M. Waters

Email: susan@quamasheco.com

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Abstract

Restoration efforts often focus on changing the composition and structure of invaded plant communities, with two implicit assumptions: (1) functional interactions with species of other trophic levels, such as pollinators, will reassemble automatically when native plant diversity is restored and (2) restored communities will be more resilient to future stressors. However, the impact of restoration activities on pollinator richness, plant–pollinator interaction network structure, and network robustness is incompletely understood. Leveraging a restoration chronosequence in Pacific Northwest prairies, we examined the effects of restoration-focused prescribed fire and native forb replanting on floral resources, pollinator visitation, and plant–pollinator network structure. We then simulated the effects of plant species loss/removal scenarios on secondary extinction cascades in the networks. Specifically, we explored three management-relevant plant loss scenarios (removal of an abundant exotic forb, removal of an abundant forb designated a noxious weed, and loss of the rarest native forb) and compared them to control scenarios. Pyrodiversity and proportion of area recently burned increased the abundance and diversity of floral resources, with concomitant increases in pollinator visitation and diversity. Pyrodiversity also decreased network connectance and nestedness, increased modularity, and buffered networks against secondary extinction cascades. Rare forbs contributed disproportionately to network robustness in less restored prairies, while removal of typical “problem” plants like exotic and noxious species had relatively small impacts on network robustness, particularly in prairies with a long history of restoration activities. Restoration actions aimed mainly at improving the diversity and abundance of pollinator-provisioning plants may also produce plant–pollinator networks with increased resilience to plant species losses.

KEYWORDS

extinction cascade, grassland, native, network, plant–pollinator network, prescribed fire, pyrodiversity, restoration, robustness

This paper is dedicated to the memory of Jim (“Doc”) Waters.

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INTRODUCTION

Pollination services are critical to maintaining biodiversity and ecosystem function in terrestrial ecosystems, yet pollinator diversity is declining globally (Dicks et al., 2021). Although there is an increasing degree of awareness of the importance of managing to support pollination services, restoration projects rarely target animals such as pollinators directly. Instead, “restoration” usually connotes plant community-focused strategies such as prescribed fire, exotic plant removal, and augmenting native plant diversity, with the implicit expectation that these changes will drive increases in animal diversity and/or abundance (Guiden et al., 2021). A corollary is the hope that an ecosystem containing greater overall diversity will also be better able to withstand species extirpations in a rapidly changing world. However, at present, it is unclear whether typical actions aimed at restoring native plant communities consistently lead to (1) richer pollinator assemblages and (2) plant–pollinator communities with increased robustness to future species losses.

Although both grassland restoration and pollinator conservation are pressing (Bardgett et al., 2021; Dicks et al., 2021; Lark, 2020), common grassland restoration approaches such as invasive removal, prescribed fire, and even native replanting may not always benefit pollinators. For example, targeted removal of noxious or invasive shrubs or forbs could have local negative impacts on pollinators, since these plants often provide floral resources and easily integrate to become highly connected within pollinator networks (Parra-Tabla & Arceo-Gomez, 2021). The effects of fire on pollinators generally appear positive, but there may be differences between the effects of wildfires and prescribed fire. Typically, prescribed burning is intended to suppress non-fire-adapted invasive or woody plants and remove moss and litter, thereby reducing competition and promoting the spread of fire-adapted herbaceous native plants, whether already present or planted into the burn (Hamman et al., 2011). A locally pyrodiverse fire history can increase floral resource abundance, floral diversity, and bare ground availability for nesting, all of which may benefit pollinators (Burkle et al., 2019; Duquette et al., 2022; Potts et al., 2003; Van Nuland et al., 2013). However, fire effects are mediated by burn timing and intensity, and the lower-intensity fires that are typical of prescribed burns may have weaker or neutral effects on pollinators (Carbone et al., 2019; Glenney et al., 2022; Ponisio et al., 2016). Even the seeding or plugging of native herbaceous plant species will add floral resources for pollinators only if (1) a high proportion of the species being planted are forbs and (2) planted forb species survive,

establish, and persist (Lybbert et al., 2022; Wilkerson et al., 2014).

Even when restoration of plant communities does enhance pollinator abundance and diversity, the resilience of resulting plant–pollinator communities is unclear, in part because restored habitat fragments are often small and widely dispersed on the landscape. As isolated, fragmented plant communities are restored, adding pollinator richness requires pollinators to immigrate from grazed, cropped, forested, urban, or suburban areas, requiring considerable habitat flexibility and perhaps limiting immigration to generalist species (e.g., Ferreira et al., 2020; Ponisio, de Valpine, et al., 2019). Overall, fragmentation is associated with simplified plant–pollinator networks (Grass et al., 2018; Librán-Embid et al., 2021), changes in proportional representation of key pollinator traits such as body size, which may affect visitation patterns (Gerard et al., 2021; Warzecha et al., 2016) and isolation of unique interactions persisting only in small habitat fragments, making them especially vulnerable to additional habitat or species losses (Ferreira et al., 2020; Librán-Embid et al., 2021). Given that restored “islands” of habitat are now a norm in a fragmented world, these conditions may in turn reduce the robustness of pollinator networks and alter the likelihood of coextinction following the loss of one or more species, depending on rewiring capacity (i.e., capacity for species to alter interaction partners; Grass et al., 2018; Ramos-Jiliberto et al., 2012). Overall, there is good reason to ask whether restoration taking place in the context of extensive habitat fragmentation can effectively reassemble robust plant–pollinator communities.

Plant species losses that test network robustness to coextinction might arise both from typical management actions and stochastic fluctuations in rare plant populations. First, pollinator coextinctions (local extirpations of pollinators associated with local extirpation of a plant species) could occur if managers frequently target specific invasive or noxious pollinator-provisioning plant species for removal. These exotic forb species are often highly abundant, high-density resources when control is initiated, and as such, they may support foraging by multiple pollinator species and play central roles in networks (Grindeland et al., 2005; Kunin, 1993; Parra-Tabla & Arceo-Gomez, 2021). Therefore, losses (or very strong reductions in abundance) of exotic floral resources could potentially lead to secondary local coextinctions of pollinator taxa, at least when such resources are not immediately replaced with phenologically and/or architecturally comparable native flora. Second, pollinator coextinctions could occur when small remnant populations of rare native forbs are lost. This could occur if the native forb

provided pollinator-provisioning traits distinct from other plants at the site (i.e., high functional complementarity). These two possibilities, pollinator dependence on exotic forbs and pollinator dependence on rare native forbs, would suggest different management responses. For example, if exotic forbs are important to pollinators, efforts at control should be temporally and spatially distributed to conserve floral resources while replanting native forbs that could replace those resources. Conversely, if rare native forbs are important, efforts should focus on conserving those populations.

