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Research

Wildfire severity alters drivers of interaction beta-diversity in plant–bee networks

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Spatial variation in species interactions (interaction β-diversity) and its ecological drivers are poorly understood, despite their relevance to community assembly, conservation and ecosystem functioning. We investigated effects of wildfire severity on patterns and four proximate ecological drivers of interaction β-diversity in plant–bee communities across three localities in the northern Rocky Mountains (Montana, USA). Wildfires decreased interaction β-diversity but increased interaction frequency (number of visits) and richness (number of links). After controlling for interaction frequency and richness, standardized effect sizes of interaction β-diversity were highest following mixed-severity wildfires, intermediate following high-severity wildfires and lowest in unburned landscapes, suggesting that wildfire increases spatial aggregation of plant–bee interactions. Moreover, higher effect sizes in burned landscapes were largely determined by turnover in the species composition of both trophic levels rather than by interaction rewiring (spatial turnover in local species interactions not due to species turnover). The underrepresented level of rewiring indicated spatial consistency in post-disturbance patterns of interactions among co-occurring species. Together, our findings suggest that wildfire alters the β-diversity of mutualistic species interactions via linked assembly of plant–bee communities and provide insights into how environmental change alters complex networks of species interactions.

Keywords: beta diversity, community assembly, environmental gradients, homogenization, interaction turnover, plant–pollinator networks, pollination, pyrodiversity, rewiring, species turnover, wildfire disturbance

Introduction

One of the central challenges in community ecology is to understand the causes of variation in species interactions across space and the consequences of this variation for species diversity, ecosystem functioning and evolutionary processes (Travis 1996, Thompson 2005). Among-site variation in species composition within trophic levels – β-diversity – has been used to gain insights into the processes structuring communities,

effects of climate change and altered disturbance regimes (Leprieur et al. 2011, Myers et al. 2015, LaManna et al. 2021), and the efficacy of conservation and restoration efforts (Vellend et al. 2007, Chalcraft et al. 2008, Grman and Brudvig 2014). Despite long-standing interest in patterns of β-diversity within single trophic levels, patterns of β-diversity across interacting trophic levels – such as pollinators and plants, or predators and prey – are poorly understood (Holland et al. 2005, Novotny 2009, Burkle et al. 2016, Myers and LaManna 2016). Recently, there has been a surge of interest in extending conceptual frameworks of β-diversity at single trophic levels to explore the β-diversity of species interactions across trophic levels, a pattern known as interaction β-diversity or interaction turnover (Poisot et al. 2012). Interaction β-diversity may provide key insights into mechanisms of community assembly, species coexistence and the responses of trophic interactions and ecosystem services to global change (Novotny 2009, Tylianakis et al. 2010, Burkle and Alarcón 2011, Burkle et al. 2016). Yet little is known about how or why interaction β-diversity responds to environmental change (Pellissier et al. 2018).

Theory suggests that environmental change may influence interaction β-diversity via four fundamental, proximate ecological processes: species turnover of the lower trophic level, species turnover of the higher trophic level, simultaneous turnover of both trophic levels and interaction rewiring (spatial turnover in local species interactions not due to species turnover) (Petanidou et al. 2008, Novotny 2009, Poisot et al. 2012, CaraDonna et al. 2017). Spatial turnover within a single trophic level can be caused by dispersal limitation, ecological drift or niche selection (Vellend 2010). In turn, these processes can increase interaction β-diversity among trophic levels linked by antagonistic (e.g. plant–herbivore) or mutualistic (e.g. plant–pollinator) interactions. Interaction rewiring reflects spatially variable foraging preferences or interaction partners among co-occurring species that depend on the abundances, phenologies, morphologies and behaviors of interacting species in a community (Vazquez et al. 2009). In a pioneering study of β-diversity in plant–herbivore food webs, Novotny (2009) found that turnover of interactions between tropical trees and their insect herbivores was determined more by spatial turnover of tree species and simultaneous turnover in tree and herbivore species than by turnover of herbivore species or rewiring. However, empirical tests of the effects of these processes on interaction β-diversity and how they respond to environmental change are limited, particularly for trophic levels linked by mutualistic interactions (Simanonok and Burkle 2014, Burkle et al. 2016, Pellissier et al. 2018).

