

Biotic and abiotic drivers of plant–pollinator community assembly across wildfire gradients

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Abstract

1. Understanding how abiotic disturbance and biotic interactions determine pollinator and flowering-plant diversity is critically important given global climate change and widespread pollinator declines. To predict responses of pollinators and flowering-plant communities to changes in wildfire disturbance, a mechanistic understanding of how these two trophic levels respond to wildfire severity is needed.
2. We compared site-to-site variation in community composition (β -diversity), species richness and abundances of pollinators and flowering plants among landscapes with no recent wildfire (unburned), mixed-severity wildfire and high-severity wildfire in three sites across the Northern Rockies Ecoregion, USA. We used variation partitioning to assess the relative contributions of wildfire, other abiotic variables (climate, soils and topography) and biotic associations among plant and pollinator composition to community assembly of both trophic levels.
3. Wildfire disturbance generally increased species richness and total abundance, but decreased β -diversity, of both pollinators and flowering plants. However, reductions in β -diversity from wildfire appeared to result from increased abundances following fires, resulting in higher local species richness of pollinators and flowers in burned than unburned landscapes. After accounting for differences in abundance, standardized effect sizes of β -diversity were higher in burned than unburned landscapes, suggesting that wildfire enhances non-random assortment of pollinator and flowering-plant species among local communities.
4. Wildfire disturbance mediated the relative importance of mutualistic associations to β -diversity of pollinators and flowering plants. The influence of pollinator β -diversity on flowering-plant β -diversity increased with wildfire severity, whereas the influence of flowering-plant β -diversity on pollinator β -diversity was greater in mixed-severity than high-severity wildfire or unburned landscapes. Moreover, biotic associations among pollinator and plant species explained substantial variation in β -diversity of both trophic levels beyond what could be explained by wildfire and all other abiotic and spatial factors combined.
5. *Synthesis.* Wildfire disturbance and plant–pollinator interactions both strongly influenced the assembly of pollinator and flowering-plant communities at local and regional scales. However, biotic interactions were generally more important drivers of community assembly in disturbed than undisturbed landscapes. As wildfire

regimes continue to change globally, predicting its effects on biodiversity will require a deeper understanding of the ecological processes that mediate biotic interactions among linked trophic levels.

KEYWORDS

beta-diversity, disturbance severity, global environmental change, mutualism, plant-pollinator networks, pollination, species interactions, species sorting

1 | INTRODUCTION

Biotic interactions among species are critical to the maintenance of biodiversity (Bascompte et al., 2006), the responses of ecosystems to environmental change (Brooker, 2006; Suttle et al., 2007) and the stability of ecosystem services (Dobson et al., 2006). Among the many types of biotic interactions that contribute to ecosystem services, mutualistic interactions among pollinators and flowering plants play key roles in the production of food for humans and many other animal species and the maintenance of biodiversity across trophic levels (e.g. Burkle et al., 2013; Sargent & Ackerly, 2008; Wolowski et al., 2017). However, plant-pollinator interactions and pollination services may be strongly affected by global environmental change (Ponisio et al., 2016; Tylianakis et al., 2008). While substantial progress has been made in determining the effects of global-change drivers on plant-pollinator interactions and biodiversity (Knight et al., 2018), the relative importance of abiotic and biotic processes that underlie the assembly of plant-pollinator communities remains poorly understood (Burkle et al., 2016).

Alterations to natural fire regimes may have some of the most important impacts on the assembly, composition and diversity of plant and pollinator communities (Burkle et al., 2015; Pausas & Verdú, 2008; Ponisio et al., 2016; Simanonok, 2018). In many ecosystems worldwide, the frequency and severity of wildfire disturbance is predicted to increase with global environmental change (Abatzoglou & Williams, 2016; McLauchlan et al., 2020; Westerling et al., 2006). Some of the largest ecological effects of disturbances may be their influence on site-to-site variation in community composition (β -diversity; Catano et al., 2017; Dornelas et al., 2014). β -diversity can be important for the maintenance of species diversity at regional scales when disturbance increases species turnover among sites (Anderson et al., 2011; Myers et al., 2015). Understanding the processes that drive β -diversity is also important because β -diversity can determine several important large-scale ecosystem functions such as crop pollination (Winfree et al., 2018).

Theory predicts that wildfire severity could influence several key assembly processes that determine plant and pollinator β -diversity. First, high-severity fires may decrease β -diversity by homogenizing species composition across sites. For example, high-severity fires might cause biotic homogenization by selecting for traits that confer fire tolerance in plant communities (Burkle et al., 2015; Pausas & Verdú, 2008). Pausas and Verdú (2008) found that Mediterranean plant communities with high fire frequency were more phenotypically

clustered in terms of fire-persistence traits than communities with low fire frequency. In addition, fire may homogenize species composition by increasing the total number of individuals in local communities (local abundance) so that more species from the regional species pool occur at each site, leading to higher local species richness (Burkle et al., 2019; Catano et al., 2017). For example, fire disturbance may increase local abundances of pollinators and plants by increasing the availability of resources necessary for reproduction or establishment (Burkle et al., 2019).

Second, fires may increase β -diversity through deterministic or stochastic assembly processes. High β -diversity may result from deterministic sorting of species among sites when mixed-severity fires ('pyrodiversity') increase heterogeneity in environmental factors that select for species with different fire tolerances or resource requirements across sites. At least two studies have shown that pyrodiversity increases β -diversity. Across three forest ecosystems in the Northern Rocky Mountains, Burkle et al. (2015) found higher β -diversity of herbaceous plants (forbs) in sites with mixed-severity wildfire compared to sites with high-severity wildfire. In mixed-conifer forest, Ponisio et al. (2016) found that β -diversity of flowering plants, but not pollinators, increased more strongly with geographical distance among sites with low and medium wildfire severity compared to sites with high wildfire severity. Alternatively, high β -diversity may result from ecological drift when fire decreases local abundance (i.e. community size) at random with respect to species identity (Myers et al., 2015). In oak-hickory forest, Myers et al. (2015) found that higher β -diversity of woody plants in burned than unburned sites was associated with smaller community size, rather than stronger species sorting, in burned sites. Finally, fire may alter the composition and relative abundances of species in the regional species pool (Burkle et al., 2015), which may influence the effect of fire on β -diversity and local species richness (Burkle et al., 2016). Despite growing interest in the responses of pollinator and plant biodiversity to changing fire regimes (Carbone et al., 2019; Koltz et al., 2018; McLauchlan et al., 2020; Ponisio et al., 2016), the extent to which fire disturbance plays similar or different roles in the assembly of plant and pollinator communities remains largely unknown.