To understand how management activities affect floral resources, plant–pollinator network structure, and network robustness in highly fragmented landscapes, we quantified floral resources and pollinator visitation and constructed plant–pollinator networks for six prairie fragments covering a gradient of restoration, which we followed for 4 years. We then modeled secondary coextinction cascades and examined the relationship between extinction cascade size and the history of prescribed fire and replanting effort over the previous 10 years. Finally, we compared predicted extinction cascade sizes when rare native forbs or highly abundant exotic weeds were removed from the community. We posed the following questions: (1) Do pollinators respond positively to the changes in the floral environment produced by restoration activities, despite fragmented habitat? (2) How do typical prairie restoration activities (e.g., prescribed fire, native forb reseeding) shape the robustness of pollinator networks to plant species losses? (3) How do losses of rare plants versus removals of common exotic weeds differ in their effects on simulated secondary coextinctions in plant–pollinator networks? We hypothesized that positive changes in floral abundance and diversity would lead to increases in pollinator abundance and that management activities that promote floral abundance and diversity would improve metrics of pollinator networks correlated with robustness. We expected that losses of low-abundance rare plants from the floral community would have a smaller impact on secondary coextinctions than the removal of high-abundance exotic weeds.

METHODS

Study location

Our study takes place in remnant and restored prairie fragments in the southern Puget Sound Region, Washington State, USA. Specifically, we used six prairie sites spanning a restoration gradient and encompassing a range of initial forb species richnesses

in 2017 (Appendix S1: Table S1). The majority of western Washington prairie-oak savannah was historically burned by native inhabitants (Boyd, 1999) but has since been converted to agriculture or developed (Dunwiddie & Bakker, 2011). Remaining prairie fragments are typically small (10–50+ ha), disconnected, and located on preserves (Appendix S1: Figure S1). These fragmented prairies provide an excellent opportunity to examine how management actions aimed at returning native plants to degraded landscapes impact pollinators and their interactions with the plant community, because a relatively consistent management approach across multiple sites, starting at different times, has created a chronosequence of restoration actions and a resulting gradient of native forb richness (Appendix S1: Table S1). We took advantage of this gradient to establish study areas at six prairie fragments (Appendix S1: Figure S1) that ranged in site history from unrestored (no previous restoration actions; extremely low native plant richness; $n = 2$ native forb species) to highly restored (more than 15 years of prescribed fire, targeted removal of invasive plants, and seeding of native grasses and forbs; $n = 37$ native forb species, Appendix S1: Table S1).

Characterizing restoration actions

We characterized restoration and management actions at our sites for the 10 years preceding our study (2006–2016), as well as for the duration of the study (2017–2020), using spatially explicit records kept by land managers for each prairie fragment. A lack of consistent spatially explicit records stretching earlier than 2006 prevented us from extending the retrospective scope of the study; however, because these prairies are dominated by short-lived perennial species, 10 years is adequate time to document strong changes in plant community composition as “degraded” sites undergo restoration (Rook et al., 2011). Typical restoration and management actions in a “degraded” western Washington prairie, which may be iterative, include (1) preparing the site via prescribed fire in the fall; (2) seeding or plugging native grasses and forbs, also in the fall; and (3) removing persisting invasive grasses and forbs with low-intensity spot-spraying of herbicide (Rook et al., 2011).

For each year of our study (2017–2020), we created a set of spatially explicit explanatory variables reflecting restoration activities that might influence plant and pollinator grassland communities. We first used GIS to define buffers around our study area and then calculated the spatial overlap between these buffers and the area affected by the restoration action at the site in each year. Selecting an appropriate spatial buffer to examine the

effect of restoration on a whole plant–pollinator community is challenging. The proximity and extent of pollinator habitat adjacent to the focal restoration area may affect both (1) the abundance and (2) the species composition of local pollinators available to forage on new floral resources. We therefore evaluated the effects of restoration actions on our focal sites using a buffer of 250 m, which should accommodate foraging distances traveled by the majority of medium-sized solitary bees (Gathmann & Tscharntke, 2002), though larger-bodied bees may be affected by resources available outside this buffer (Greenleaf et al., 2007).

We chose to focus on variables describing restoration-associated prescribed fire and replanting of native forbs at our sites, two actions that are both likely to affect overall floral resource abundance and diversity and, therefore, pollinators. For prescribed fire, we calculated pyrodiversity (Jones & Tingley, 2022; Ponisio et al., 2016), an integrated measure of the spatial and temporal variation in fire history, for each site in each year, using spatially explicit burn data for the previous 10 years. Most prescribed burning took place in or adjacent to our buffer areas because we focused on areas actively undergoing habitat restoration for an endangered butterfly, Taylor's checkerspot (*Euphydryas editha taylori*). Pyrodiversity integrates fire history over time but does not reflect the effect of recent burning, which can lead to a flush of floral resources (Carbone et al., 2019); therefore, we also calculated the proportion of our buffer areas that had been burned within the past year ("recent burn"). To estimate the effects of management efforts to revegetate with native forbs, we combined records of the total grams of native forb seed sown and the total numbers of forb seedlings planted, to generate estimates of forb seed and seedlings added per buffer unit area for each year (excluding wind-pollinated forbs). Seeding and plugging are complementary strategies that may increase floral resources, but they were highly correlated with one another within sites and had been implemented inconsistently over time. We therefore combined the two variables to generate a single measure of "replanting effort" by scaling both variables by their maxima and adding scaled values together. Prescribed fire, seeding, and plugging often took place simultaneously, so we tested for multicollinearity between fire and replanting variables by verifying that variance inflation values were less than 3 for each factor.

After initial data exploration, we excluded exotic removal as a variable because hand-pulling and spot-spraying had been recorded as a yes/no at most of our sites, rather than as spatially explicit actions. This made it impossible to calculate the proportion of the buffer affected since exotic removal was opportunistic and since

all sites underwent these opportunistic removals in most years.

