Final Report to Boulder County Parks and Open Space and City of Boulder Open Spaces and Mountain Parks

Effects of fire and thinning disturbances on biodiversity of wild bee communities in the Front Range of Colorado

Thomas Seth Davis[1*], Ryleigh Gelles[1], Boris Kondratieff[2], Camille Stevens-Rumann[1]

[1]Forest and Rangeland Stewardship, Warner College of Natural Resources, Colorado State University, Fort Collins, CO, USA

[2]Bioagricultural Sciences and Pest Management, College of Agricultural Sciences, Colorado State University, Fort Collins, CO, USA

*Correspondence: Thomas Seth Davis, Primary Investigator, email: seth.davis@colostate.edu, phone: 970-491-6980, mailing address: 1472 Campus Delivery, Fort Collins, CO, USA 80523-1472.

BCPOS sponsor: Stefan Reinold

OSMP sponsor: Chris Wanner

Executive Summary

This project examined the response of native pollinator communities to forb cover and diversity, as mediated by wildfire and wildfire mitigation treatments in ponderosa pine stands managed by OSMP and BCPOS. At least 57 unique native bee species were detected in the study, and there was no evidence that forest thinning negatively impacted bee richness or abundance. Approximately 35% of detected bee genera varied seasonally in their abundances, but bumblebees (*Bombus* spp.) were by far the most common genus captured (97% of sites) and were present in high abundance throughout the growing season. Bee abundance and species richness were positively correlated with floral abundances and coarse woody debris loadings. Floral resources and woody debris were greatest in sites that had experienced low- and high-severity wildfire. Distinct bee communities were identified in burned, thinned, and non-treated sites, and indicated the presence of both habitat specialists and generalists. In addition, the presence of exotic forbs at study sites was not associated with bee abundance or diversity. Collectively these results suggest that a mosaic of cover types reflecting multiple disturbance categories may maximize regional bee biodiversity, and ecosystem management efforts that impact either floral resources or woody debris are likely to have direct effects on site-level native bee assemblages.

Management Implications

(1) Ponderosa pine forest stands on BCPOS and OSMP lands provide habitat for a surprisingly diverse native bee community and represent an important conservation resource.

(2) Forest thinning has no detectable effect on native bee abundance or species richness.

(3) Floral resources and coarse woody debris are positively associated with site occupancy by native bees and can be targeted by vegetation management efforts.

(4) Exotic (forb) species are not expected to have negative effects on bee communities or pollination services.

(5) Regional bee biodiversity can be managed by retaining both anthropogenic (thinning) and natural (low- or high-severity fire) disturbance processes on the landscape.

Abstract

Using blue vane traps native bee community assemblages were sampled across the growing season (early, middle, and late) in 39 ponderosa pine-forest sites in central Colorado to evaluate the effects of fire and forest thinning disturbances on bee populations. We quantified bee abundance, richness, and diversity as well as foraging resources (flower abundance and richness), nesting habitat (woody material), and proportion of invasive forbs (%) to understand factors that predict bee distributions. Five key findings emerged: (1) overall γ-diversity was high and consisted of 4 families (Andrenidae, Apidae, Halictidae, and Megachilidae), 20 genera, and at least 57 unique bee species. Predominant genera consisted of bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.) which accounted for 59, 9, and 4% of total bee specimens, respectively. (2) Pooled bee abundances did not vary due to the effects of thinning or fire, but bee species richness was highest in stands that experienced high-severity fires. (3) Both floral resources and coarse woody debris were significantly more abundant in burned sites; floral resources were positively correlated with bee abundance and species richness and coarse woody debris was positively correlated with bee species richness. (4) Bee community composition varied across disturbance types, with ~40% of genera found only in specific habitats. (5) The presence of exotic plant species at study sites did not significantly impact bee abundance or diversity. We conclude that forest thinning operations are not associated with reductions in bee abundances or species richness, and fire disturbances generate foraging and

nesting habitats that are important for native bee diversity. However, community structure does vary across disturbance types and specific assemblages tend to be associated with non-treated, thinned, and burned sites, indicating that managers can use thinning and burning treatments as tools for conserving bee biodiversity on the landscape.