Mutualistic interactions among pollinators and flowering plants may complement or mediate the influence of fire disturbance on plant-pollinator community assembly. Yet, little is known about the relative contributions of biotic and abiotic factors to patterns of β -diversity (Chase, 2010) because relatively few studies

in community ecology have explicitly examined the influence of the biotic environment on β -diversity (Bagchi et al., 2014; Chase et al., 2009; Dyer et al., 2007; Myers & LaManna, 2016; Özkan et al., 2014). On the one hand, fire may drive the structure both pollinator and flowering-plant communities such that relatively little pollinator or plant β -diversity is uniquely explained by species composition of the other trophic level. In this case, differences in species composition of one trophic level may be associated with differences in species composition of the other trophic level, but these differences would also be associated with differences in fire disturbance. This pattern would indicate that an understanding of the effects of fire on either pollinators or flowering plants may be sufficient to predict responses of both trophic levels to changes in fire regimes anticipated under global climate change (Abatzoglou & Williams, 2016; Westerling et al., 2006). Alternatively, because pollinators and flowering plants are linked through mutualistic interactions, plant β -diversity may also have a strong influence on pollinator β -diversity (and vice versa) that is independent from the influence of fire. In this case, biotic linkages among trophic levels that are unassociated with fire may themselves be important predictors of β -diversity of each trophic level. Finally, wildfire disturbance may increase the relative contribution of mutualistic associations to community assembly of pollinators and plants if mutualism plays a more important role in determining differences in community composition among localities in disturbed than undisturbed landscapes. Each of these mechanisms remains largely unexplored.

Here, we tested a series of related hypotheses about the effects of wildfire severity and biotic interactions on pollinator and flowering-plant community assembly. We compared β -diversity, species richness and total abundances of pollinators and flowering plants among landscapes with no recent wildfire (unburned), mixed-severity wildfire and high-severity wildfire in three sites across the Northern Rockies Ecoregion, USA. We examined patterns of β -diversity at two spatial scales: (a) β -diversity among local communities that have experienced the same wildfire-severity level (unburned, mixed severity and high severity) and (b) β -diversity among local communities with different wildfire severities.

At the first spatial scale (within wildfire-severity levels), we tested whether abiotic and biotic factors influence pollinator and plant β -diversity within burned and unburned landscapes. We predicted that high-severity wildfire would reduce β -diversity by deterministically selecting for fire-tolerant species across local communities with similar local fire conditions, whereas mixed-severity wildfire would increase β -diversity by increasing species sorting among local communities that differ in local fire conditions. We tested these predictions by comparing observed differences in β -diversity among the three levels of wildfire severity to null models that accounted for the influence of wildfire and site on the local species pool and the total abundance of all species in local communities (Kraft et al., 2011; Myers et al., 2013). We also tested the predictions that species would sort more strongly along abiotic gradients in mixed-severity wildfire and that wildfire would

increase the importance of plant-pollinator interactions to community assembly. We tested these predictions using variation partitioning and co-occurrence analyses. If wildfire mediates species sorting along abiotic gradients, we predicted that a greater proportion of variance in β -diversity would be explained by abiotic factors in burned than unburned landscapes and especially in mixed-severity wildfire. If wildfire mediates the importance of plant-pollinator interactions to community assembly, we predicted that (a) a greater proportion of variance in β -diversity would be explained by biotic factors in burned than unburned landscapes and (b) more non-random co-occurrences among plant and pollinator species pairs would be present in burned than unburned landscapes.

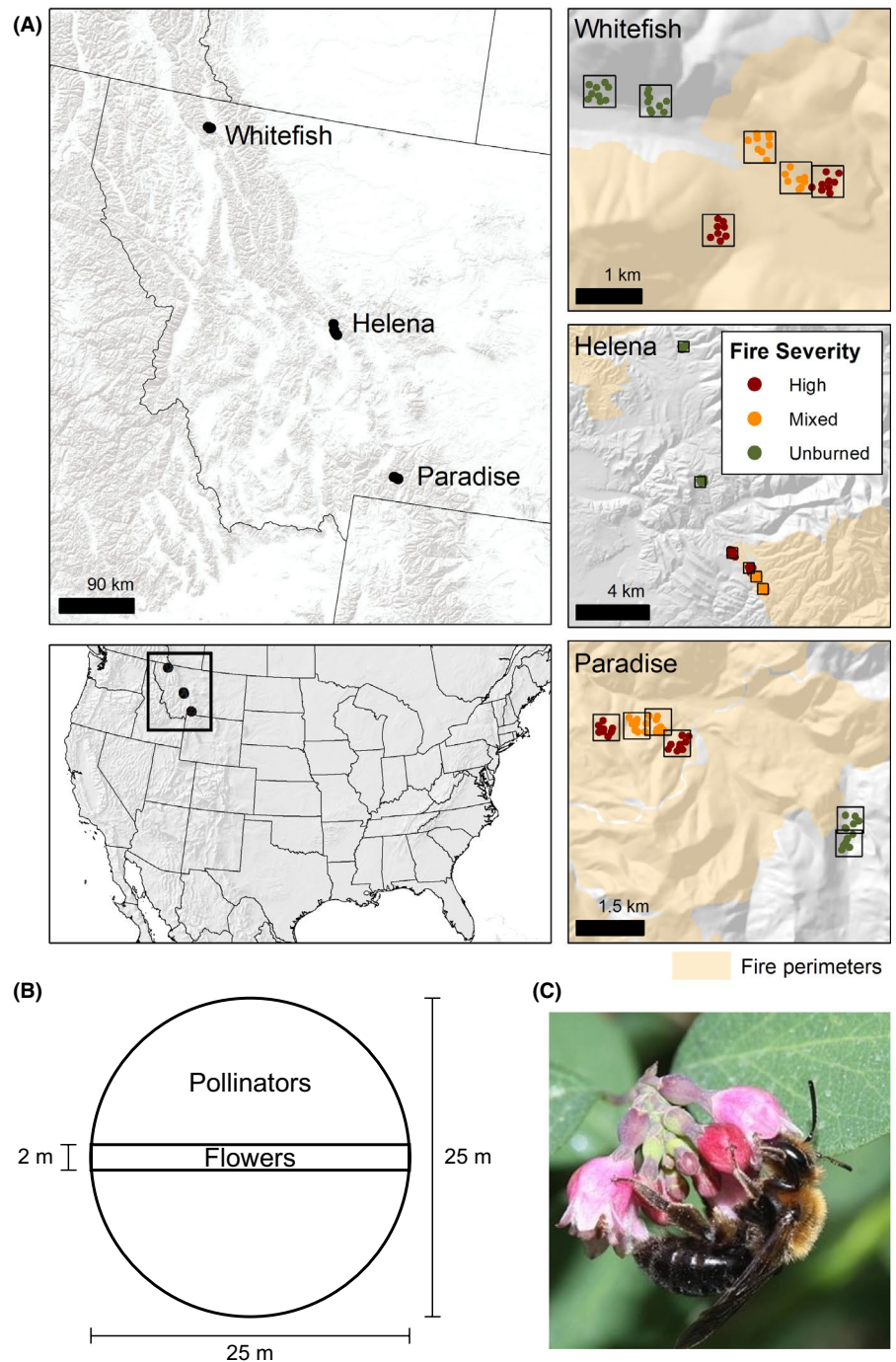
At the second spatial scale (among wildfire-severity levels), we tested the relative importance of abiotic and biotic factors on pollinator and plant β -diversity across wildfire gradients. If plant-pollinator interactions play an important role in community assembly of each trophic level, we predicted that the species composition of pollinator and flowering plants would uniquely contribute to the β -diversity of the other trophic level (i.e. independent from the influence of wildfire and all other factors combined). Alternatively, if community composition is primarily determined by effects of wildfire, we predicted that the contribution of pollinator and flowering-plant species composition to β -diversity of the other trophic level would be indistinguishable from the contribution of wildfire (i.e. no unique biotic contribution). We tested these predictions using similar variation partitioning analyses as described above, but where β -diversity was compared across all wildfire-severity levels rather than within each level.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study took place in three sites (named Helena, Paradise and Whitefish) within the Northern Rocky Mountains (Figure 1; Burkle et al., 2015). Historically, these sites have experienced mixed-severity wildfire regimes (Baker, 2009), which favour understorey and early successional plant species and a mosaic of forest-successional stages (Perry et al., 2011). Wildfires have largely been suppressed over the past century, however, leading to denser stands and more intense and extensive wildfires in the past few decades (e.g. Miller et al., 2009). Additional information on these sites are provided in the Supporting Information. Within each site, 48–52 plots were selected (152 total plots across all three sites) that differed in the recent presence and severity of wildfire (Figure 1), including 12–18 plots with no recent wildfire within at least the past 60 years (hereafter unburned), 17–18 plots with recent (<10 years old) mixed-severity wildfire and 17–18 plots with recent high-severity wildfire (Burkle et al., 2015). Within each wildfire-severity level in each site, plots were located in one of two previous wildfire burn units or unburned units (hereafter referred to as units). Data and R scripts to reproduce our analyses are archived on Dryad (LaManna et al., 2020).