Among the many drivers of global environmental change, alterations to fire regimes may have some of the most profound impacts on the β-diversity of mutualistic species interactions (Burkle et al. 2016, Ponisio et al. 2016, McLauchlan et al. 2020, LaManna et al. 2021). Fire may increase interaction β-diversity by increasing spatial turnover in local species composition of single or multiple trophic levels (Novotny 2009, Burkle et al. 2016). For example, mixed-severity wildfires may increase spatial turnover of flowering plants (Burkle et al.

2015, Ponisio et al. 2016, LaManna et al. 2021) via species sorting among sites that differ in abiotic or biotic conditions (LaManna et al. 2021). Alternatively, fire, or its absence, may influence spatial turnover within trophic levels by decreasing the total number of individuals in a community (community size) at random with respect to species identity, resulting in ecological drift (Myers et al. 2015, Catano et al. 2017). For example, Myers et al. (2015) found that higher β-diversity of woody plants in burned than unburned forests was associated with smaller numbers of individuals in burned communities rather than stronger selection among sites with different environmental conditions. Fire may also increase interaction β-diversity by increasing interaction rewiring. Given that fire can increase interspecific and intraspecific variation in floral traits important for interactions with pollinators as well as interspecific variation in pollinator body size (Ne'eman et al. 2000, LoPresti et al. 2018, Burkle et al. 2019), potential opportunities exist for shifts in pollinator foraging choices and rewiring after wildfire. However, the extent to which fire alters interaction β-diversity via its effects on interaction rewiring, species turnover within or across trophic levels or multiple processes remains unknown.

In this study, we investigated the effects of wildfire on patterns and ecological drivers of interaction β-diversity among plants and bees across three localities in the northern Rocky Mountains of Montana, USA. Within each locality, we surveyed plant–bee interactions at plots in landscapes with no recent wildfire (unburned), mixed-severity wildfire and high-severity wildfire. To test the hypothesis that wildfire influences the relative strength of proximate ecological drivers of interaction β-diversity, we first partitioned the interaction β-diversity observed in each landscape into four components: spatial turnover of flowering-plant species composition, spatial turnover of bee species composition, simultaneous turnover of plant and bee species composition and interaction rewiring. Following Burkle et al. (2016), we refer to these four components of interaction β-diversity as proximate drivers. Second, we used a null model to simulate patterns of interaction β-diversity and its four components that were expected due to differences in the local frequency (number of visits) and landscape richness (number of links) of plant–bee interactions observed in unburned and burned communities. In our study sites, unburned communities generally have fewer individuals and lower species richness of flowers and pollinators than burned landscapes (Burkle et al. 2015, 2019, LaManna et al. 2021). Therefore, we expected higher interaction β-diversity in unburned landscapes due to lower interaction frequency and richness (Burkle et al. 2016). Third, we calculated standardized effect sizes (relative measures of effect magnitudes) of interaction β-diversity and its four components that accounted for differences in interaction frequency and richness. Larger standardized effect sizes in burned than unburned landscapes would indicate more spatial aggregation (clumping) of plant–bee interactions than expected given observed interaction frequency and richness. Spatial aggregation of species interactions could, in turn, be driven by wildfire's influence on community assembly

processes such as species sorting and dispersal limitation (LaManna et al. 2021). Our study provides insights to the relative contributions of plant species turnover, bee species turnover and interaction rewiring and the influence of ecological assembly processes in structuring plant–bee interactions across disturbed and undisturbed landscapes.

Material and methods

Study localities

We studied plant–bee interactions in three distinct localities – Helena, Paradise Valley (hereafter Paradise), and whitefish – in the Northern Rockies Ecoregion of Montana, USA (Supporting information). Historically, mixed-severity wildfires in this biogeographic area (Fischer and Bradley 1987, Baker 2009) promoted landscape heterogeneity through a mosaic of forest successional stages (Hessburg and Agee 2003, Perry et al. 2011). Due to fire suppression and fuel buildup over the past century, wildfire severity is increasing (Miller et al. 2009). The Helena locality is characterized by low primary productivity (ca 450 g C m^{-2} year^{-1}) ponderosa pine *Pinus ponderosa* woodlands, the Paradise locality by intermediate productivity (ca 500 g C m^{-2} year^{-1}) lodgepole pine *P. contorta* and Douglas fir *Pseudotsuga menziesii* forests, and the whitefish locality by high productivity (ca 600 g C m^{-2} year^{-1}) mixed-conifer forests (Burkle et al. 2015). Within each locality, a wildfire had occurred within the past 6–12 years. Study sites were selected to span mixed-severity fire (18 sites in each locality), high-severity fire (18 sites in each locality) and unburned areas (16–18 sites with no wildfire within at least the last 60 years). Distance between sites within a fire severity class or within a locality was not a strong contributor to β-diversity of plants or pollinators (LaManna et al. 2021). Detailed descriptions of fire characteristics and site-selection methods are available in Burkle et al. (2015). Furthermore, patterns of alpha and beta diversity, species composition and traits, among other information about this system, are in Burkle et al. (2015, 2019), Reese et al. (2018) and LaManna et al. (2021).