Keywords

Ecosystem management, biodiversity, community ecology, fire, native bees, ponderosa pine

Introduction

Wild pollinator species, especially native bees, have important impacts on the assembly and genetic structure of plant communities, maintenance of ecological networks (Loveless and Hamrick 1984), and provisioning of ecosystem services (Kremen et al. 2007). For instance, an estimated 75% of crops rely on pollination by insects for sustained yield or crop quality (IPBES 2016), and wild pollinator communities are often equivalent or superior to managed bees for crop pollination services (Winfree et al. 2009). It is increasingly recognized that pollination services are driven by landscape factors, and proximity of natural ecosystems including forests and rangelands enhances pollination services in nearby agricultural systems (Ricketts et al. 2008, Carvalheiro et al. 2010). This is because natural systems often contain specific nesting and foraging resources that may drive site occupancy by native bees in adjacent land cover types (Walther-Hellwig and Frankl 2003, Potts et al. 2006) and promote overall pollinator population growth (Williams et al. 2012). However, variation in structural characteristics of natural systems can alter bee foraging and nesting habitats, and these resources are directly affected by ecosystem management practices.

Disturbances, both anthropogenic and natural, are key drivers of ecosystem structure, function, and composition (Franklin et al. 2002). In coniferous forest systems of western North America, fire is one of the most prevalent and dramatic natural disturbances. Although it is increasingly recognized that fire disturbances are an important process for maintaining desirable ecosystem structures, many forest management efforts are also aimed at mitigating fire risk in wildland-urban interfaces (Cohen 2000). The Front Range region of central Colorado has experienced considerable population growth in recent decades and is probably one of the largest and most continuous wildland-urban corridors in the western United States (Manfredo and Zinn 1996). Dominant vegetation in forest landscapes on the eastern slope of the Front Range (where the majority of population centers are located) is generally distributed along an elevational gradient, with spruce/fir forests occurring at elevations >2500 m, and pine forests typically predominating below this threshold (Peet 1978). In particular, ponderosa pine forest is widespread in the region, and stands are often heavily managed for multiple use values but also with the specific goal of decreasing surface fuel loads to reduce wildfire risk near population centers (Liu et al. 2015).

Reduction of forest density and basal area (i.e., 'thinning') is the primary approach by which ecosystem managers address this goal. Recent studies have demonstrated that high forest basal areas are negatively correlated with bee abundance and species richness (e.g., Rhoades et al. 2018), likely via cascading effects whereby removal of canopy cover facilitates increased penetration of sunlight to the forest floor, favoring the growth of forbaceous species that are resources for pollinators including native bees (Eltz et al. 2002, Jha and Vandermeer 2010). However, very few studies have examined the effects of thinning on forest bee communities (Hanula et al. 2016), and no studies have yet examined the effects of thinning or fire disturbances

on bee assemblages in ponderosa pine forests. This is a critical knowledge gap, as forest vegetation management could have beneficial or deleterious effects on pollinator abundances and crucial ecosystem services. To address this gap in knowledge, we ask the question "How do disturbances from wildfire and fuels reduction (thinning) treatments affect bee communities?". To address this question, we specifically test the following working hypotheses: (1) bee abundance and diversity differs between burned stands, stands that have experienced forest density reduction, and non-treated high-density stands; (2) thinning promotes bee abundance and diversity as compared to non-treated control sites (treated vs. control sites); (3) fire severity has differential impacts on bee abundance and diversity ('low' vs 'high' severity); and (4) the presence of invasive forbs is associated with a reduction in bee abundance or diversity. Our studies provide a first description of basic bee biodiversity in ponderosa pine forests of central Colorado and elucidate how both anthropogenic and natural disturbances interact with site structural elements to predict variation in native bee species assemblages and community structure.

Methods and Materials

Study system. A total of N=39 sites were selected across the landscape of the Front Range of Colorado to represent four different disturbance types, including sites that had experienced (1) low-to-moderate severity wildfire, (2) high-severity wildfire, (3) sites treated with forest density reductions, and (4) non-treated control sites with high basal area (Figure 1). Sites were selected as a subset of the stands sampled and defined in Stevens-Rumann and Fornwalt (2018); the authors from that study comprehensively described understory plant community assemblages at study sites, including the total number of native and invasive forb, grasses and shrubs. These data