FIGURE 1 Study area and design. (A) Map of the Northern Rockies Ecoregion in western Montana, USA, with insets showing the spatial distribution of study plots (points), burn units (black boxes around points) and extent of wildfire (red shaded area) within each site (Helena, Paradise and Whitefish). (B) Schematic of floral and pollinator sampling design at each plot. Flowers were sampled in a 25×2 m band transect, and pollinators were hand-netted within a 25 m diameter circular plot centred on the floral transect. (C) *Andrena* spp. on snowberry plant (*Symphoricarpos albus*) at one of this study's plots (photo: Laura Burkle)



2.2 | Data collection

2.2.1 | Flowering-plant community sampling

Throughout the 2014 and 2015 growing seasons, we visited each plot once per week. During each visit, we quantified floral densities, species richness and composition by recording the number of open flowers of each species along a 25×2 m band transect (Figure 1B). Although there were additional plant species present at these plots (see Burkle et al., 2015 for a description of forb, grass, and tree diversity in the study sites), we focused on herbaceous and woody plant species in bloom as they represent floral resources for pollinators.

Importantly, all open flowers were surveyed (i.e. not only those flowers where pollinators were present).

2.2.2 | Pollinator community sampling

During each floral-transect visit, we also quantified the densities, species richness and composition of pollinators by hand-netting within a 25 m diameter circular plot centred on the 25×2 m floral transect (Figure 1B) for 20 min during sunny, calm weather and peak pollinator activity (c. 09:00–16:30). Plots were visited in random order during these hours. We considered pollinators to be any

insect visitor that was observed flying among flowers and contacting floral reproductive parts. Plots in Helena were observed 12 times in 2014 and 9 times in 2015. Plots in Paradise were observed nine times each in 2014 and 2015. Plots in Whitefish were observed seven times each in 2014 and 2015. Total observation time varied per plot depending mainly on growing season length, which varied among sites. Each pollinator was collected individually and identified to species later. Bees (Hymenoptera), flies (Diptera) and butterflies (Lepidoptera) were all sampled during our surveys and are included in our analyses. However, most of the pollinators sampled were Hymenoptera (Burkle et al., 2019; Reese et al., 2018), and results were similar if we conducted all analyses using only Hymenoptera.

2.2.3 | Abiotic environmental factors

We measured several abiotic environmental variables at each plot that are thought to influence pollinator and plant community composition, including wildfire severity, climate, soil chemistry, topography and other variables associated with wildfires and pollinator nesting habitat, including coarse-woody debris (CWD), bare ground, stumps and other legacies that can result from wildfires (Moretti et al., 2009; Williams et al., 2010). Detailed explanations of these variables are provided in the Supporting Information.

2.3 | Statistical analyses

We calculated β -diversity among plots within each wildfire-severity level (i.e. high severity, mixed severity and unburned) using mean distance-to-centroids calculated from Bray–Curtis distances that measure differences in species composition and relative abundances of species across plots (Anderson et al., 2011). The distances to the centroid of each wildfire-severity level in each site were calculated with function 'betadisper' in the R VEGAN package (Oksanen et al., 2019; R Core Team, 2015). We then performed null-model analyses to disentangle potential wildfire effects on β -diversity via alteration of species pools and local abundance from wildfire effects on β -diversity via non-random effects on local species composition of plants and pollinators (Kraft et al., 2011; Myers et al., 2013). Individual pollinators or flowers from each wildfire-severity level in each site were randomly re-distributed among plots in that wildfire-severity level in that site while preserving local abundance (i.e. the total number of pollinators or flowers in each plot) and species-abundance distributions in each site \times wildfire combination (Kraft et al., 2011; Myers et al., 2013). Thus, these null assemblages were the product of stochastic assembly from the observed species pool and local abundance alone, and all local-scale mechanisms that might cause additional spatial aggregation of pollinators or flowers (e.g. habitat partitioning, local interactions among species, dispersal limitation) were removed. Distance-to-centroids for simulated communities (β_{SIM}) were then compared to observed distance-to-centroid (β_{OBS}) relative to the standard deviation of β_{SIM} (σ_{SIM}) after

2,000 iterations, and a standardized effect size of the difference was calculated as follows: $\beta_{\text{SES}} = (\beta_{\text{OBS}} - \beta_{\text{SIM}}) / \sigma_{\text{SIM}}$. Therefore, β_{SES} represent β -diversity that remains unexplained by stochastic assembly from the species pool determined by site and wildfire-severity level (Kraft et al., 2011), and are a way to measure the influence of wildfire at the local plot-to-plot scale (as opposed to wildfire effects on the species pool itself). We tested for differences in β -diversity among wildfire-severity levels using generalized linear mixed models (GLMMs) with distance-to-centroid as the response that included site and unit nested within site as random effects. The unit of replication in these GLMMs was the distance of each plot to its wildfire-severity-level centroid in a study site (i.e. one data point per plot per wildfire-severity level per site). These distances are calculated from Bray–Curtis dissimilarities using function 'betadisper' from R package VEGAN and are directly comparable across different sites and wildfire-severity levels (Anderson et al., 2011; Oksanen et al., 2019). We report results from both a parametric and non-parametric statistical model. For the parametric model, we used GLMMs that allowed residual variance to differ among wildfire-severity levels using function 'lme' from R package NLME. For the non-parametric model, we used permutational GLMMs using function 'permanova.lmer' from R package PREDICTMEANS (Luo et al., 2020; Pinheiro et al., 2020). Briefly, non-parametric permutational GLMMs randomly re-assign data points in a mixed-model ANOVA to different groups in each iteration (we used 9,999 iterations) and compare a distribution of null-expected F values to the observed F value. We summed pollinator and floral abundances at each plot across both years for analyses presented here. Results were qualitatively similar if we analysed 2014 and 2015 separately except β -diversity for pollinators differed among wildfire-severity levels in 2014 and 2014–2015 combined, but not in 2015 when considered separately. However, three times as many pollinators were sampled in 2014 compared to 2015, so inferences were made with the larger dataset of 2014 and 2015 combined, and these results matched results considering only 2014.