Field methods: plant–bee interactions

We quantified plant–pollinator interaction networks at each site by observing floral visitors at open flowers in a 25 m diameter plot (491 m^2) weekly for 20 min during times of greatest visitor activity (sunny, calm, 9:00–16:00 h) over the growing season (late-May–August, depending on the locality). Pollinators were those floral visitors contacting the reproductive parts of flowers and moving among flowers, and we captured them with hand nets. Plant and floral visitor species presence at a site was determined by their participation in at least one plant–pollinator interaction. We did not consider plant species with flowers that were never visited. Plots in Helena were observed twice in 2013, 12 times in 2014, 9 times in 2015 and 7 times in 2016. Plots in Paradise were observed twice in 2013, 9 times each in 2014 and 2015 and 5 times in 2016. Plots in Whitefish were observed twice in 2013 and 7 times each in 2014 and 2015 (Burkle et al. 2019). Therefore, although sampling effort was somewhat variable among years and localities, sampling was consistent within each locality and our analytical approaches and null models take this into account (below). Floral visitors were frozen, pinned and identified to species (Reese et al. 2018). Because bees were 89% of individual visitors to flowers, we focused on this group and pooled plant–bee interactions for each site across all observations for analyses.

Statistical methods

We tested the hypothesis that wildfire influences proximate drivers of interaction β-diversity in four main steps. First, we calculated the observed plant–bee interaction β-diversity ($β_{TOTAL-OBS}$) among sites within each fire severity class in each locality following Simanonok and Burkle (2014), which is modified from betalink (Poisot et al. 2012). $β_{TOTAL-OBS}$ uses the Jaccard index of dissimilarity and reflects the presence or absence of plant–bee interactions (links between plant and bee species) among sites. $β_{TOTAL-OBS}$ was calculated as $(b + c)/(a + b + c)$, where a is the number of interactions (links) shared between the plant–bee networks of two sites, b is the number present only in the network of the first site and c is the number present only in the network of the second site (Novotny 2009). We used this measure because it incorporates differences in interaction richness (broad-sense measure of β-diversity) that more narrow-sense measures ignore (Koleff et al. 2003). Furthermore, this measure can be easily partitioned into additive components that allow investigation of the underlying proximate drivers of interaction β-diversity. Results that were based on Bray–Curtis dissimilarity, which incorporates interaction frequency, yielded qualitatively similar results (Supporting information).

Second, we partitioned the observed plant–bee interaction β-diversity ($β_{TOTAL-OBS}$) into four additive components representing turnover resulting from simultaneous plant and bee species turnover ($β_{PA-OBS}$), plant species turnover ($β_{P-OBS}$), bee species turnover ($β_{A-OBS}$) or interaction rewiring ($β_{0-OBS}$) among sites within each fire severity class in each locality following Simanonok and Burkle (2014). Interaction rewiring represents the proportion of $β_{TOTAL-OBS}$ unexplained by the three species turnover components ($β_{PA-OBS}$, $β_{P-OBS}$, $β_{A-OBS}$), and therefore reflects spatially variable foraging preferences or interaction partners among co-occurring species. In the simplest case comparing two communities with identical species composition of plants and bees, $β_{0-OBS}$ equals $β_{TOTAL-OBS}$.