were also used in the present investigation. Dominant forest tree vegetation at study sites is typical of dry mixed-conifer forests in the Front Range of Colorado, and were focused in ponderosa pine (*Pinus ponderosa*) – dominant stands interspersed with Douglas-fir (*Psuedotsuga menziesii*). Wildfire disturbance sites included locations within the Fourmile Canyon fire (2010), the Dome fire (2010), and the Flagstaff fire (2012); fire severity was assigned based on the criteria of proportion of overstory tree mortality where high-severity was classified as stands that experienced 80-100% tree mortality and low-to-moderate severity was classified as stands that experienced 10-79% tree mortality (Stevens-Rumann and Fornwalt 2018). Stands disturbed by thinning had no recent burn history but were treated by density reduction to an average residual overstory basal area of 19.0 m^2/ha $\pm$ 2.0 m^2/ha between 2009-2013; similarly, mean basal area at non-treated control stands was 30.0 m^2/ha $\pm$ 3.0 m^2/ha, and mean basal area at low- and high-severity wildfire stands was 13.5 m^2/ha $\pm$ 1.4 m^2/ha and 0.2 m^2/ha $\pm$ 0.0 m^2/ha, respectively.

Bee sampling procedures. Bee diversity, abundance, and community composition fluctuate seasonally in central Colorado forest ecosystems (Rhoades et al. 2018), accordingly, at each site, bee assemblages were sampled at multiple time points representative of 'early' (Apr-May), 'middle' (Jun), and 'late' (Aug) in the growing season. Bee assemblages were sampled by placing specialized site-based 'blue-vane traps' (SpringStar, Inc., Woodinville, WA, USA) at study sites for a period of 48 h in each collection period. These traps are visually attractive to bees and highly effective at capturing them, consequently, trapping times were minimized to reduce potential impacts on bee communities. Minimum distance between trapping locations was 200 m to control for spatial autocorrelation in bee sampling efforts (Rhoades et al. 2018). Traps were hung from existing vegetation at a distance of ~1 m between the base of the trap and the ground surface, and a single trap was placed at each site in each sampling period.

After 48 h, trap contents were collected and returned to the laboratory for curation. All collected bees were sorted, labelled, pinned, and mounted for preservation and identification. Collected specimens were identified to the lowest taxonomic grouping possible; in most cases, to the genus- or species-level. The collection and representative voucher specimens are maintained in the Colorado State University Gillette Museum of Arthropod Diversity (Fort Collins, Colorado, USA). From specimen identifications, site-level species- and genus-abundance matrices were produced for use in statistical analysis and hypothesis-testing.

Measuring components of bee habitat. In addition to characterizing bee communities, we measured site structural elements important to bee foraging and nesting. At each collection period (n=3 for each study site), floral abundances were measured at sites using quadrats. At each site and collection period, five 1×1 m^2 quadrats were deployed and the total number of active floral displays (number of individual flowering plants, as determined from stem density) counted within each quadrat; species richness (number of putative species represented by active floral displays) within each quadrat was also be recorded. One quadrat was placed directly under the trap location, with additional quadrats placed 2 m in each cardinal direction. Quadrat measurements were treated as a subsample, and values from all 5 quadrats at each site were averaged together to yield a site-level mean floral abundance and richness for each collection period.

In addition to floral resources, coarse woody debris (both sound or rotting wood material on the ground surface >7.6 cm in diameter) is an important predictor of potential nesting habitat, especially for solitary bees (Rodriguez and Kouki 2015). To measure the availability of coarse woody debris fuels planar transects (Brown 1974) were used to generate estimates of woody debris loadings in MG/ha (megagrams per hectare); transects originated at the trap location in

each site and extended for 10 m in each cardinal direction (40 m total transect length per collection site). Tallied planar intercepts were aggregated across the four transects to provide a single site-level estimate of coarse woody debris surface loadings.

Data analysis. Two-way ANOVA was used to analyze the fixed effects of site disturbance type (low severity fire, high severity fire, density reduction treatment, and non-treated control), seasonality (early, middle, and late), and the disturbance type × seasonality interaction on the responses of mean bee abundance (number of bees) and mean species richness (number of species), treating each site × collection period observation of the bee community as an experimental unit. Post-hoc contrast tests were used to determine 1) whether thinning operations are associated with changes in the bee community assemblage relative to non-treated control sites, and 2) whether the effects of high severity fire on bee assemblages differ from those of low severity fire.