Plant community

At each site, we established a series of permanently marked 50-m transects, along which we collected floral density and composition data. In 2017, floral density and composition were collected at 15 points along each of 10 transects (150 m² per site); from 2018 to 2020, the same data were collected at 10 points along 12 transects per site (120 m² per site). We identified and counted floral units (inflorescences or flowers, depending on what was most easily counted) in 1-m² sampling quadrats approximately every 3 weeks for 1–2 days at each site between late April and July. We used these counts to estimate floral resource abundance by species in each quadrat, based on per-flowering-unit resource estimates from floral trait measurements described below and in Appendix S2.

In two cases, unplanned management actions and funding gaps affected our ability to collect a full data set across all sites in all years, although data were still adequate to address our questions. Specifically, in 2019, a funding gap made it impossible to sample one of the six sites, Glacial Heritage. In addition, mowing events prevented us from completing the fourth sampling date at another site, Deschutes, in 2017 and 2018. Mowing did not occur at our other sites over the duration of our study, and this disturbance at Deschutes was unlikely to affect our results because it was completed after virtually all forb flowering had finished at this forb-depauperate site.

Estimating floral resources by species

For best estimates of floral resources, we multiplied floral unit counts by estimates of per-floral-unit resources based on trait measurements collected both in the field and from the literature (Hegland & Totland, 2005). In 2021, we collected floral trait measurements at Glacial Heritage Preserve, where most forbs occurred ($n = 59$ species). We counted the number of flowers per floral unit (defined as either flower or inflorescence for ease of counting; see Appendix S2) on up to three floral units on each of 20 individuals for each species. We then measured floral dimensions for up to three flowers per floral unit and estimated resources provided per floral unit by calculating floral volume as described in Appendix S2. For an additional 18 species, we lacked floral measurements, usually either because the species flowered very

briefly in 2021 or because it was a small weedy species that was not abundant in 2021. We estimated resources for these species using floral measurements found in floras and herbarium specimens (Appendix S2: Figure S1). We multiplied per-floral-unit floral resource estimates by floral unit counts in quadrats to estimate floral resources for each species during each floral survey event and used these estimates as the floral resource response variable in all analyses.

Quantifying pollinator visitation

We performed floral patch-focused observation for each forb species in flower at a site, at approximately the same seasonal time points as the floral density data were collected. Overall observation time at a site on a given sampling date was therefore proportional to the number of forb species in flower. We selected an observation patch by choosing a random transect number to provide a general location in the field, then located the nearest floral patch for the target species where the number of observable floral units exceeded a minimum of 20 within an estimated area of approximately 2 m². We used this threshold to reject very low-density forb species for which visual display was unlikely to attract pollinators. Observers performed 15-min timed observations between approximately 08:00 am and 04:00 pm, when temperatures were between 15°C and 30°C, humidity was above 20%, and wind speed was less than 3 m/s. Observers captured and dispatched all insect visitors that contacted stamens or stigmas. Lepidoptera and queen bumble bees were excluded from captures and identified on the flower, due to conservation considerations. Timing was paused during specimen handling. Two observations were performed for every forb species at a site at each time point, carried out by different observers and with different diurnal timing to the greatest degree possible. Specimens were later identified to the lowest taxonomic level possible by taxonomic experts (e.g., genus or species for most bees and flies).

Plant and pollinator mutualism dependence

We estimated plant dependence on pollinators for reproduction and pollinator dependence on floral resources for every taxon and used these values to parameterize matrices in coextinction simulations. Plant dependence on pollinators was estimated with field experimental pollinator exclusions for 31 forb species (Appendix S3: Table S1). We performed literature searches for an additional 44 species, which were

binned into “high,” “medium,” or “low” categories and assigned a value between 0 and 1 using a random draw based on category (Appendix S3). Pollinator dependence on plants was assigned similarly, using literature-based life history information to assign a range of values between 0 and 1 for various taxonomic groups (e.g., dependence values limited between 0.9 and 1 for bees, which require floral resources to complete their life cycle), then performing a random draw within the designated range.

Analytical methods

All analyses were performed in R version 4.1.2 (R Core Team, 2021).

Restoration actions, floral resources, and pollinator abundance and diversity

We built a series of generalized additive models to explore how restoration actions affected floral resource availability and pollinator activity at our sites (mgcv package; Wood, 2011). Specifically, we modeled both site-level floral resources and site-level Shannon floral diversity as a function of pyrodiversity, proportion of area burned in the previous year (recent burn), and cumulative replanting (scaled cumulative grams of forb seed spread over the previous 10 years + scaled cumulative number of forb plugs planted over the previous 10 years; all wind-pollinated forb species excluded). In these and all floral and pollinator models, we explored interactions between the restoration variables and iteration (seasonal time point) and compared models with and without site and iteration used as random intercepts to account for repeated measures over multiple years. We also evaluated models that incorporated variance structure based on differential variance in sites and iterations. We were unable to explore interactions between restoration variables to accommodate potential contingencies between replanting and prescribed fire due to high variance inflation factors when interaction terms were introduced, so all models are additive only. For these and all models, we first compared a set of full models with alternative distributional assumptions appropriate to the data type (e.g., Tweedie vs. Gaussian models for continuous data) and selected an appropriate full-model structure using likelihood ratio tests by comparing Akaike information criterion values.

Pollinator visitation (total pollinator visits for all pollinator species observed) and Shannon diversity of visiting pollinators were calculated for a given site, iteration, and year. In some cases, a forb species had a flowering patch that had been observed for pollinator visits but was too

rare to have been detected in our floral abundance transects. We considered the undetected forb species to have the minimum nonzero floral resource value and added the same value to floral resource measurements for all other observed plant species within each site/year in order to convert these zero floral resource measures to tiny values that reflected the fact that the plant species was present and allowed us to include their observations in the model data. In addition, for 0.7% of floral observations, a second 15-min observation was missed; in these cases, counts from the single observation were doubled to estimate visitation. We used models for visitation and pollinator diversity that included site-level floral diversity and log-transformed site-level floral resources as explanatory variables. We also included pyrodiversity and percentage recently burned (but not replanting, since it was correlated with floral diversity) as additional explanatory variables, since fire might affect pollinators directly as well as via floral resources. We included a random intercept for site to account for repeated measures across years.