To assess effects of wildfire on floral and pollinator species richness and total abundance at the fire-unit scale, we compared total abundances and rarefied species richness (rarefied to the minimum number of individuals across burn units after first rarefying to the minimum number of plots in each wildfire \times site \times unit combination) for each unit among the three wildfire-severity levels. We calculated fire-unit abundance as the total number of pollinators or flowers of all species combined across plots in a burned or unburned unit. We then tested for differences in mean fire-unit abundances and mean rarefied species richness across wildfire-severity levels with GLMMs that included site as a random effect. At the plot (local) scale, we tested for differences in local total abundance (total count of flowers or pollinators at each plot), local species richness and local rarefied species richness among wildfire-severity levels with GLMMs that included site and unit nested within site as random effects. For rarefaction analyses, species richness was rarefied to the minimum number of individuals across burn units or plots. The only exception to this was for local pollinator species richness, where species richness was rarefied to the 15th percentile of total abundances across sites

because only one pollinator was detected at seven plots. However, results are similar and inferences the same if we exclude these seven plots. Six of the seven plots where only one pollinator was detected were in unburned landscapes, where pollinator abundances were much lower than in burned landscapes. Moreover, plots with only one pollinator were surveyed with equal effort as plots with many more pollinators. Therefore, we retained plots with only one pollinator because they reflect biologically-meaningful differences in pollinator abundances across wildfire-severity levels. For all analyses, we report both GLMMs that allowed residual variance to differ among wildfire-severity levels using function 'lme' from R package NLME and non-parametric permutational GLMMs using function 'permanova.lmer' from R package PREDICTMEANS. We summed pollinator and floral abundances at each plot across both years for analyses presented here, but results were qualitatively similar if we analysed 2014 and 2015 separately. We also visualized these patterns using non-metric multidimensional scaling (NMDS) in R package VEGAN.

We used variation partitioning at two scales to determine the relative importance of various ecological factors to differences in species composition among plots within each wildfire-severity level and among plots across wildfire-severity levels. This allowed us to evaluate (a) the relative importance of species sorting along abiotic and biotic gradients within each wildfire-severity level and (b) the relative importance of wildfire severity and biotic interactions to differences in species composition across wildfire-severity levels. Factors examined in these analyses included plant-pollinator associations (i.e. the extent to which variation in floral species composition predicts pollinator species composition and vice versa), wildfire severity, other abiotic factors (i.e. climate, topography, and other variables associated with wildfires and pollinator-nesting habitat), and spatial variables associated with dispersal limitation (geographical distance) and unmeasured environmental variables (Peres-Neto et al., 2006). We used the 'varpart' and 'rda' functions in the R VEGAN package. Prior to conducting variation partitioning analyses, we first performed a parallel analysis for our abiotic environmental data using function 'paran' of R package PARAN (Dinno, 2018), which tests how many principal components (PCs) are different from random variation. This parallel analysis indicated retaining the first four abiotic principal components. We also used forward model selection ('forward.sel' function in the ADESPATIAL R package) to reduce the number of variables used to predict variation in floral and pollinator species composition (Borcard et al., 2011; Legendre & Legendre, 2012). Forward model selection is a standard approach recommended for variation partitioning analyses that first tests for the overall significance of a predictor matrix and, if significant, assesses the significance of each column of the matrix to evaluate its contribution in light of other columns (Borcard et al., 2011; Legendre & Legendre, 2012). Only significant columns are retained up to the adjusted- R^2 of the overall predictor matrix (Borcard et al., 2011; Legendre & Legendre, 2012). Variation partitioning calculates the proportion of total variation in the response matrix explained by each explanatory matrix (i.e. abiotic matrix, biotic matrix and spatial matrix) and the proportion of variation that is shared among explanatory matrices (Legendre &

Legendre, 2012; Peres-Neto et al., 2006). Here, we used the proportion of variation in pollinator or floral species composition explained by the other trophic level alone (i.e. the extent to which variation in floral species composition not associated with the abiotic environment or geographical distance predicts pollinator species composition and vice versa) as a measure of the degree to which plant-pollinator associations influence species composition of pollinators and flowering-plants independently of the abiotic environment or geographical distance. We pooled across both years for analyses presented here, but results were qualitatively similar if we analysed 2014 and 2015 separately.

To complement the variation-partitioning analyses and to assess whether certain pollinator species co-occurred with certain plant species across plots in each site and wildfire-severity level, we performed an analysis of co-occurrence using *c*-scores (Gotelli & Ulrich, 2010). The *c*-score, a measure of co-occurrence across plots, was calculated for each pollinator-plant species pair in each site and wildfire-severity level. For any pollinator-plant species pair, the *c*-score ranges from 0 (the species pair only occurs together) to 1 (the species pair never occurs together). We used a null-model approach to calculate the *c*-score expected if species occurrence was randomly distributed across plots within a site (Gotelli & Ulrich, 2010). Additional details are provided in the Supporting Information.

3 | RESULTS

Overall, we identified 329 pollinator species and morphospecies (241 Hymenoptera species, 62 Diptera species and 26 Lepidoptera species) and 193 flowering-plant species (164 herbaceous-plant species and 29 woody-plant species) at 152 plots across the three study sites (Figure 1; Reese et al., 2018). Non-metric multidimensional scaling indicated that the three sites differed widely in species composition of pollinators and plants (Figure S1).

3.1 | How do abiotic and biotic factors influence pollinator and plant β -diversity within burned and unburned landscapes?

Observed patterns of β -diversity (β_{OBS}) were consistent with the prediction that wildfire homogenizes species composition of both pollinators and flowering plants (Figure 2A). For both pollinators and plants, β_{OBS} within high-severity wildfires was lower than β_{OBS} within unburned landscapes (Figure 2A; Figure S2; Table S1). For pollinators, β_{OBS} within mixed-severity wildfires did not differ significantly from β_{OBS} within high-severity wildfires (Figure 2A). For flowering plants, in contrast, β_{OBS} within mixed-severity wildfires was higher than β_{OBS} within high-severity wildfires, but not significantly different from β_{OBS} within unburned landscapes (Figure 2A).