Mean floral abundance/richness, as well as woody debris loadings (MG/ha), were treated as proxies for foraging and nesting habitat, respectively, and were also analyzed as responses within this framework. The relationship between these metrics (floral abundance/richness and coarse woody debris loadings) and bee community metrics (abundance and richness) were subsequently investigated using linear regression models to test the directional hypotheses that 3) greater abundance or diversity of floral resources is associated with increased abundance or diversity of native bees, and 4) more nesting opportunities are associated with an increased abundance or diversity of native of native bees. Lastly, bee abundances and diversity were aggregated across all collection periods and regressed against the total proportion of forb cover identified as 'invasive species' (i.e., the % of forbs that are invasive) using botanical data from

Stevens-Rumann and Fornwalt (2018) to test the hypothesis that 5) presence of invasive forbs is associated with a reduction in bee abundance or diversity.

Bee community composition was also compared across sample collection periods and disturbance types at the genera scale to evaluate whether these factors were associated with shifts in bee assemblages. Chi-square tests were used to test the null hypothesis that the proportion of genera at study sites was similar across collection periods and disturbance types. Pie charts were used for visualization of these results.

All statistical tests were performed in the R programming language and incorporate a Type I error rate of α=0.05 for assigning 'statistical significance', though marginally significant effects (α=0.10) were also interpreted.

Results

Bee diversity across the study region. A total of 676 specimens were collected during the study; overall bee γ-diversity in ponderosa pine forests was high and consisted of 4 families (Andrenidae, Apidae, Halictidae, and Megachilidae), 20 genera, and at least 57 unique bee species. Predominant genera consisted of bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.) which accounted for 59, 9, and 4% of all collected bee specimens, respectively (Table 1). Rarefaction analysis indicated that the sampling design was robust for estimating γ-diversity across the study area (Figure 2); for instance, by solving the term in 2b it can be shown that including an additional 11 sites (50 total sites, an additional 22% sampling effort) would likely have resulted in the sampling of only one additional species, or an additional 1.8% species richness. Rates of detection of species richness was similar in all habitat types.

Effects of disturbance type and seasonality on bee assemblages. Abundances of captured bees were not affected by disturbance type ($F_{3, 90}$=0.122, P=0.946), collection period ($F_{2, 90}$=1.104, P=0.366), or a disturbance type $\times$ collection period interaction ($F_{6, 90}$=0.704, P=0.646), although mean bee abundances were greatest in the early-season (June) collection period. Similarly, bee species richness was not affected by disturbance type ($F_{3, 90}$=2.039, P=0.114), collection period ($F_{2, 90}$=1.738, P=0.186), or a disturbance type $\times$ collection period interaction ($F_{6, 90}$=0.615, P=0.717; Figure 3). However, when bee abundances were analyzed at a genus level, 35% of genera exhibited significant seasonal variation including *Anthophora*, *Diadasia*, *Halictus*, *Hoplitis*, *Lasioglossum*, *Megachile* and *Osmia*; all other genera were either relatively constant in their abundances across the growing season, or were too rare to evaluate their phenology (Table 2).

When specific contrasts were made between disturbance types, there was no evidence that mean bee abundance ($F_{1, 90}$=0.284, P=0.595) or species richness ($F_{1, 90}$=0.028, P=0.862) differed between thinned and non-treated control sites. There was also no evidence that mean bee abundance differed between high-severity fire and low-severity fire sites ($F_{1, 90}$=0.013, P=0.908); however, there was a marginally significant difference in mean species richness between high- and low-severity fire sites with approximately 23% greater species richness in sites that had experienced high-severity fire ($F_{1, 90}$=3.016, P=0.085; Figure 4). In addition, two rarely captured genera (*Melecta* and *Sphecodes*) were found only in sites disturbed by fire.

Effects of disturbance type on foraging and nesting habitats. Components of foraging (floral resources) and nesting habitat (coarse woody debris) were responsive to differences in disturbance type.

Mean floral abundance differed significantly due to the effect of disturbance type ($F_{3, 90}$=2.852, P=0.041) and was greatest in high-severity fire sites, intermediate in low-severity fire sites, and lowest in thinned and non-treated sites (Figure 5a). Mean floral abundances did not vary across sample periods ($F_{2, 90}$=0.896, P=0.411), but there was a marginal effect of the disturbance type × sample period interaction on floral abundances ($F_{6, 90}$=1.939, P=0.082). Mean floral species richness in quadrats also varied in response to disturbance type and was highest in high-severity fire sites, intermediate in low-severity fire sites, and did not differ between thinned and non-treated sites ($F_{3, 90}$=5.778, P=0.001; Figure 5b). There was also a significant effect of seasonality on floral species richness, and floral richness was greatest during August ($F_{2, 90}$=4.461, P=0.014; Figure 5c); however, the disturbance type × collection period interaction did not impact floral species richness ($F_{6, 90}$=1.146, P=0.197). Coarse woody debris loadings (MG/ha) also varied due to the main effect of disturbance type ($F_{3, 90}$=13.613, P<0.0001), and coarse woody debris loadings in high-severity fire sites were on average 50, 82, and 89% higher than in low-severity fire, thinned, and non-treated control sites, respectively (Figure 5d).