Plant–pollinator interaction networks

We built interaction networks for each site and year, weighting interactions by mean floral resource abundance of the plant and visitation frequency of the insect. Given that one goal of restoration in these systems is explicitly to increase network size (i.e., support greater plant and pollinator richness), we did not use *z*-score standardization; rather, comparisons between sites were made in the context of management goals and considered in light of changing network sizes. We used the bipartite package in R (Dormann et al., 2008, 2009) to produce metrics of network size, connectance, nestedness, modularity (*Q*), and interaction diversity (*H2'*) for each network in each year. Nestedness (measured as nestedness metric based on overlap and decreasing fill [NODF]; Almeida-Neto et al., 2008) is a measure of the degree to which species interact with a subset of the interaction partners of more generalized species in the community (Bascompte et al., 2003; Vázquez et al., 2007). Modularity measures compartmentalization within networks, in which subgroups (modules) of species interact more frequently among themselves than with other members of the network (Girvan & Newman, 2002; Olesen et al., 2007; Ponisio, Valdovinos, et al., 2019).

Using generalized linear mixed-effects models via the glmmTMB and lme4 packages in R (Bates et al., 2014; Brooks et al., 2017), we modeled all six of these network metrics for whole-year networks as a function of pyrodiversity, proportion area recently burned, and cumulative replanting, using site as a random intercept.

Simulating secondary extinction cascades in response to management actions

We followed the approach of Vieira and Almeida-Neto (2015) to simulate secondary extinction cascades initiated by loss of a specific native or exotic plant species (stochastic coextinction models [SCMs]). This approach entails building matrices of plant–pollinator interactions, in which interactions are parameterized by (1) their proportional frequency and (2) the intrinsic demographic dependence of each species on the mutualism (i.e., nutritional dependence of pollinators on floral resources and reproductive dependence of plants on insect-mediated pollen transfer).

We compared six species loss scenarios, which we executed for every network (within site and year). The first three scenarios attempted to establish scales of cascades for comparison: (1) Loss of the forb in the network with the greatest richness of visiting insect taxa, that is, the one with the highest normalized species degree. This scenario was intended to provide an upper bound for secondary cascade size. (2) Loss of the forb with the lowest species degree. (3) Loss of a randomly selected forb, simulating stochastic species loss. We compared these with three scenarios mimicking management-relevant scenarios: (4) Loss of a dominant exotic forb. This scenario could occur through deliberate management, for example, by spraying to control an invasive species. We simulated this scenario by removing the most abundant exotic plant species from every network. (5) Loss of the most abundant forb that was also designated as a noxious weed, which in some circumstances might be both a target for mandated control and an important pollinator resource. We simulated this scenario by removing the most abundant noxious weed from every network. (6) Loss of a rare native forb. Loss of a rare native could occur stochastically due to small population sizes or as a result of climate change or other global change agents, especially if the species is near its range limit. We simulated this by removing the lowest-abundance native forb from every network. We performed 500 simulations of each scenario and divided each resulting secondary extinction cascade size by its associated network size. Using generalized linear mixed-effects models, we modeled log(cascade size) as a function of pyrodiversity, proportion area recently burned, cumulative replanting, and scenario, using site as a random intercept.

RESULTS

We performed 1206 observations and documented 6227 plant–pollinator interactions between 84 plant species and 330 insect taxa. Flower visitation was dominated by

bees (48.0%) and flies (38.0%), with lower visitation from beetles (5.7%), wasps (3.6%), Lepidoptera (0.5%), and others (e.g., ants) (4.2%).

Management actions changed both the abundance and diversity of floral resources available to pollinators (Appendix S1: Figure S2a–d, Table S2). Mean floral resource abundance increased with the proportion of the site burned the previous year (“recent burning”) and with pyrodiversity (contingent on seasonal time point; Appendix S1: Table S2, Figure S2a,b). Floral diversity likewise increased with pyrodiversity and recent burning (Appendix S1: Table S2). We did not detect an effect of cumulative replanting on either floral resource abundance or floral diversity (Appendix S1: Table S2, Figure S2d). Mean proportion of floral resources attributed to native forbs also increased in response to both pyrodiversity ($\chi^2[1] = 4.86$, $p < 0.027$) and recent burning ($\chi^2[1] = 4.73$, $p = 0.030$).

Mean pollinator visitation frequency and mean pollinator diversity were positively affected by changes in floral resource abundance and diversity (Figure 1a; Appendix S1: Table S3). Pyrodiversity also increased pollinator diversity directly (i.e., beyond the effect of changes to the floral environment; Figure 1b). Estimated plant dependence by flower-visiting taxa averaged 0.68 ± 0.02 , and pollinator dependence by forbs (both measured and estimated) averaged 0.64 ± 0.09 for native forbs and 0.45 ± 0.13 for exotic forbs (Appendix S3: Table S1).

Management by burning increased network size marginally, both via pyrodiversity ($\chi^2[1] = 4.21$, $p = 0.040$) and via effects of recent burning ($\chi^2[1] = 4.00$, $p = 0.045$; Appendix S1: Table S4). Burning and replanting history also affected network structure (Figure 2). Increasing pyrodiversity was associated with increased modularity ($\chi^2[1] = 7.38$, $p = 0.007$; Figure 3b), decreased connectance ($\chi^2[1] = 9.42$, $p = 0.002$, Figure 3b), and slightly decreased nestedness (nodf $\chi^2[1] = 4.51$, $p = 0.034$, Figure 3b), mediated by a strong negative relationship between network size and both of these metrics. There was a similar but nonsignificant decreasing trend in connectance in response to replanting effort (Figure 3a; $\chi^2[1] = 2.85$, $p = 0.091$). We did not detect significant effects of burning or replanting on interaction diversity (H2'; Figure 3a–c; Appendix S1: Table S4).

In all six species loss/removal scenarios, the magnitude of secondary extinction cascades diminished as pyrodiversity increased ($\chi^2[1] = 16.218$, $p < 0.001$) and as replanting effort increased ($\chi^2[1] = 5.36$, $p < 0.021$), with slopes differing among species removal scenarios ($\chi^2[1] = 100.19$, $p < 0.001$; Figure 4a,b; Appendix S1: Table S5). As expected, the largest secondary cascades occurred in response to loss of the highest-degree forb and the smallest cascades in response to loss of the