Differences in β_{OBS} appeared to largely mirror differences in species pools and local abundances of pollinators and flowering plants

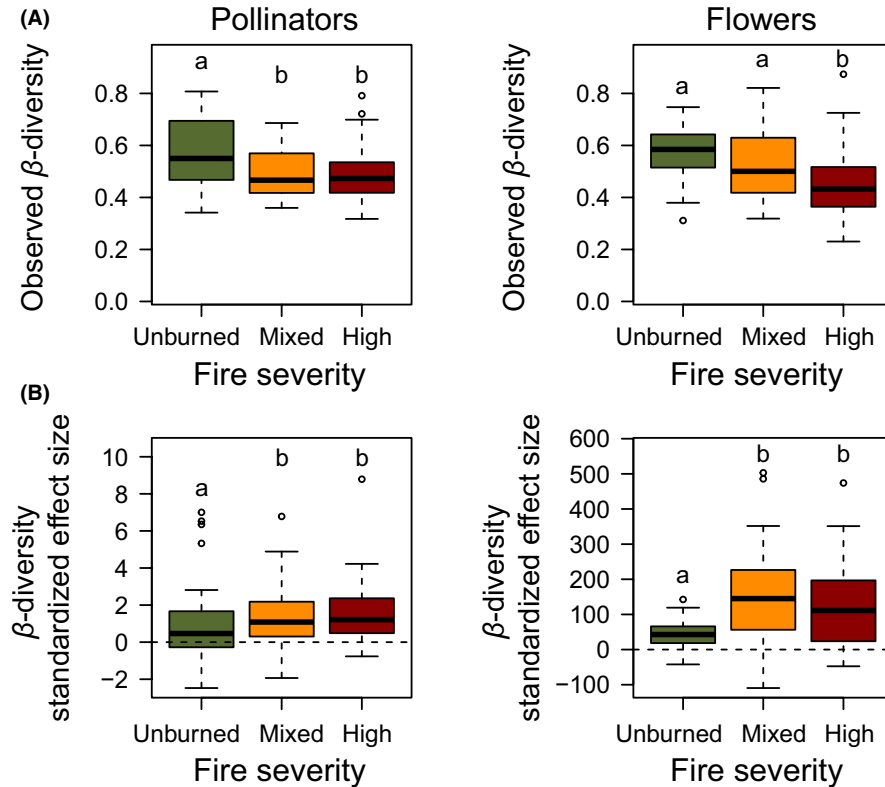


FIGURE 2 β -diversity within each wildfire-severity level for pollinator and flowering-plant communities. Boxplots of distance-to-centroids for each wildfire-severity level \times site combination are calculated from Bray–Curtis dissimilarities ($N = 46$ – 53 plots per wildfire-severity level). Observed values of β -diversity (A), and standardized effect sizes of β -diversity (B; observed value minus the mean expected value from the null model divided by the standard deviation of the expected values) are shown for pollinators and plant communities. Unburned plots are in green, plots with mixed-severity wildfires are in yellow and plots with high-severity wildfire are in red. Standardized effect sizes of β -diversity that fall near zero represent differences in species composition that are no different from the null model assuming random assembly of local communities (see text for details of the null model). Lower-case letters indicate the results of post-hoc comparisons (different letters indicate significant contrasts), and lack of lower-case letters indicates that the overall GLMM ANOVA test was not significant ($p > 0.05$, Table S1). Random effects are included for burn unit (block) nested within site

between burned and unburned landscapes. Regional species richness, regional abundances, and local abundances and species richness of both pollinators and flowering plants were generally higher within mixed-severity wildfires compared to unburned landscapes (Figure 3; Figures S3 and S4; Table S1). In addition, regional rarefied species richness (rarefied to account for differences in abundance of individuals across wildfire-severity levels) of flowers, but not pollinators, was significantly higher within mixed-severity wildfires compared to unburned landscapes (Figure 3; Table S1). Local rarefied species richness of pollinators, but not flowering plants, was significantly higher within mixed-severity and high-severity wildfires compared to unburned landscapes (Figure 3; Table S1).

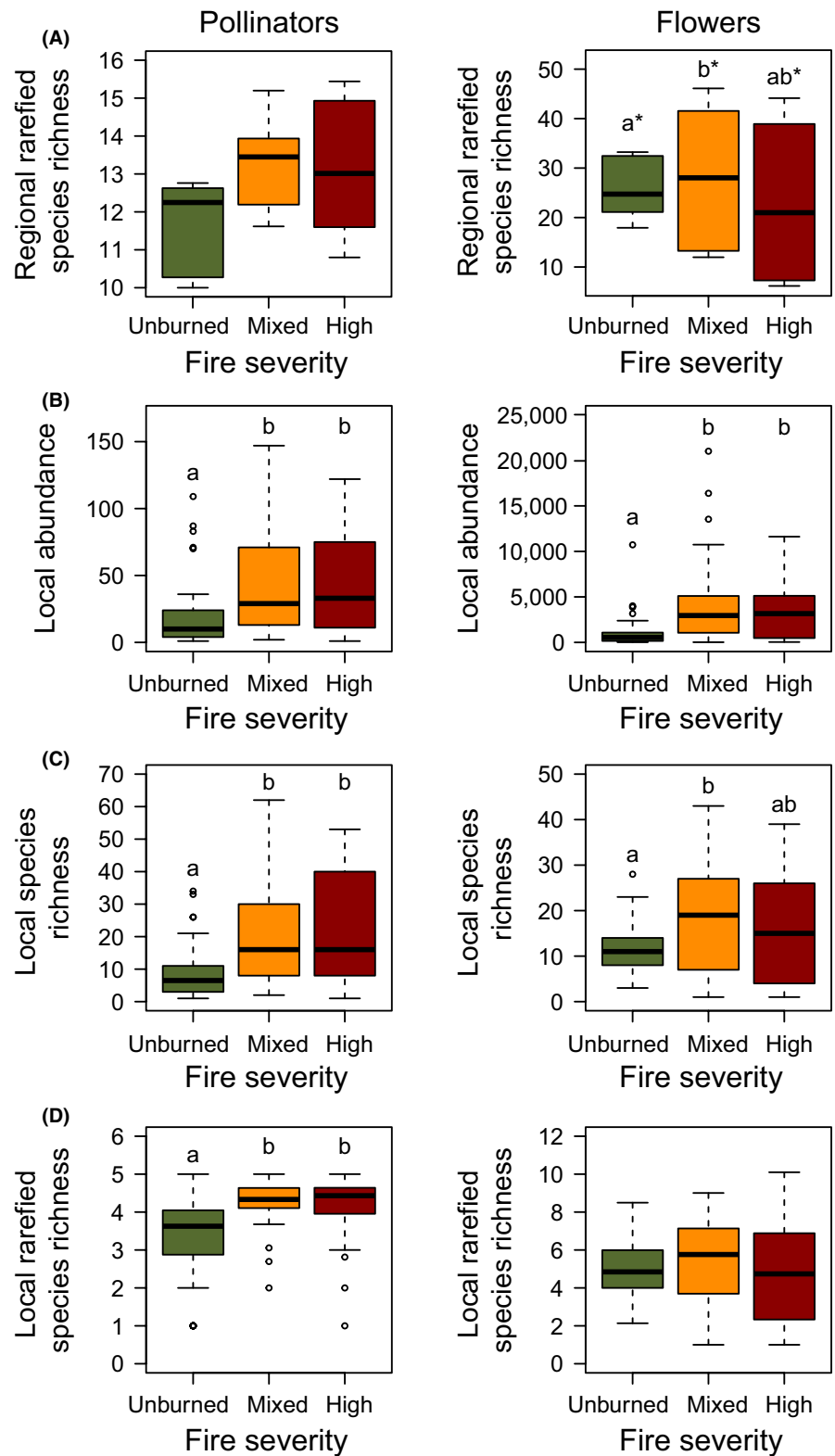
The effects of wildfire on species pools and local abundances of pollinators and flowering plants (Figure 3) led to the expectation that simulated patterns of β -diversity from the null model (β_{SIM}) should also be lower in burned landscapes relative to unburned landscapes (Figure S5). However, β_{OBS} declined in burned landscapes less than β_{SIM} . In other words, while wildfire homogenized species composition among sites, it was less than what would be expected given increases in local abundances and species richness in burned

landscapes. Consequently, standardized effect sizes of β -diversity (β_{SES}) were greater within mixed-severity and high-severity wildfires compared to unburned landscapes (Figure 2B). β_{SES} were also mostly positive within both mixed- and high-severity wildfires (Figure 2B), indicating non-random assortment of both pollinator and plant species among local communities.