Regression analysis revealed that the abundance and species richness of bee assemblages were generally positively correlated with the abundance of foraging and nesting resources, although overall effect sizes were relatively small. Bee abundance at study sites were significantly positively associated with mean floral abundances ($F_{1, 100}$=5.079, P=0.026; Figure 6a), but not floral species richness ($F_{1, 100}$=0.550, P=0.459) or coarse woody debris ($F_{1, 100}$=0.381, P=0.538). Bee species richness at study sites was also positively correlated with mean floral abundances ($F_{1, 100}$=3.912, P=0.050; Figure 6b) as well as coarse woody debris ($F_{1, 100}$=4.601, P=0.034, Figure 6c), but not floral species richness ($F_{1, 100}$=2.036, P=0.156). The proportion of invasive forbs (expressed as a percent of all forbs at a given study site) was not

associated with captured bee abundances ($F_{1, 100}$=0.097, P=0.755) or species richness ($F_{1, 100}$=2.708, P=0.103).

Effects of disturbance type on bee community structure. There was a significant shift in bee community composition over the course of the growing season (χ^2=214.784, df=40, n=676, P<0.001). Although *Bombus* was a dominant component of the bee community throughout the sample period, assemblages were generally more even in July and August. Generic richness was overall greatest in July, but early-season *Agapostemon* and *Halictus* were present but by late-season these genera were no longer found and instead several genera including *Megachile* and *Diadasia* became more frequent (Figure 7). Similarly, bee community composition varied across disturbance types (χ^2=92.917, df=60, n=676, P=0.004), indicating a preference of some genera for specific habitats; however, generic richness was comparable across all disturbance types.

Discussion

This study provides a first systematic inventory of the bee fauna in disturbed and non-disturbed ponderosa pine forest stands of the Colorado Front Range region and demonstrates that ponderosa pine forests are habitat for a variety of bee species (Table 1). By comparison with other recent studies of bee biodiversity in Colorado habitats, bee community assemblages in ponderosa pine forests (57 unique species detected) are intermediate in their richness and suggest that elevation and temperature are key drivers of bee γ-diversity. For instance, in a survey of bee assemblages in high elevation (>2800 m) spruce-fir forests near Woodland Park (CO) Rhoades et al. (2018) found approximately 39 unique species; in contrast, Kearns and Oliveras (2009) detected >100 bee species in grassland habitats near Boulder (CO).

There was not strong evidence for direct effects of disturbance type or seasonality on pooled bee abundances or species richness (Figure 3), although ~35% of bee genera fluctuated seasonally. Bumblebees (*Bombus* spp.) were by far the most abundant pollinator resource and were found at virtually all sites and in relatively continuous abundances across the season, comprising 59% of the total collection. The single most abundant species was *Bombus appositus* Cresson (white-shouldered bumblebee), which comprised 17% of the total collection and is a generalist pollinator that feeds on and transfers pollen for a variety of plants including thistles, gentians, clovers, locoweeds, penstemons, buttercups, asters, and others (Wright 1988, Whittington et al. 2004). Interestingly, *B. appositus* was most concentrated in thinned stands (40% of captures were in thinned stands), indicating that forest density reduction efforts may provide habitat for this abundant generalist species. However, our surveys also detected two sensitive bumblebee species including *B. fraternus* Smith (southern plains bumblebee) and *B. fervidus* F. (golden northern bumblebee) which were only found in high density non-thinned stands and high-severity fire stands, respectively. These findings indicate that ponderosa pine forests in the Front Range are habitat for both abundant and rare bee species, and that pollination services are likely to be consistent in the region across most of the growing season due in part to the high abundance of bumblebees.