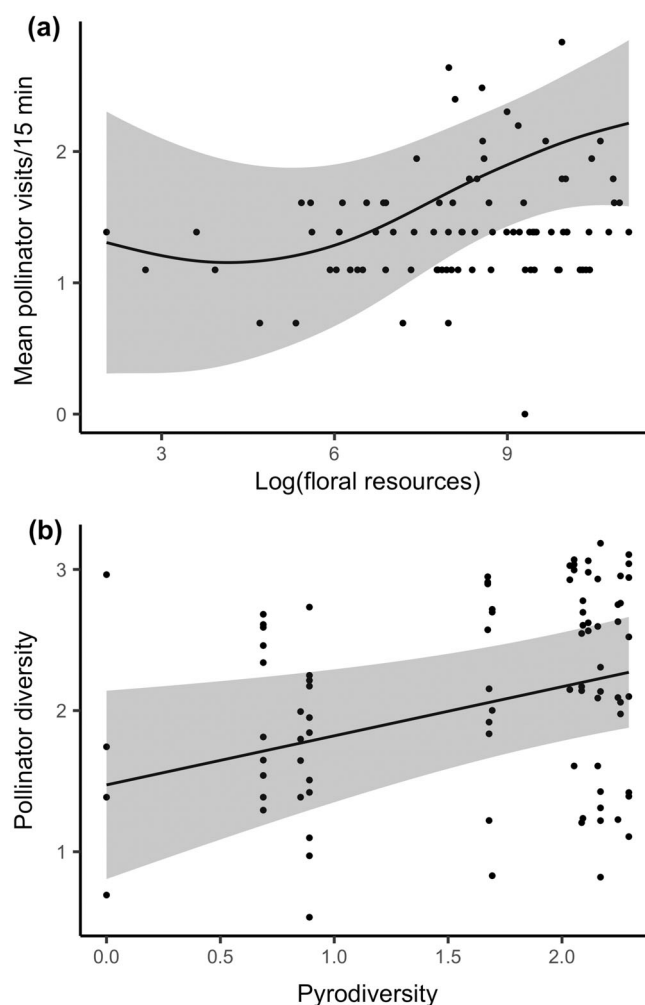


FIGURE 1 Pollinator responses to floral resources availability and management via prescribed fire. (a) Pollinator visitation increases with floral resources in the early season, which in turn increase with pyrodiversity and proportion of area burned with the past year (Appendix S2: Table S2). (b) Pollinator diversity increases in response to pyrodiversity, over and above pyrodiversity effects on floral resource abundance and floral diversity.

lowest-degree forb, with loss of a random forb producing cascades of intermediate size (Figure 5; Appendix S1: Table S6). At low levels of replanting effort and low levels of burning, loss of a rare forb produced mean secondary extinction cascade sizes similar to those produced by loss of a high-degree forb. Cascade size decreased strongly with pyrodiversity and replanting in the rare-forb-loss scenario (Figure 4a,b; Appendix S1: Table S6). Removal of the dominant exotic forb or the most abundant noxious weed produced smaller cascade sizes than loss of a highly connected forb or a rare forb, particularly when pyrodiversity and replanting effort were low.

The mean degree of the plant species removed was equivalent for random, rare native, dominant exotic, and dominant noxious weed removal scenarios, and these

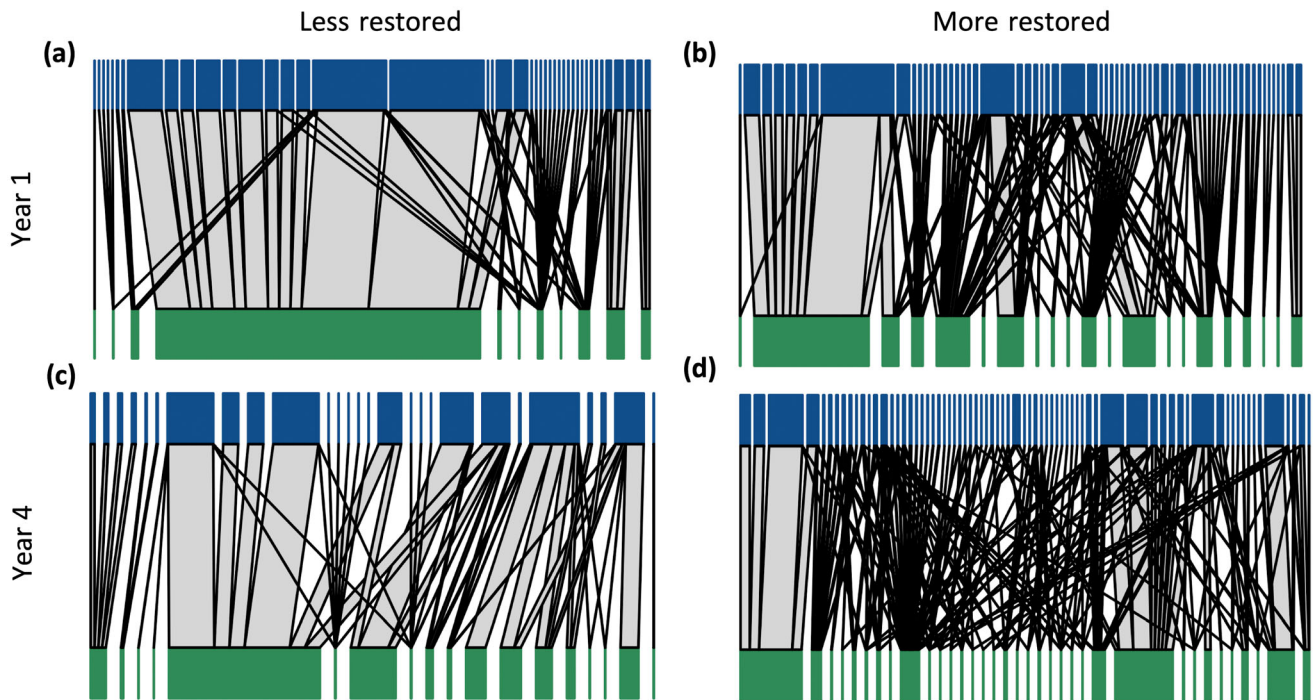


FIGURE 2 Sample network structures at a less-restored site (left panels) and a more-restored site (right panels). In Year 1, the less-restored study area (a) had been affected by only one previous prescribed burn, with no native forb replanting, over the previous decade. By contrast, portions of the more-restored site shown here (b) had been partially burned in seven prescribed fire events, with native forbs seeded in or plugged after some of the fires. All sites continued to be managed with fire, seeding, and/or plugging throughout the 4 years of our study. Top panels (a, b) show plant–pollinator networks in the first year of the study, 2017; bottom panels (c, d) show networks for the same sites in 2020.