Associations between β -diversity and abiotic factors were consistent with the prediction that wildfire increases species sorting along environmental gradients (Figure 4A,B; Table S2). For pollinators, the total abiotic effect (variation in β -diversity associated with all abiotic factors, including variation shared between abiotic and biotic or spatial factors) was greater within high-severity wildfires compared to both mixed-severity wildfires and unburned landscapes (all orange and red bars in Figure 4A; Table S2). For flowering plants, the total abiotic effect was also greater within burned than unburned landscapes, and greater within high-severity wildfires than within mixed-severity wildfires (all orange and red bars in Figure 4B; Table S2).

Wildfire also mediated the relative importance of pollinators and flowering plants to β -diversity of the other trophic level. First,

FIGURE 3 Pollinator and flowering-plant abundances and species richness across wildfire-severity levels. (A) Regional rarefied species richness across wildfire-severity levels, rarefied to the minimum number of individuals and plots sampled across all site \times wildfire \times unit combinations ($N = 6$ plots per wildfire-severity level). (B) Local abundances (total number of pollinators or flowers at each plot) by wildfire-severity level. (C) Local species richness by wildfire-severity level. (D) Local rarefied species richness (rarefied to the minimum floral abundance and to the 15th percentile of total pollinator abundance across plots) by wildfire-severity level ($N = 46$ – 53 plots per wildfire-severity level). Unburned plots are green, plots with mixed-severity fires are yellow and plots with high-severity fire are red. Lower-case letters indicate the results of posthoc comparisons (different letters indicate significant contrasts), and lack of lower-case letters indicates that the overall GLMM ANOVA test was insignificant ($p > 0.05$, Table S1). *Results for regional floral species richness only significant for the mixed-variance GLMM, but not the permutational GLMM



both the unique and total biotic effects on β -diversity were generally greater in burned than unburned landscapes (Figure 4B; Table S2). Second, pollinators had a stronger influence on plant composition in high-severity wildfires, whereas plants had a stronger influence on pollinator composition in mixed-severity wildfires. The unique contribution of pollinators to flowering-plant β -diversity was 10% greater

in high-severity than mixed-severity wildfires (dark green bars in Figure 4B; Table S2). In contrast, the unique contribution of flowering plants to pollinator β -diversity was 30% greater in mixed-severity than high-severity wildfires (Figure 4A; Table S2). These results indicate that plant-pollinator interactions are important drivers of plant and pollinator community assembly following wildfire.

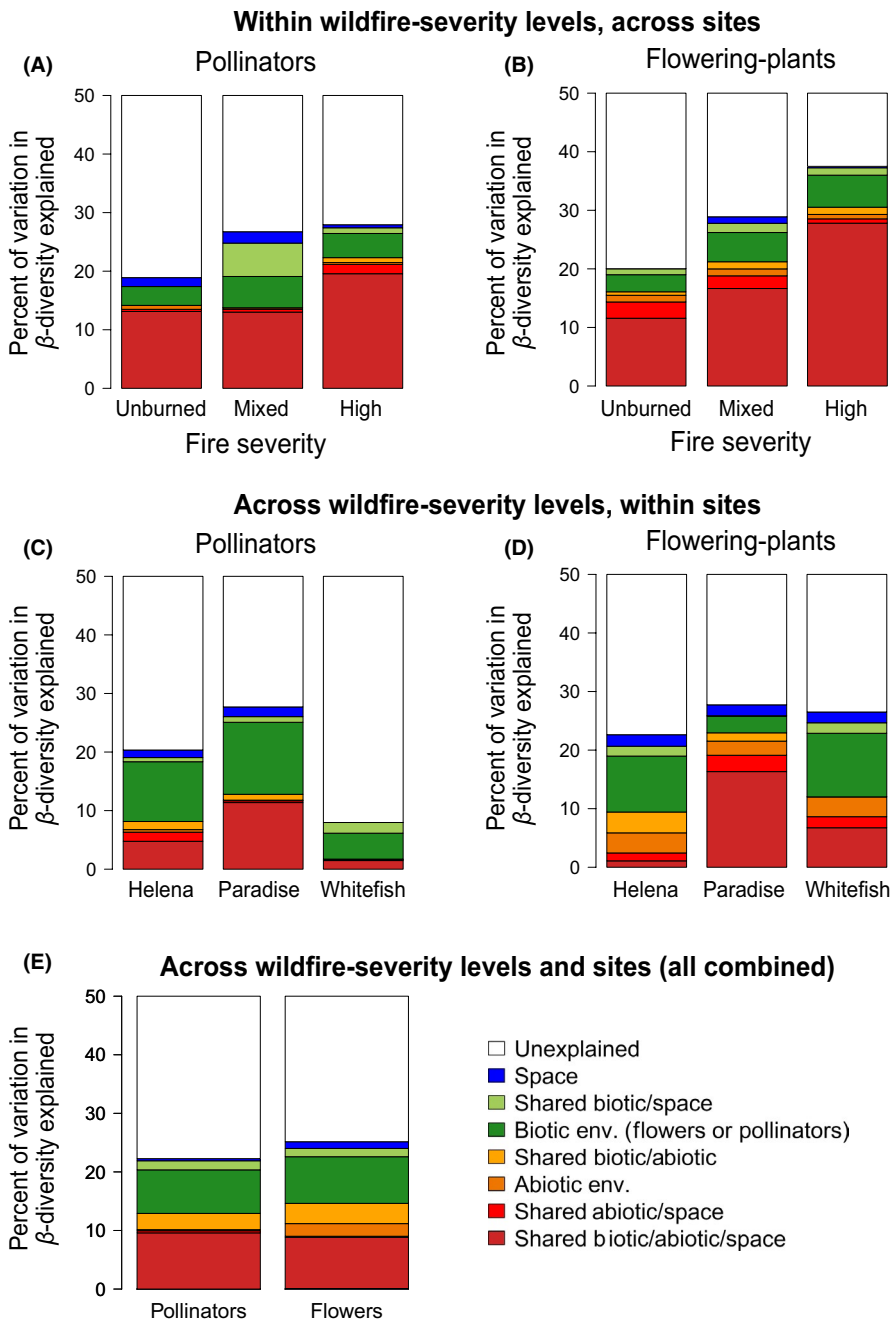


FIGURE 4 Partitioning of the variation in pollinator and flowering-plant β -diversity explained by the abiotic environment (e.g. wildfire severity, soil chemistry, climate), biotic environment (floral or pollinator communities) and geographical distance (labelled space). Results are shown at different spatial scales: (A, B) variation in β -diversity within wildfire-severity levels and across the three study sites; (C, D) variation in β -diversity across wildfire-severity levels and within the three study sites and (E) variation in β -diversity across all wildfire-severity levels and study sites. Effects are either independent (isolated) from other factors or shared (Table S2). The biotic environment refers to flowering plants when predicting pollinator β -diversity and to pollinators when predicting floral β -diversity. Biotic effects that were uncorrelated with abiotic or spatial effects are shown in dark green. See Table S2 for significance tests of these fractions. Values shown are adjusted- R^2 values that adjust for the number of explanatory variables

3.2 | What is the relative importance of abiotic factors and biotic interactions on pollinator and plant β -diversity across wildfire gradients?