Although pooled bee abundances and species richness did not vary with disturbance types or collection period, there was evidence that community composition was responsive to both factors, and there were specific community assemblages associated with different collection periods and different disturbances (Figure 7, 8). Generic richness was elevated in July and August as compared to June, with a notable increase in the genus *Anthophora* spp. (solitary digger bees) by mid-season, and a notable absence of *Halictus* spp. (eusocial sweat bees) after

June. In addition, some genera were only found in disturbed sites: *Agapostemon* spp., *Anthidium* spp., and *Augochlorella* spp. were found only in thinned stands or those that experienced low-severity wildfire, whereas *Coelioxys* spp. and *Eucera* spp. were found only in non-treated stands. In contrast, *Melecta* and *Sphecodes* were found only in stands that experienced high-severity fire. Other taxonomic groups were habitat generalists and were found in all habitats including *Anthophora* spp., *Bombus* spp., *Diadiasia* spp., *Halictus* spp., *Hoplitis* spp., *Lasioglossum* spp., *Lithurgopsis* spp., *Megachile* spp., and *Osmia* spp. (Figure 8). Thus, a mix of habitat specialists and habitat generalists are found in the region, with specific assemblages associated with thinned, burned, and high-density non-treated stands. This corresponds to the findings described in Stevens-Rumann and Fornwalt (2018), who demonstrated that distinct plant assemblages were associated with different disturbances across the same sampling network. Our results also match those of Galbraith et al. (2019), who found that high-severity fire was associated with enhanced bee species richness in mixed-conifer forests. Accordingly, maintaining a landscape that is comprised of a mosaic of these respective disturbance types is probably important for maximizing bee biodiversity. In addition, for ecosystem management project implemented during summer months, concentrating activities in June (as opposed to July or August) may directly impact fewer bee species—this was the period during which per-capita impact on floral resources would likely be limited (i.e., floral abundances were intermediate) and the lowest level of bee richness was observed.

This work also highlights the importance of indirect effects of both natural and anthropogenic disturbances on foraging and nesting resources that are important for native bees: both floral abundances and coarse woody debris (surface fuel loadings) were strongly affected by disturbance types (Figure 5). Floral abundances and coarse woody debris were positively

associated with abundance and species richness of bee community assemblages, indicating that
(a) higher availability of floral resources is likely to increase site occupancy by bees, and (b)
higher availability of coarse woody debris is likely to increase bee species richness (Figure 6).
These relationships provide targets for managers concerned with conserving bee biodiversity and
suggest that a cascade of effects is likely to result from removal or reduction of forest canopy,
with generally positive effects on bee populations. Creating canopy gaps that provide additional
growing space or competitive release for understory forbs will provide additional foraging
resources for native bees (Walters and Stiles 1996, Rankin and Tramer 2002), but our data also
suggest that it may be desirable to leave some amount of coarse woody debris on-site following
fuels or density-reduction treatments to provide bee nesting habitats (Rodriguez and Kouki
2015). The specific effects of coarse woody debris on bee species richness could be examined
experimentally in future work to determine threshold values for target levels of bee diversity.

Several limitations of the present study should be considered when interpreting the results
discussed here. First, this study only considers a single collection year. An additional year of bee
collection in summer 2020 will strengthen our conclusions and allow for estimates of year-to-
year variability in bee population abundances and the climate signals associated with that
variability. Given the infrequency of our collections, an additional year of sampling is not
expected to have detectable effect on regional bee populations (Gezon et al. 2015). Second, there
were unmeasured aspects of variability at study sites that could strengthen our understanding of
factors regulating bee population distributions. In particular, physical conditions such as mean
site temperature, average windspeeds, and rate of degree day accumulations are likely to have
substantial impacts on both plant phenology as well as insect behavior (Fucini et al. 2014).
Lastly, our study design does not incorporate landscape structural elements such as habitat

connectivity, cover richness, or urbanization—all of which are known to drive the distribution of sensitive insect populations at landscape scales (Williams and Kremen 2007, Holzschuh et al. 2010). It is our intention to characterize these sources of variability in a second year of study and use generalized linear mixed modelling approaches to evaluate and compare overall effect sizes due to microsite, local, and regional factors.