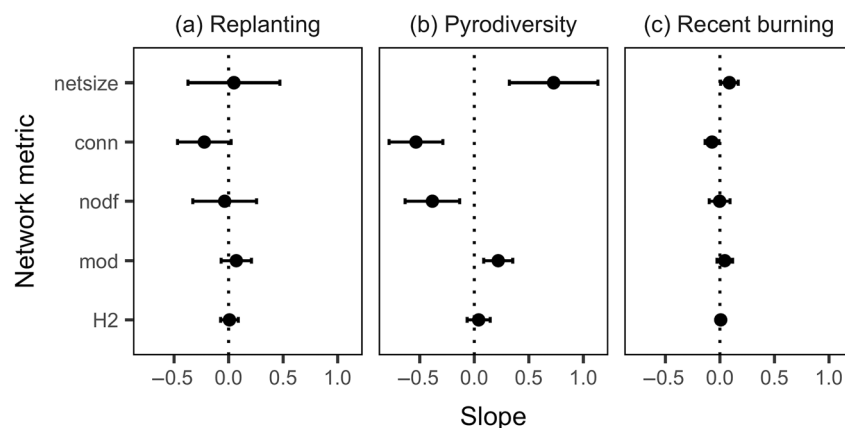


FIGURE 3 Slopes and 95% CIs for generalized linear models relating six network structural metrics to (a) replanting effort, (b) pyrodiversity, and (c) proportion of area burned within the previous year.

values were bracketed by the mean species degrees for low-degree and high-degree plant species removals (Figure 5). However, equivalent mean species degree among these scenarios did not lead to similar effect sizes when species were removed. Specifically, the scenarios with equivalent species degree nevertheless differed in the mean magnitude of secondary extinction cascade size produced by species removal (Figure 5), with the removal of rare native species associated with cascades up to twice

as large as those produced when noxious or exotic plant species were removed.

DISCUSSION

Our results demonstrate that the cumulative effects of typical restoration activities like prescribed fire and replanting restructured plant–pollinator networks,

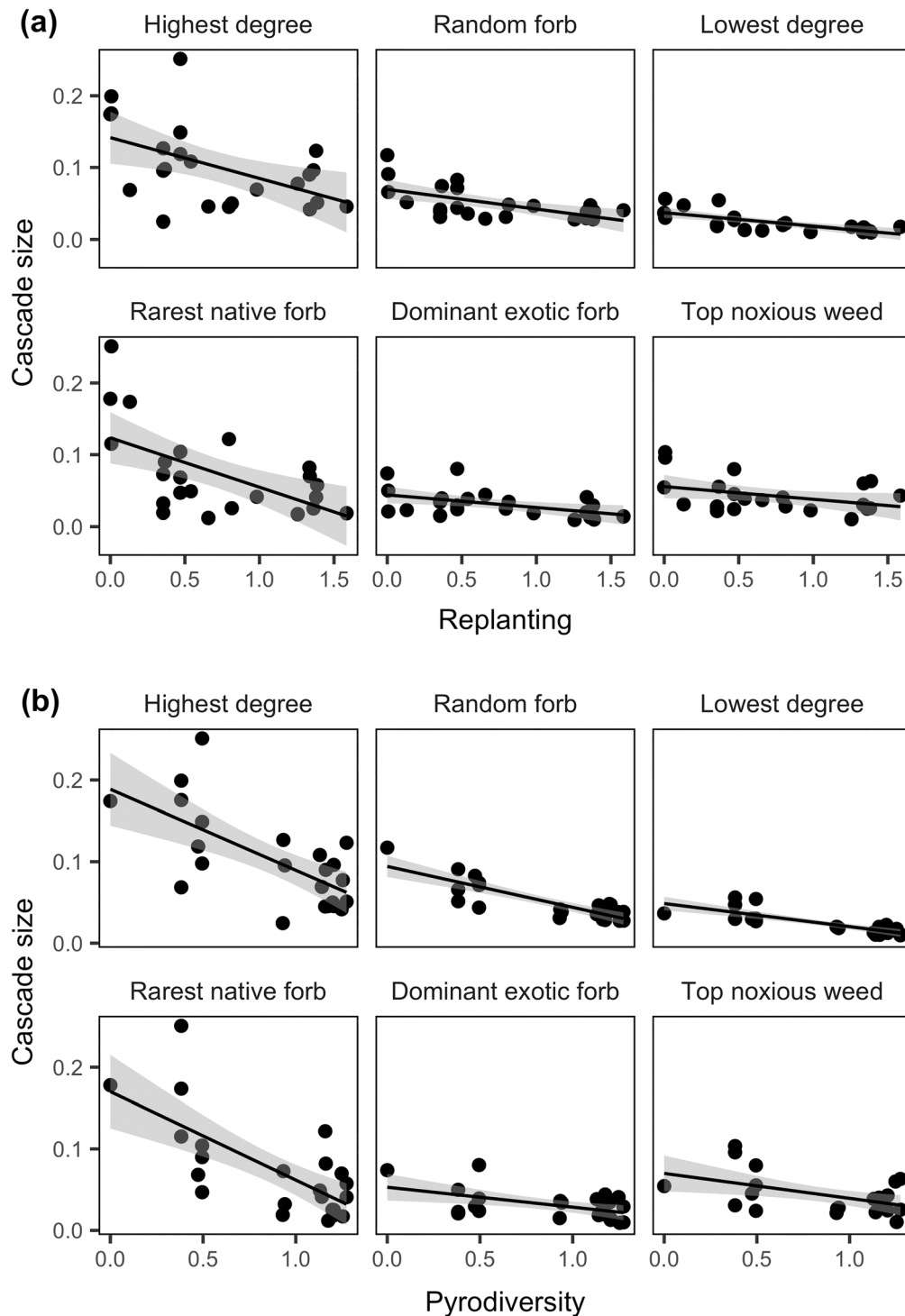


FIGURE 4 Relationship between secondary extinction cascade size and management history for six species loss/removal scenarios. Cascade size is the mean proportion of secondary extinctions. (a) Cascade size in relation to cumulative replanting effort (scaled mean grams of seed plus scaled mean number of plugs); (b) cascade size in relation to pyrodiversity. Each data point is the mean of 500 extinction cascade simulations for one site in 1 year.

leading to greater network robustness to secondary extinctions across multiple species loss scenarios. Like other grassland restoration studies, we find that management actions such as prescribed fire and replanting are

positively related to floral resource availability and pollinator visitation rates. In addition, we documented changes in community structure via decreased connectance, decreased nestedness, and modestly