Third, we used a null model to calculate standardized effect sizes of plant–bee interaction β-diversity and its four components that preserves differences in local interaction frequency (total number of observed visits made by bees to flowers per site) and the composition and richness of plant–bee interactions (observed links, i.e. plant–bee species pairings) within each fire severity class per locality (Supporting information). Sites with lower interaction frequency and richness

(Fig. 1) are expected to have higher interaction β-diversity than sites with higher interaction frequency and richness due to random sampling alone (Burkle et al. 2016). In each of 2000 iterations of the null model, we simulated the expected interaction β-diversity ($\beta_{TOTAL-SIM}$) among sites within each fire-severity class (unburned, mixed-severity wildfire, high-severity wildfire) in each locality. We then calculated standardized effect sizes of interaction β-diversity ($\beta_{TOTAL-SES}$) as the difference between $\beta_{TOTAL-OBS}$ and mean $\beta_{TOTAL-SIM}$ (n = 2000), divided by the standard deviation of $\beta_{TOTAL-SIM}$. To do this, we modified the Kraft et al. (2011) null model for the analysis of β-diversity within a single trophic level. We calculated $\beta_{TOTAL-SIM}$ by randomly sampling plant–bee visits for each site from all of the plant–bee visits observed across all sites in each fire-severity class in each locality. Therefore, $\beta_{TOTAL-SES}$ represents deviation from the null-expected β-diversity of plant–bee interactions, given local interaction frequencies and landscape interaction composition for each fire severity class. Positive values of $\beta_{TOTAL-SES}$ indicate processes that increase spatial aggregation of plant–bee interactions within sites (e.g. species sorting, dispersal limitation), whereas negative values of $\beta_{TOTAL-SES}$ indicate processes that homogenize plant–bee interactions across sites. In each iteration of the null model, we also simulated the expected values for each of the four components (β_{PA-SIM}, β_{P-SIM}, β_{A-SIM} and β_{0-SIM}), and calculated SES for each component (β_{PA-SES}, β_{P-SES}, β_{A-SES} and β_{0-SES}) following the same method used for $\beta_{TOTAL-SES}$ described above. Positive values of SES for any component indicate that the observed component contributes more to $\beta_{TOTAL-SES}$ than

expected, whereas negative values indicate that the observed component contributes less to $\beta_{TOTAL-SES}$ than expected.

Fourth, we used mixed-effect PermANOVA models to test whether observed interaction β-diversity ($\beta_{TOTAL-OBS}$), the four observed components (β_{PA-OBS}, β_{P-OBS}, β_{A-OBS} and β_{0-OBS}), standardized effect sizes of interaction β-diversity ($\beta_{TOTAL-SES}$) and the four standardized components (β_{PA-SES}, β_{P-SES}, β_{A-SES} and β_{0-SES}) differed among fire severity classes (fixed effect), with locality included as a random effect (Borcard et al. 2011, Legendre and Legendre 2012). Results for individual localities are provided in the Supporting information. We conducted PermANOVAs with *permanova.lmer* in the predictmeans package (Luo et al. 2020). We followed significant PermANOVAs with contrastmeans to test for pairwise differences between fire severity classes. Values of SES that overlap zero are not different from the null expectation (null model above), but may differ between fire severity classes (via contrastmeans). All analyses were performed in R ver. 3.5.3 (<www.r-project.org>).

Results

Observed effects of wildfire on plant–bee interaction β-diversity and its ecological components

Wildfire significantly decreased observed plant–bee interaction β-diversity (Table 1: $\beta_{TOTAL-OBS}$). $\beta_{TOTAL-OBS}$ was generally high in all landscapes (above 85% on average; Fig. 2). However, $\beta_{TOTAL-OBS}$ was slightly higher in unburned landscapes (Fig. 2).
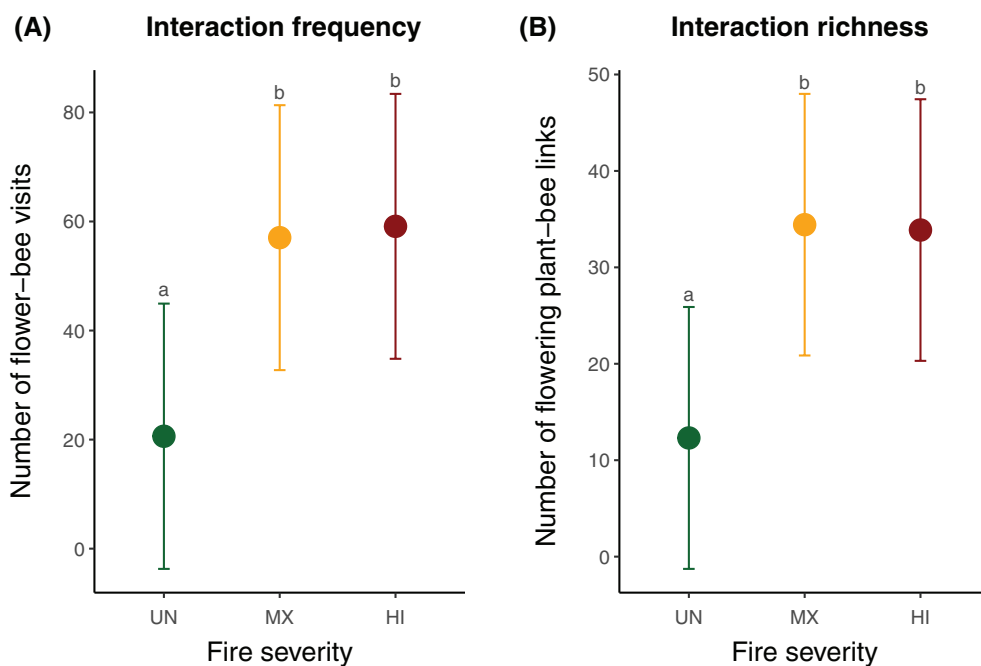