The study of forest bee ecology is still in a nascent state, especially in temperate coniferous forests of western North America. Basic studies in biodiversity (such as the present investigation) are needed and can inform natural resource management by generating several useful tools including: (1) inventories of both sensitive and rare species, (2) estimates of the effects of implementation actions on bee community assemblages, and (3) simple models that relative specific and tangible resource targets to bee communities (e.g., coarse woody debris loadings). Here, we conclude that forest thinning operations are not associated with a loss of bee abundance or species richness, and that thinning may provide habitat for at least one abundant and generalist pollinator (*B. appositus*). Although basic site structural elements including floral abundances and large surface fuels were better predictors of site occupancy by native bees than disturbance type or collection period, bee community structure differed between disturbance types and each type was associated with a distinct assemblage of bee genera. Consequently, natural resource managers can target manipulation of both floral resources and woody debris for direct control of site-level bee assemblages but should also seek to actively maintain a range of natural disturbance processes including both low- and high-intensity fire to conserve landscape-scale bee biodiversity. Additional studies aimed at elucidating the mechanisms underlying bee responses to forest disturbances, including both thinning and burning, will help to develop a causal understanding of the cascades that promote or suppress key ecosystem services.

Acknowledgements

References

Brown JK. 1974. Handbook for inventorying downed woody material. General Technical Report INT-16. Ogden, UT. USDA-USFS, Intermountain Forest and Range Experiment Station. 24 p.

Carvalheiro LG, Seymour CL, Nicolson SW, Veldtman R. 2010. Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. Journal of Applied Ecology 49:1373-1383.

Cohen J. 2000. Preventing disaster: home ignitability in the wildland-urban interface. Journal of Forestry 98:15-20.

Eltz T, Bruhl CA, van der Kaars S, Linsenmair EK. 2002. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia 131:27-34.

Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, et al. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Fucini S, Uboni A, Lorenzi MC. 2014. Geographic variability in air temperature leads to intraspecific variability in the behavior and productivity of a eusocial insect. Journal of Insect Behavior 27:403-410.

Galbraith SM, Cane JH, Moldenke AR, Rivers JW. 2019. Wild bee diversity increases with local fire severity in a fire-prone landscape. Ecosphere 10: e02668.

Gezon ZJ, Wyman ES, Ascher JS, Inouye DW, Irwin RE. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. Methods in Ecology and Evolution 6:1044-1054.

Hanula JL, Ulyshen MD, Horn S. 2016. Conserving pollinators in North American forests: a review. Natural Areas Journal 36:427-439.

Holzschuh A, Steffan-Dewenter I, Tscharntke T. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? Journal of Animal Ecology 79:491-500.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). 2016. Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Potts SG, Imperatriz-Fonseca VL, Ngo HT, Biesmeijer JS, Breeze TS, Dicks LV, et al. (Eds.). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 36 pages.

Jha S, Vandermeer JH. 2010. Impacts of coffee agroforestry management on tropical bee communities. Biological Conservation 143:1423-1431.

Kearns CA, Oliveras DM. 2009. Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. Journal of Insect Conservation 13:655-665.

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters 10:299-314.

Liu Z, Wimberly MC, Lamsal A, Sohl T, Hawbaker TJ. 2015. Climate change and wildfire risk in an expanding wildland–urban interface: a case study from the Colorado Front Range Corridor. Landscape Ecology 30:1943-1957.

Loveless MD, Hamrick JL. 1984. Ecological determinants of genetic structure in plant populations. Annual Review of Ecology and Systematics 15:65-95.

Manfredo MJ, Zinn HC. 1996. Population change and its implications for wildlife management in the New West: A case study of Colorado. Human Dimensions of Wilflide 1:62-74.

Peet RK. 1978. Forest vegetation of the Colorado Front Range: Patterns of species diversity. Vegetatio 37:65-78.

Potts SG, Petanidou T, Roberts S, O'Toole C, Hulbert A, Willmer P. 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biological Conservation 129:519-529.

Rankin WT, Tramer EJ. 2002. Understory succession and the gap regeneration cycle in a *Tsuga canadensis* forest. Canadian Journal of Forest Research 32:16-23.

Rhoades PR, Davis TS, Tinkham WT, Hoffman CM. 2018. Effects of seasonality, forest structure, and understory plant richness on bee community assemblages in a southern Rocky Mountain mixed conifer forest. Annals of the Entomological Society of America 111:278-284.

Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, et al. 2008. Landscape effects on crop pollination services: are there general patterns? Ecology Letters 11:499-515.

Rodriguez A, Kouki J. 2015. Emulating natural disturbance in forest management enhances pollination services for dominant Vaccinium shrubs in boreal pine-dominated forests. Forest Ecology and Management 350:1-12.

Stevens-Rumann CS, Fornwalt P. 2018. Forest vulnerability to disturbances. Final Report to Boulder County Open Space, Small Grants Program. 17 p.