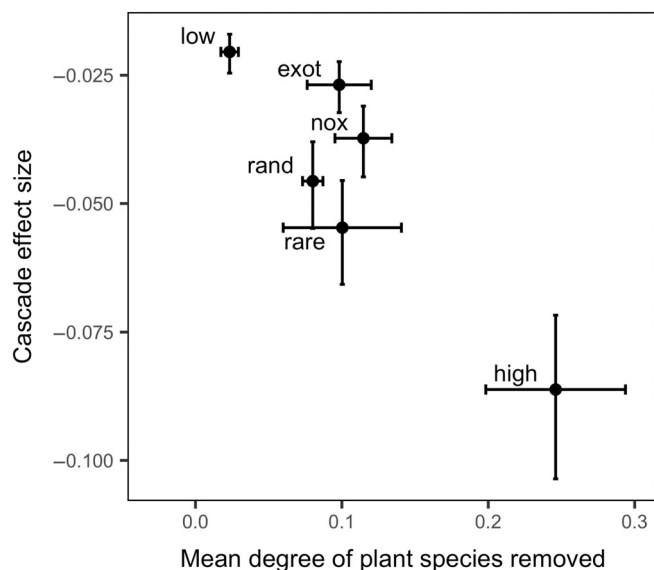


FIGURE 5 Mean reduction in secondary extinction cascade size as a function of mean species degree of the plant species removed in each scenario.

increased modularity as restoration progressed and plant and insect richness increased. These patterns were detectable even as highly fragmented and disconnected prairie habitats were restored. Finally, we found that at the early stages of restoration (little burning or replanting history), loss of a low-abundance native forb led to larger predicted secondary coextinction cascades than loss of a dominant exotic forb or a noxious weed, suggesting that rare native plants may have played a disproportionately important role in structuring networks in these florally depauperate sites.

Both long-term fire history (pyrodiversity) and short-term fire effects (proportion of area burned within the previous year) increased the diversity and abundance of floral resources for pollinators, in keeping with results from many previous studies in grassland restoration (Lettow et al., 2018; Mola & Williams, 2018; Valko et al., 2016). Fire alters competitive interactions and may favor native fire-adapted forbs over the invasive perennial grasses that have more recently played large roles in western Washington prairies (Hamman et al., 2011). We did not detect a clear effect of replanting effort; this may reflect uneven efforts (both seeding and plugging were inconsistent in intensity after fires) or the fact that a high proportion of seeding and plugging fails across restoration projects generally (Lybbert et al., 2022; Wilkerson et al., 2014).

Pollinators responded positively to the changes in the floral environment, supporting the notion that restoration at one trophic level benefits diversity at other trophic levels (Guiden et al., 2021; Kaiser-Bunbury et al., 2017).

Greater community floral diversity may support more pollinators by providing a wider array of floral architectures, phenologies, and resource types, which in turn offers more scope for pollinator dietary niche complementarity and reduction of competition (Kratschmer et al., 2021; Loy & Brosi, 2022; Tilman et al., 2014). These benefits accrue to populations already occupying these fragmented and degraded sites, and if nearby refugia harbor additional species, augmenting floral diversity may promote recolonization of the site and possibly even connectivity of the metacommunity (Ponisio, de Valpine, et al., 2019). Other recent work has also documented increases in pollinator diversity in response to prescribed fire (Ponisio et al., 2016; Ulyshen et al., 2022). Interestingly, pollinators responded to prescribed fire over and above floral diversity, suggesting that fire had direct effects on pollinators as well as indirect effects via floral resources. We speculate that the restructuring of perennial grass-invaded habitat through repeated burning may increase access to nesting habitat for ground-nesting pollinators by removing mosses, lichens, or thatch and increasing bare ground, especially if native bunchgrasses benefit (Calabria et al., 2016; Hamman et al., 2011). However, other mechanisms, such as changes to rates of larval survival or predation on pollinators, might also be mediated by the habitat restructuring.

Network robustness to species losses increased with burning and replanting in all species removal scenarios regardless of the identity of the species removed, implying that network-level characteristics were responding to restoration. In particular, we observed changes in four key network structural metrics in tandem with increasing management by prescribed fire. First, network size, or overall richness of interactors, increased with both pyrodiversity (a measure of fire history) and with the proportion of area recently burned (Appendix S1: Table S4). Prescribed fire has also been associated with increased network size in other studies (Glenny et al., 2022; Ponisio et al., 2016). Second, as network size increased, we observed decreased connectance, a pattern often documented by others (e.g., Campbell et al., 2015; Olesen & Jordano, 2002). We speculate that this reduction in connectance arises as the increasing number of forb species offers pollinators more foraging choices, thereby reducing the number of pollinator taxa that visit any particular forb and decreasing the overall connectance of the network. Lower connectance, in turn, is associated with fewer secondary extinctions in SCMs (Vanbergen et al., 2017; Vieira & Almeida-Neto, 2015), and the reduction in connectance may explain why extinction cascade size decreased with prescribed fire. Third, networks also became less nested in response to increasing pyrodiversity, implying less dietary niche

overlap for pollinators and/or less sharing of pollinators by plants. This change may be due to a diminishing influence of invasive perennial forbs since invasive forbs attractive to flower-visiting insects can be associated with higher nestedness (Bartomeus et al., 2008; Campbell et al., 2015). Finally, modularity increased slightly with pyrodiversity.

Our simulated species removals highlighted the importance of rare forbs to plant–pollinator network robustness in highly degraded prairies. Our findings suggest that small, remnant populations of native forbs can play outsized roles in sustaining plant–pollinator networks when floral diversity is low (in contrast to the mass ratio hypothesis; Grime, 1998). Despite the fact that the rare native forbs we removed (1) appeared proportionally unimportant in terms of overall floral resources provided and (2) had normalized species degree (number of mutualist partners) equivalent to the exotic and noxious forbs we removed, their mean effect on coextinction when lost from the network was greater than that of other simulated plant losses, especially in sites that had experienced little restoration (Figures 4a,b and 5). We speculate that these rare native forbs might host visiting pollinator assemblages that have a higher mean dependence on the mutualism (depend more heavily on flowers for nutrition, e.g., more bee taxa and fewer nonsyrphid fly taxa). Higher mean plant dependence among target plants' pollinators could lead to stronger propagation of extinctions. Similarly, exotic forbs whose removal caused small effects might be provisioning less-dependent pollinators on average, for whom losing a floral resource would have a lower impact. This in turn could result from traits such as provision of particular floral resource types (e.g., rare native forbs providing nutritional profiles of nectar or pollen that are locally rare in heavily invaded sites). This opens an area for further inquiry: what traits or evolutionary histories of rare native forbs might contribute to strong effects in secondary extinction cascades? Regardless, these findings highlight the importance of conserving small existing populations of native forbs to the greatest degree possible.