Figure 1. Least-squared mean (A) interaction frequency (number of flower–bee visits) and (B) interaction richness (number of flowering plant–bee links) per site among fire severity classes (colors). Unburned is in green, mixed-severity fire is in orange and high-severity fire is in red. Letters indicate significant differences among fire severity classes at α < 0.05. Within-locality patterns are shown in the Supporting information.

Table 1. Mixed-effects PermANOVA of the effects of wildfire severity on observed interaction β-diversity and its components and on standardized effect sizes of interaction β-diversity and its components. Locality was included as a random effect. PermANOVAs used the Kenward–Roger approximation for degrees of freedom (df = 1297). p-values at α < 0.05 are in boldface.

Response	F	p
Observed		
B_{TOTAL}	162.99	**0.001**
B_{PA}	367.96	**0.001**
B_P	75.51	**0.001**
B_A	297.98	**0.001**
B_0	316.66	**0.001**
SES		
B_{TOTAL}	41.10	**0.001**
B_{PA}	18.39	**0.001**
B_P	17.58	**0.001**
B_A	29.15	**0.001**
B_0	59.47	**0.001**

Ecological components of observed interaction β-diversity differed among fire-severity classes (Table 1, Fig. 2). The contribution of simultaneous plant and bee species turnover (β_{PA-OBS}) ranged from 24 to 59%, and this was the strongest contributor to $\beta_{TOTAL-OBS}$ in unburned areas. β_{PA-OBS} was lower in burned landscapes, especially following high-severity wildfires. The contribution of plant species turnover (β_{P-OBS}) was highest in unburned landscapes (23%) and lowest following high-severity wildfires (13%). The contribution of bee species turnover (β_{A-OBS}) ranged from 11 to 37%, and this was the strongest contributor to $\beta_{TOTAL-OBS}$ in burned landscapes. β_{A-OBS} was highest following high-severity wildfires, and

lowest in unburned landscapes. Interaction rewiring (β_{0-OBS}) was generally the least important contributor to $\beta_{TOTAL-OBS}$ (3–15%). Like β_{A-OBS}, β_{0-OBS} was highest following high-severity wildfires, intermediate following mixed-severity wildfires, and lowest in unburned landscapes.

Effects of wildfire on standardized effect sizes of interaction β-diversity and its ecological components

Wildfire increased standardized effect sizes of interaction β-diversity (Table 1: $\beta_{TOTAL-SES}$; Fig. 3). $\beta_{TOTAL-SES}$ were higher than the null expectation (zero) following mixed-severity and high-severity wildfires. $\beta_{TOTAL-SES}$ were also higher following mixed-severity wildfires than high-severity wildfires. In contrast, $\beta_{TOTAL-SES}$ did not differ from the null expectation in unburned landscapes.