When examining β -diversity across wildfire-severity levels, differences in wildfire severity were associated with differences in species composition of both pollinator and plant communities across sites (Figure 4C–E). All abiotic factors combined (i.e. wildfire severity, climate, topography, soil chemistry, and other factors associated with wildfire effects and pollinator-nesting habitat) explained between 1% and 13% of total pollinator β -diversity within each site and between 9% and 23% of total flowering-plant β -diversity within each site (Table S2). Within all

three study sites, wildfire severity was the most important abiotic factor explaining variation in plant β -diversity and the most important or second-most important abiotic factor explaining variation in pollinator β -diversity (Table S3). The principal component that primarily captured differences in wildfire severity among sites included correlated differences in woody debris and soil chemistry (Table S3).

Across wildfire gradients in each site (Figure 4C,D) and across all sites combined (Figure 4E), plant–pollinator associations explained substantial variation in β -diversity above and beyond what could be explained by wildfire severity, other abiotic factors or geographical distance. Flowering-plant β -diversity explained between 8% and 26% of total pollinator β -diversity within each site,

and pollinator β -diversity explained between 16% and 21% of total flowering-plant β -diversity within each site (Figure 4C,D; Tables S2 and S4). When averaged across all three sites, the independent influence of flowering-plant β -diversity on pollinator β -diversity reflected over half (53%) of the total explained variation in pollinator β -diversity (Figure 4C; Table S2). The independent influence of pollinator β -diversity on flowering-plant β -diversity reflected one-third (32%) of the total explained variation in plant β -diversity (Figure 4D; Table S2). These results indicate that in addition to determining responses of plant and pollinator communities to wildfire, biotic interactions play an important role in determining plant and pollinator community assembly that is independent of wildfire or other abiotic factors.

Co-occurrence analyses largely supported results from the variation-partitioning analysis, indicating that a greater proportion of plant and pollinator species had non-random associations with species in the other trophic level in burned than unburned landscapes (Table S5). Moreover, these non-random associations were predominantly positive associations (Table S5), which indicate mutualisms. According to the most-restrictive criteria (Bayes mean-based criterion), an average of 29.1% of pollinator species and an average of 47.0% of flowering-plant species across the three sites were involved in at least one non-random positive or negative association with species in the other trophic level (Tables S5, S6 and S7).

4 | DISCUSSION

Local biotic interactions among trophic levels may combine with the abiotic environment to determine community-level responses to wildfire and other effects of global environmental change, yet this hypothesis has remained largely untested. Here, we found that wildfire disturbance had an important influence on β -diversity, local and regional abundance, and species richness of pollinator and flowering-plant communities across three sites in the Northern Rocky Mountains. Wildfire also mediated the importance of biotic associations between pollinators and flowering plants to β -diversity of each trophic level, increasing the importance of mutualism in structuring communities following wildfire disturbance. Moreover, biotic associations between pollinator and plant species explained substantial variation in β -diversity beyond what could be explained by wildfire severity, other abiotic factors and spatial factors. Such influences on β -diversity are important because β -diversity affects the maintenance of biodiversity at landscape-to-regional spatial scales and can determine several important ecosystem functions such as pollination services (Winfree et al., 2018). Our results suggest that a thorough understanding of pollinator–plant associations and how those associations are altered by wildfire may be as or more important to the conservation of pollinator and plant species diversity than an understanding of abiotic influences (e.g. disturbance severity, climate, soil chemistry, topography) on plants and their pollinators.

4.1 | How do abiotic and biotic factors influence pollinator and plant β -diversity within burned and unburned landscapes?

In contrast to a recent meta-analysis of disturbance effects on plant β -diversity (Catano et al., 2017), our results indicate that fire disturbance homogenizes species composition (reduces β -diversity) among pollinator and plant communities. Reductions in β -diversity indicate that local communities are more similar to each other in the composition and relative abundances of species and also indicates that γ -diversity (or regional species richness) is more similar to α -diversity (or mean local species richness). We found that high-severity wildfires homogenized species composition of both pollinators and flowering plants, whereas mixed-severity wildfires only homogenized species composition for pollinators but not flowering plants. In our study, homogenization from wildfire did not appear to be the result of selection for a subset of species that can tolerate wildfire conditions. Instead, homogenization resulted from increased local floral and pollinator abundances following wildfires, which allowed more species from species pools to be present in local communities (i.e. increased local species richness). Interestingly, β -diversity effect sizes (β_{SES}), which account for differences in total pollinator and floral abundances across wildfire-severity levels, were greater in burned than unburned landscapes. This result indicates non-random assortment of both pollinator and plant species among local communities. Pollinators and flowering plant species also sorted more strongly along abiotic gradients in burned than unburned landscapes, suggesting that wildfire enhances the importance of environmental heterogeneity and niche partitioning for determining differences in species composition across localities (Legendre & Legendre, 2012; Vellend, 2016). Although these results involve total abiotic effects, which contain shared variance with biotic and spatial effects, we attribute any shared variance with abiotic factors to abiotic influences on those other factors. These results collectively indicate that wildfire increases abundances and species richness of flowering plants and pollinators while also enhancing opportunities for non-random community assembly processes like species sorting, dispersal limitation or species interactions that lead to clumped species distributions (LaManna et al., 2017; Myers et al., 2015).

Our results also indicate that wildfire mediates the importance of mutualistic associations between pollinators and flowering plants to β -diversity of each trophic level. Variation-partitioning and co-occurrence analyses indicate that stronger associations between flowering-plant and pollinator species in burned than unburned landscapes reflect greater effects of plant–pollinator interactions on community assembly in burned than unburned landscapes. These effects were independent of wildfire and other important abiotic factors. Co-occurrence analyses further showed many positive associations between flowering-plant and bee species (order Hymenoptera), especially in the Apidae and Megachilidae families, that were likely important drivers of plant and pollinator communities to wildfire. In addition,

variation partitioning revealed that pollinators play a relatively more important role in flowering-plant community assembly in high-severity than in mixed-severity wildfires, whereas flowering plants play a more important role in pollinator community assembly in mixed-severity than in high-severity wildfires. These results suggest that the importance of mobile associates of plants, such as pollinators, to the assembly of early-successional plant communities that emerge following wildfire disturbance increases with the severity of the disturbance. In high-severity wildfires, where fire burns most if not all existing vegetation, pollinator activities likely contribute strongly to spatial patterns of plant establishment and reproductive success. However, in mixed-severity wildfire, where the effects of fire are more heterogeneous across the landscape (Perry et al., 2011), remnant plant populations likely influence the relative abundances and distributions of pollinator species. The influence of pollinators and other plant mutualists on plant community assembly in highly disturbed landscapes may explain some of the contingencies in responses of plant communities to wildfire and other disturbances (Belyea & Lancaster, 1999; Catano et al., 2017). However, little is known about how pollinators and flowering plants influence each other's community assembly following disturbance, and future studies are needed that test potential mechanisms by which communities linked through mutualism influence each other following wildfires and other types of ecological disturbance.