The impact of losing a rare native forb also depended strongly on burning and replanting history, while the impact of removing a dominant exotic or noxious forb showed a weaker relationship. When sites were less restored, the effect of losing a rare native forb was high; however, at high levels of pyrodiversity or replanting, loss of a rare species produced smaller cascades, of similar magnitude to removal of noxious weeds or numerically dominant exotic forbs. One possible explanation for this result is that the size and/or connectance of the networks interact with the functional roles of individual forb species. For example, it is possible that rare forbs that play

key roles at lower network size (i.e., in less-restored sites) play increasingly functionally redundant roles as network size increases with restoration (e.g., Devoto et al., 2012; Ponisio, 2020) and, therefore, trigger smaller losses when removed. This result bolsters the importance of restored plant and pollinator species richness in buffering potential stochastic plant species losses in the context of climate change and other environmental stressors. However, since we cannot disentangle the effects of changing network size and architecture from other potential direct effects of burning and replanting (e.g., changes in pollinator nest site availability), it is possible that factors besides species richness and network structure also mediate the effect of losing a rare native forb.

Despite the abundant floral resources that can be provided by dominant noxious or exotic weeds and the fact that these species tend to easily integrate into existing pollinator networks (Parra-Tabla & Arceo-Gomez, 2021), simulated removal does not always have strong negative effects on pollinators. Contrary to our initial hypothesis, loss of dominant exotic forbs or noxious weeds in less-restored sites did not produce large cascades. This result was somewhat surprising. These exotic species were foraged on regularly in our study by multiple insect taxa, showing that they were not intrinsically undesirable. In the field, exotic species frequently formed large, showy patches, and floral neighborhood display frequently plays a strong role in attracting pollinators to forage at a patch of flowers (Ghazoul, 2006; Grindeland et al., 2005; Mitchell et al., 2004; Waters et al., 2014, 2020). Furthermore, on the basis of density, we might expect the resource patches produced by dominant exotic forbs to be preferred to the more diffuse, smaller patches created by remaining native forbs in degraded prairie, at least when pollinators forage optimally (Kunin, 1993; Pyke, 1984). Yet removing exotic forbs (whether noxious or not) produced a weaker effect than removing rare natives, again suggesting that qualities other than abundance govern the impacts of weed removal on pollinators. This provides support for the common management practice of targeting abundant weeds, even when they do supply floral resources.

Though our simulations benefit from recent innovations in modeling the dynamics of coextinction cascades in plant–pollinator networks, they still cannot fully account for the role of pollinator behavior in mediating cascades. SCMs have provided significant improvements to early modeling of coextinction cascades by incorporating estimates of species' dependence on mutualistic interactions (Vieira & Almeida-Neto, 2015). However, pollinator behavioral flexibility may still affect outcomes. The majority of pollinators have the capacity to forage at multiple

flowering species, and with the loss of a floral resource, insects are likely to alter their foraging patterns to accommodate the loss (Brosi et al., 2017), potentially including movement to plants we have not previously seen them visit (rewiring; Ramos-Jiliberto et al., 2012). This dietary flexibility could attenuate the extinction cascades we modeled. However, even if true cascade size is smaller than our simulations predict, the floral resource removals would certainly increase pollinator niche overlap and, thus, increase resource competition between pollinator taxa for plants remaining in the rewired network. In addition, switching to a less-preferred host plant can result in inferior nutrition for pollinators (Donkersley et al., 2017).

Our finding that pyrodiversity increased resilience to coextinction losses contrasts with other recent work (e.g., Ponisio, 2020). This contrast may be due either to true differences in the effects of fire on the plant–pollinator communities studied or to methodological differences in modeling coextinction. For example, variation in fire intensity, which we were unable to incorporate in our study, would certainly affect the composition of plant and pollinator assemblages; very hot fires could eliminate some ground-nesting bees, while cooler fires might leave some patches of floral resources intact. In addition, accounting for the dependences of plant and pollinator species on the mutualism affects the outcome of coextinction models (Vieira & Almeida-Neto, 2015). As coextinction modeling becomes ever more nuanced, we advocate for continuing to explore the effects of restoration and prescribed fire with models that incorporate indirect effects.

We incorporated 10 years of spatially explicit native forb replanting and prescribed fire into our analysis, but there are additional restoration variables we were unable to include. Specifically, opportunistic maintenance via spot spraying or hand pulling of invasive exotic plants such as tall oatgrass (*Arrhenatherum elatius*) and Scotch broom (*Cytisus scoparius*) typically took place at least annually at the preserves where we worked, but we were unable to obtain spatially explicit records to determine where these activities overlapped with our study areas. We are therefore unable to determine the role that these variables may play. However, spot spraying and hand pulling were typically focused on exotic plants that either (1) were not pollinator resources (invasive grasses) or (2) already had been managed to very low density by the time we began our study. Therefore, we believe it is likely that the majority of the change we observed resulted from the variables we measured. In addition, all of our exotic and noxious removal simulations focused on species that were still occurring at high density.

Given the ongoing biodiversity crisis and the particular vulnerability of pollinator species globally, there is

an urgent need to understand the nuances of how plant restoration influences biodiversity at multiple trophic levels and to use practices that can best support ecological function and robustness to future species losses. We encourage further work to investigate how restoration and management actions affect plant–pollinator network robustness and whether the traits of relatively rare interactors can play key roles in low-richness systems. We also advocate for further exploration of how restoration affects networks that involve additional interactors that remain relatively understudied in restored plant communities, such as insect herbivores, seed predators, and soil biota. Understanding such networks and how they respond to restoration can continue to refine adaptive management and support conservation.

AUTHOR CONTRIBUTIONS

Susan M. Waters conceived of the experimental design, collected and analyzed data, and led manuscript writing and editing. Rachel M. Mitchell contributed to analysis, manuscript writing, and editing. Emily R. Brown and Ethan M. Taber contributed to analysis of spatial data.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Waters, 2023) are available in Dryad at <https://doi.org/10.5061/dryad.crjdfn38j>.

ORCID

Susan M. Waters  <https://orcid.org/0000-0003-2696-349X>

Rachel M. Mitchell  <https://orcid.org/0000-0002-0867-9068>

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SUPPORTING INFORMATION

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

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