The SES for each of the ecological components of interaction β-diversity differed among fire-severity classes (Table 1, Fig. 3). In unburned landscapes, the SES for all four components overlapped with the null expectation, whereas components in burned landscapes were positive, neutral or negative. The SES for the component of $\beta_{TOTAL-OBS}$ due to simultaneous plant and bee species turnover (β_{PA-SES}) were significantly positive following mixed-severity wildfires and marginally positive following high-severity wildfires, indicating that spatial turnover of pairs of plant and bee species among sites was more common than expected. In contrast, SES for the component of $\beta_{TOTAL-OBS}$ due to plant species turnover (β_{P-SES}) and bee species turnover (β_{A-SES}) were no different from the null expectation, regardless of fire severity (but see Supporting
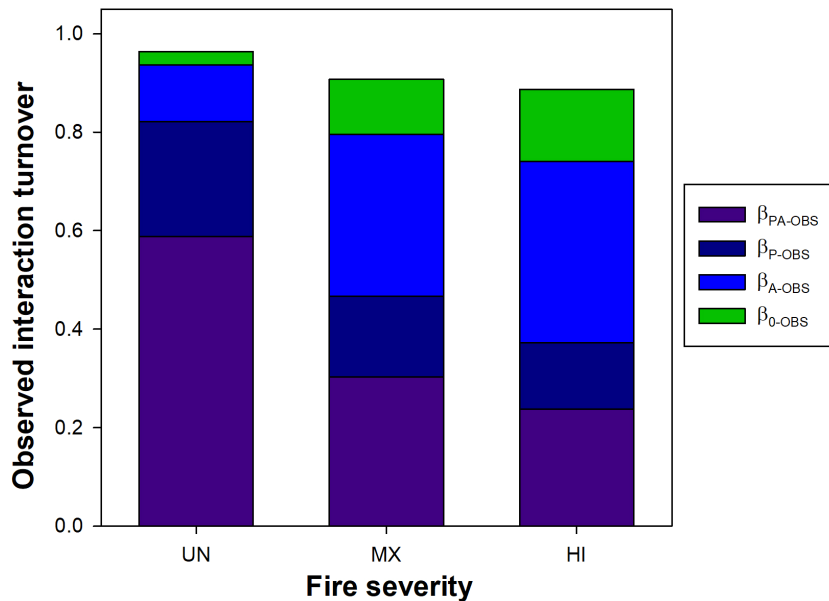

Figure 2. Observed plant–bee interaction β-diversity among fire severity classes: unburned (UN), mixed severity (MX) and high severity (HI). Total interaction turnover ($\beta_{TOTAL-OBS}$) is the sum of the four partitions: β_{PA-OBS} (purple) is the contribution of simultaneous plant and bee species turnover to observed interaction turnover, β_{P-OBS} (dark blue) is the contribution of plant species turnover, β_{A-OBS} (blue) is the contribution of bee species turnover and β_{0-OBS} (green) is the contribution of rewiring. Observed values of interaction turnover can range from 0 (all interactions shared between pairs of sites) to 1 (no interactions shared between pairs of sites).
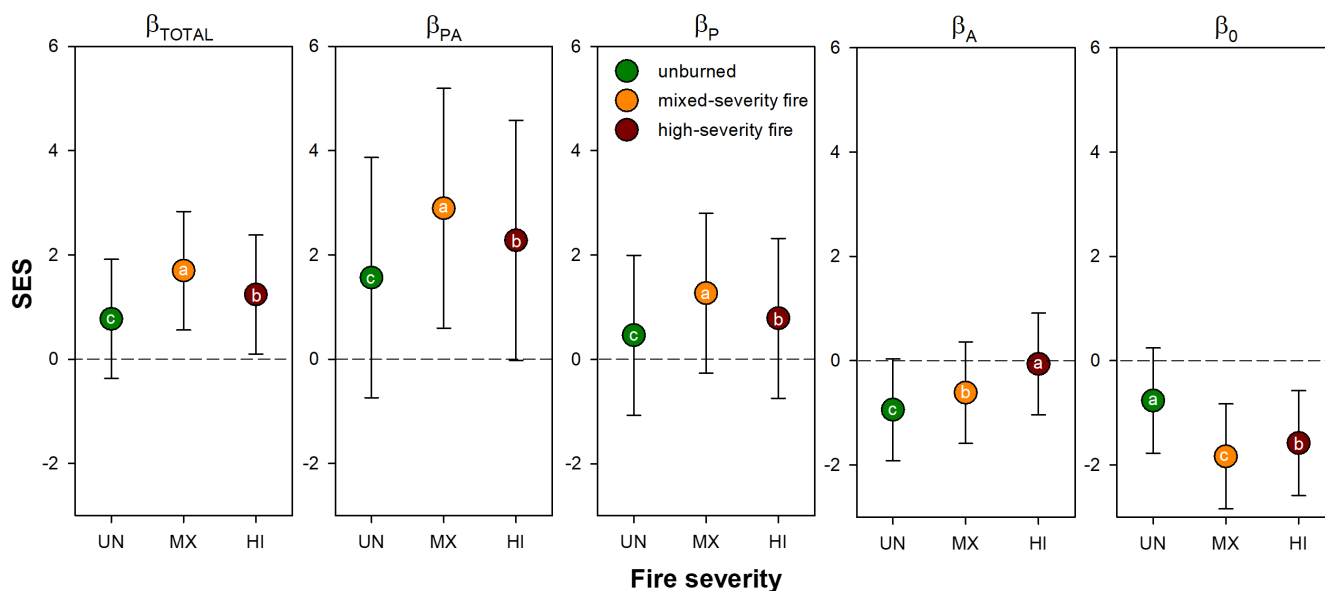
Figure 3. Standardized effect sizes (SES) of plant–bee interaction β-diversity ($\beta_{TOTAL-SES}$) among fire severity classes (colors) and SES for the partitioned contributors to interaction β-diversity (i.e. β_{PA-SES}, β_{P-SES}, β_{A-SES} and β_{0-SES}). β_{PA-SES} is the SES of the contribution of simultaneous plant and bee species turnover, β_{P-SES} is the SES of the contribution of plant species turnover, β_{A-SES} is the SES of the contribution of bee species turnover and β_{0-SES} is the SES of the contribution of rewiring. Unburned (UN) is in green, mixed-severity wildfire (MX) is in orange and high-severity wildfire (HI) is in red. Error bars are 95% confidence intervals. SES of interaction β-diversity with confidence intervals that overlap zero indicate that between-site differences in the composition of interactions are no different from the null-expectation. Letters indicate significant differences among fire severity classes at α < 0.05 (Supporting information).