Wildfire was likely associated with patterns of pollinator β -diversity because it was associated with differences in woody debris cover and soil chemistry that influence the availability of pollinator nesting habitat (e.g. Morato & Martins, 2006; Moretti et al., 2009). In addition, fire disturbance was likely associated with patterns of flowering-plant β -diversity because it can alter several abiotic factors that are important to plant growth, including soil chemistry and light availability (Rieske, 2002). These factors may explain why wildfire severity was strongly associated with variation in pollinator and floral species composition across plots within each of the three study sites. While standardized effect sizes of β -diversity (β_{SES}) were generally greater for flowers than for pollinators (compare panels in Figure 2B), this likely reflects our use of flowers (instead of individual plants) as a measure of abundance for flowering-plant species. This was done because number of flowers of a given plant species in an area reflects a more biologically meaningful measure of flowering-plant relative abundance to pollinators. Larger, more vigorous plants produce more flowers and represent greater resources for pollinators. For these reasons, however, we caution against directly comparing the magnitude of β_{SES} between pollinators and flowering plants.

Our results suggest that wildfire disturbance enhances regional and local abundances and species richness of pollinators and flowering plants, but pollinators and flowering plants differed in their response to high- versus mixed-severity wildfires. Our findings for flowering plants support the idea that mixed-severity wildfires enhance both regional and local abundance and species richness relative to high-severity wildfires or lack of wildfire. However, our

findings for pollinators did not support this idea. First, regional and local pollinator abundance, species richness and rarefied species richness were higher in landscapes with wildfires compared to unburned landscapes but did not differ among landscapes with mixed- and high-severity wildfires. Second, pollinator β -diversity was similar between mixed- and high-severity wildfires. Overall, greater diversity and abundances of pollinator and plant species following mixed- and high-severity fires highlights the importance of wildfire in general, and especially mixed-severity wildfires (i.e. pyrodiversity), for promoting diverse assemblages of critically important species like plants and pollinators (Ponisio et al., 2016).

4.2 | What is the relative importance of abiotic and biotic factors on pollinator and plant β -diversity across wildfire gradients?

Plant-pollinator interactions are important for plant reproduction, ecosystem services (Burkle et al., 2017; Ollerton et al., 2011; Sargent & Ackerly, 2008; Wolowski et al., 2017) and species coexistence (Bastolla et al., 2009). Yet, the relative importance of these mutualistic interactions in structuring species composition of pollinator and plant communities has remained unclear because both communities may respond in a correlated way to the underlying abiotic environment. Our results across wildfire-severity gradients suggest that plant-pollinator associations accounted for substantial variation in species composition of pollinators and flowering plants that was unrelated to wildfire severity or any other measured abiotic factor (dark green bands in Figure 4, indicating variation in β -diversity uniquely associated with biotic factors). The amount of shared explained variation between abiotic and biotic variables can make it difficult to infer the relative importance of abiotic and biotic mechanisms to variation in β -diversity (Legendre & Legendre, 2012; Peres-Neto et al., 2006). However, the independent contribution of the other trophic level (i.e. plants for pollinators, and pollinators for plants) was as great if not greater than the variation in β -diversity explained by all other factors in most sites (Figure 4C,D) and across sites (Figure 4E). Moreover, we found that nearly a third of all pollinator species and nearly half of all flowering-plant species across all three regions were involved in at least one non-random co-occurrence with species in the other trophic level. Collectively, these results indicate that pairs of pollinator and flowering-plant species consistently co-occur or avoid each other in ways that generate substantial β -diversity beyond what is caused by wildfire or other abiotic factors.

Relatively few studies in community ecology have explicitly examined the influence of the biotic environment on β -diversity (Bagchi et al., 2014; Dyer et al., 2007; Özkan et al., 2014). Our results strongly suggest that community assembly of one group of organisms is highly dependent on the assembly of its linked trophic levels (Barberán et al., 2015; Clements, 1916; Gleason, 1917; Wisz et al., 2013), even among sites with similar abiotic environmental conditions. Our results also indicate that biotic interactions among

trophic levels are more important drivers of community assembly in disturbed than undisturbed landscapes. These results highlight the potential for co-extinction of species brought about by the loss of biotic linkages. Our findings also suggest that studies of composition–environment relationships that ignore biotic factors might erroneously conclude that weak relationships between β -diversity and abiotic factors are the result of neutral or stochastic community assembly mechanisms (Chase & Myers, 2011).

4.3 | Conservation implications

Our results have broad implications for the conservation of biodiversity of taxa linked through mutualistic or other trophic interactions. First, our results highlight the importance of pollinator communities in determining plant community assembly following severe wildfire disturbance. Given evidence of widespread global pollinator declines and increasing severity and frequency of wildfires with global climate change (Abatzoglou & Williams, 2016; McLaughlan et al., 2020; Potts et al., 2010; Westerling et al., 2006), our findings suggests that plant community assembly and the recovery of plant species diversity following wildfire or other disturbances may be drastically altered by the lack of intact and healthy pollinator populations. Second, if plant–pollinator associations account for substantial variation in plant and pollinator species composition beyond what can be explained by the abiotic environment alone (as we find), then climate-based models meant to predict future range shifts for either pollinator or plant species (e.g. Imbach et al., 2017) may not generate accurate predictions if they do not account for biotic interactions (Wiszniewski et al., 2013). While consideration of plant associates for pollinator species appears to be an important consideration for their conservation, such a focus on a species' biotic associates is rarely considered in many climate-based species-distribution models that attempt to predict future range shifts with global climate change. One potential solution is for species-distribution models to incorporate information about biotic associations (Wiszniewski et al., 2013). Yet, for most systems, many gaps remain in our knowledge of species associations and interactions. For example, in many pollinator–plant systems, we still have little understanding of which pollinators prefer which species of plants (and vice versa; Sargent & Ackerly, 2008), how plant–pollinator interactions vary across space (Carstensen et al., 2014), and the degree to which interactions are flexible in the absence of typical or preferred species (Burkle et al., 2016).

Overall, our results suggest that a more thorough understanding of plant–pollinator interaction networks is as important to the maintenance of pollinator and plant diversity as an understanding of climate or other abiotic influences on plants and their pollinators (Morris et al., 2020). While this may have been assumed widely in pollination ecology, we now have strong evidence that this is indeed the case for pollinators and flowering plants. Thus, an expanded effort to understand plant–pollinator associations, and species–interaction networks in general, may be necessary to effectively conserve

much of the world's biodiversity (Bascompte et al., 2006; Bastolla et al., 2009).

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AUTHORS' CONTRIBUTIONS

L.A.B., R.T.B. and J.A.M. conceived the study and collected the data; J.A.L. performed statistical analyses and wrote the first draft of the manuscript. All authors contributed to revisions of the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and R scripts to reproduce analyses are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.z34tmpgbq> (LaManna et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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