information for differences among localities in β_{P-SES}). The SES for the component of $\beta_{TOTAL-OBS}$ due to interaction rewiring (β_{0-SES}) were negative in burned landscapes, especially so following mixed-severity wildfires, indicating that rewiring contributed less to interaction β-diversity than expected.

Discussion

Our results support the hypothesis that wildfire influences interaction β-diversity and its proximate ecological drivers. Wildfires homogenized observed plant–bee interactions across sites, especially following high-severity wildfires. In contrast, observed plant–bee interactions were most heterogeneous among sites in unburned landscapes. However, after accounting for fewer plant–bee interactions in unburned than burned landscapes, the high levels of interaction β-diversity observed in unburned areas largely disappeared. Instead, standardized effect sizes of interaction β-diversity were highest in burned landscapes, especially following mixed-severity wildfires, and no different from the null expectation in unburned landscapes. Standardized effect sizes of interaction β-diversity were positive in burned landscapes, indicating that plant–bee interactions become more spatially aggregated following wildfires. Patterns in the proximate drivers of interaction β-diversity were altered after controlling for differences in flower–bee interaction frequency of local communities and in interaction richness between wildfire severities of each locality, highlighting the importance of null-model approaches when considering the causes of variation in species interactions across space.

Importantly, in burned landscapes, simultaneous turnover in the composition of both plant and bee species contributed more than expected to interaction β-diversity, whereas rewiring contributed less than expected. These findings suggest that post-disturbance patterns of interactions among co-occurring species are fairly consistent across space, and wildfire alters the β-diversity of plant–bee interactions via linked assembly of both trophic levels.

Alteration of interaction β-diversity and its ecological components by wildfire

Our results suggest that wildfire – especially high-severity wildfire – homogenizes local plant–bee interactions. Although this is the first study to investigate the effects of disturbance on the spatial turnover of species interactions, our findings are consistent with other studies of species-level β-diversity that found homogenizing effects of wildfire on species composition (Pausas and Verdú 2008, Myers and Harms 2011, LaManna et al. 2021).

However, in this study, the homogenizing influence of wildfire appeared to be caused by greater frequency of plant–bee interactions in local communities and greater interaction richness across burned landscapes. In the absence of any other ecological processes, higher β-diversity is expected among local communities in landscapes that contain larger numbers of species in the regional species pool (Kraft et al. 2011, Myers et al. 2013). Via simulations, Burkle et al. (2016) found that interaction β-diversity is expected to increase as the size of the regional species pool increases,

especially for communities with small numbers of individuals. To date, other empirical studies of interaction β-diversity have not accounted for null-expected patterns due to changes in local interaction frequency or landscape-level interaction composition and richness. Here, unburned sites were relatively depauperate in flowering plants and bees (Burkle et al. 2015, 2019, LaManna et al. 2021), whereas floral resources are generally more plentiful after wildfire in the northern Rocky Mountains (Burkle et al. 2019) and other ecosystems (Potts et al. 2003, reviewed by Pyke 2017, Mola and Williams 2018). These effects of wildfire on local abundances and landscape-level species richness led to greater interaction frequency and richness in burned areas, which in turn created patterns in interaction β-diversity. By considering how disturbances such as wildfires influence interaction β-diversity via both local and landscape processes, it may be possible to increase understanding of how complex networks of species interactions respond to and recover from disturbance, especially at the large spatial and temporal scales most germane to conservation and management.

After controlling for differences in interaction frequency and richness, we found that plant–bee interactions were more heterogeneous among sites in burned landscapes, especially following mixed-severity burns. Furthermore, in unburned landscapes, none of the proximate drivers of interaction β-diversity were different from the null expectation. In burned landscapes, only two of the proximate drivers differed from the null expectation. Consistent with the hypothesis that species sorting plays a critical role in plant–pollinator interactions, we found that differences in SES of interaction β-diversity among landscapes were primarily associated with differences in the relative importance of simultaneous species turnover in both trophic levels (β_{PA} component). Among the four components of interaction β-diversity, β_{PA} emerged as a stronger proximate driver of interaction β-diversity in burned compared to unburned landscapes (Fig. 3). These results are consistent with LaManna et al. (2021), who found that associations between plant and pollinator species explained significant variation in the turnover of species in both trophic levels, beyond what could be explained by other abiotic and spatial factors in these ecosystems. Notably, there was less interaction rewiring than expected in burned landscapes, indicating stability in plant–bee interactions (i.e. bees visiting most possible plant partners and not switching hosts). Such stability of interactions in burned communities is consistent with bees competing less for plentiful floral resources post-fire and foraging mainly on their preferred flowers, or could indicate limited interaction flexibility when the occurrence of preferred interaction partners varies across space. The implications of these patterns for pollination are unknown.

Increase in spatial aggregation of plant–bee interactions by wildfire

Our results suggest that wildfire increases spatial aggregation of plant–bee interactions. We found that standardized effect sizes (SES) of interaction β-diversity were highest following mixed-severity wildfires. This finding suggests that mixed-severity wildfires not only increase heterogeneity of environmental conditions (Perry et al. 2011) and species assemblages of plants and bees (Burkle et al. 2015, Ponisio et al. 2016, LaManna et al. 2021) across space, but also increase spatial aggregation of plant–bee interactions.

Three key processes may contribute to spatial aggregation of plant–bee interactions in burned landscapes. First, dispersal limitation may constrain colonization and establishment of plants and bees following wildfire, especially when large areas are burned. Species with particular traits (e.g. long flight ranges, persistent seed banks) may be more likely to colonize post-fire (Keeley and Fotheringham 2000, Carbone et al. 2019). Second, abiotic mechanisms of species sorting can result in spatial aggregation when environmental conditions select for particular suites of species. For example, wildfire in some systems may lead to conditions that are best exploited by large-bodied bee species and taller plant species with large floral displays (LoPresti et al. 2018, Burkle et al. 2019). However, the abiotic environment alone is unlikely to drive interaction β-diversity in this system (LaManna et al. 2021). Third, biotic mechanisms of species sorting can contribute to spatial aggregation through interactions with species that are clumped. In a recent study of β-diversity within both trophic levels (LaManna et al. 2021), we found that biotic associations between plants and pollinators explained more of the variation in community structure in burned than unburned landscapes.

Pollination is essential to the recovery of plant communities after wildfire (Ne'eman et al. 2000, Potts et al. 2006, Heil and Burkle 2019). Because wildfire alters β-diversity of plant–pollinator interactions via spatial turnover of species in both trophic levels, management of both plants and bees may be necessary to conserve pollination in these and other disturbed landscapes. Investigating the mechanisms underlying interaction β-diversity, including species turnover of one or both trophic levels and rewiring, will assist in linking species-level patterns in β-diversity with spatial patterns in their interactions and in better understanding disturbances and environmental change. Furthermore, this work highlights the value of incorporating null-models that account for interaction frequency and richness at local and landscape scales when assessing the β-diversity of species interactions across environmental gradients. This study provides an example of these approaches to help guide future work on the biogeography of species interactions.

Author contributions

Laura A. Burkle: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead). **R. Travis Belote**: Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (supporting). **Jonathan A. Myers**: Conceptualization (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Writing – review and editing (equal).

Transparent Peer Review

Data availability statement

Supporting information

The supporting information associated with this article is available from the online version.

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