Walters BB, Stiles EW. 1996. Effect of canopy gaps and flower patch size on pollinator visitation of *Impatiens capensis*. Journal of the Torrey Botanical Club 123:184-188.

Walther-Hellwig K, Frankl R. 2003. Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. Journal of Applied Entomology 124:299-306.

Whittington R, Winston ML, Tucker C, Parachnowitsch AL. 2004. Plant-species identity of pollen collected by bumblebees placed in greenhouses for tomato pollination. Canadian Journal of Plant Science 84:599-602.

Williams NM, Kremen C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecological Applications 17:910-921.

Williams NM, Regetz J, Kremen C. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93:1049-1058.

Winfree R, Aguilar R, Vasquez DP, Lebuhn G, Alzen MA. 2009. A meta-analysis of bees' response to anthropogenic disturbance. Ecology 90:2068-2076.

Wright DH. 1988. Temporal changes in nectar availability and *Bombus appositus* (Hymenoptera: Apidae) foraging profits. The Southwestern Naturalist 33:219-227.

Table 1. A summary of all bee specimens captured in this study (γ-diversity), arranged by

taxonomic designation.

Family	Genus	species	abundance
Adrenidae	Unknown	sp*	1
Apidae	*Anthophora*	*bomboides*	5
		montana	2
		occidentalis	3
		porterae	8
		sp	4
		terminalis	2
		walshii	1
	Apis	*mellifera*	7
	Bombus	*appositus*	120
		bifarius	32
		californicus	1
		centralis	57
		fervidus	10
		flavifrons	12
		fraternus	1
		griseocollis	3
		huntii	10
		insularis	2
		melanopygus	18
		nevadensis	56
		occidentalis	3
		rufocinctus	71
		sylvicola	2
	Diadasia	sp	16
	Eucera	*edwardsii*	2
	Melecta	*pacifica fulvida*	4
	Melissodes	*agilis*	3
		communis	2
		rivalis	1
		sp	4
	Svastra	*obliqua*	1
	Unknown	sp	6
	Xeromelecta	*californica*	1
Halictidae	*Agapostemon*	sp	1
		texanus	1
	Augochlorella	*aurata*	1

	Halictus	sp	16
		tripartisus	1
	Lasioglossum	sp	1
		sp	17
	Sphecodes	sp	1
	Unknown	sp	3
Megachilidae	*Anthidium*	sp	2
	Coelioxys	sp	1
	Hoplitis	*albifrons*	2
		sp	11
	Lithurgopsis	*apicalis*	17
	Megachile	*fortis*	2
		gemula	1
		inupta	1
		sp	21
	Osmia	*bucephela*	6
		integra	1
		nigrifrons	2
		sp	54
	Unknown	sp	10
Unknown	Unknown	sp	32
	Total		676

* 'Sp' refers to a specimen that was unidentifiable to the species level but was designated as a

distinct morphotype

25

Table 2. Seasonal variation in abundances of bee genera. Genera which varied significantly due to the main effect of 'sample period' are highlighted in bold text.

Genus	Month			Phenology
	June	July	August	
Agapostemon	1	1	0	Rare
Anthidium	0	1	1	Rare
Anthophora	**2**	**19**	**4**	**Mid-season**
Apis	0	3	4	Rare
Augochlorella	1	0	0	Rare
Bombus	158	92	148	Continuous
Coelioxys	0	1	0	Rare
Diadasia	**0**	**3**	**13**	**Late-season**
Eucera	2	0	0	Rare
Halictus	**12**	**5**	**0**	**Early-season**
Hoplitis	**1**	**10**	**2**	**Mid-season**
Lasioglossum	**17**	**1**	**0**	**Early-season**
Lithurgopsis	0	5	12	Mid/late-season
Megachile	**0**	**3**	**22**	**Late-season**
Melecta	1	3	0	Rare
Melissodes	0	4	6	Mid/late-season
Osmia	**30**	**17**	**16**	**Early-season**
Sphecodes	0	1	0	Rare
Svastra	0	0	1	Rare
Xeromelecta	0	1	0	Rare

Figure 1. Map showing location of sampling sites within the study area (cross-hatching),

reproduced from Stevens-Rumann and Fornwalt (2018). Red= high-severity fire sites; orange=

low-severity fire sites; green= non-treated control sites; blue=thinned sites.
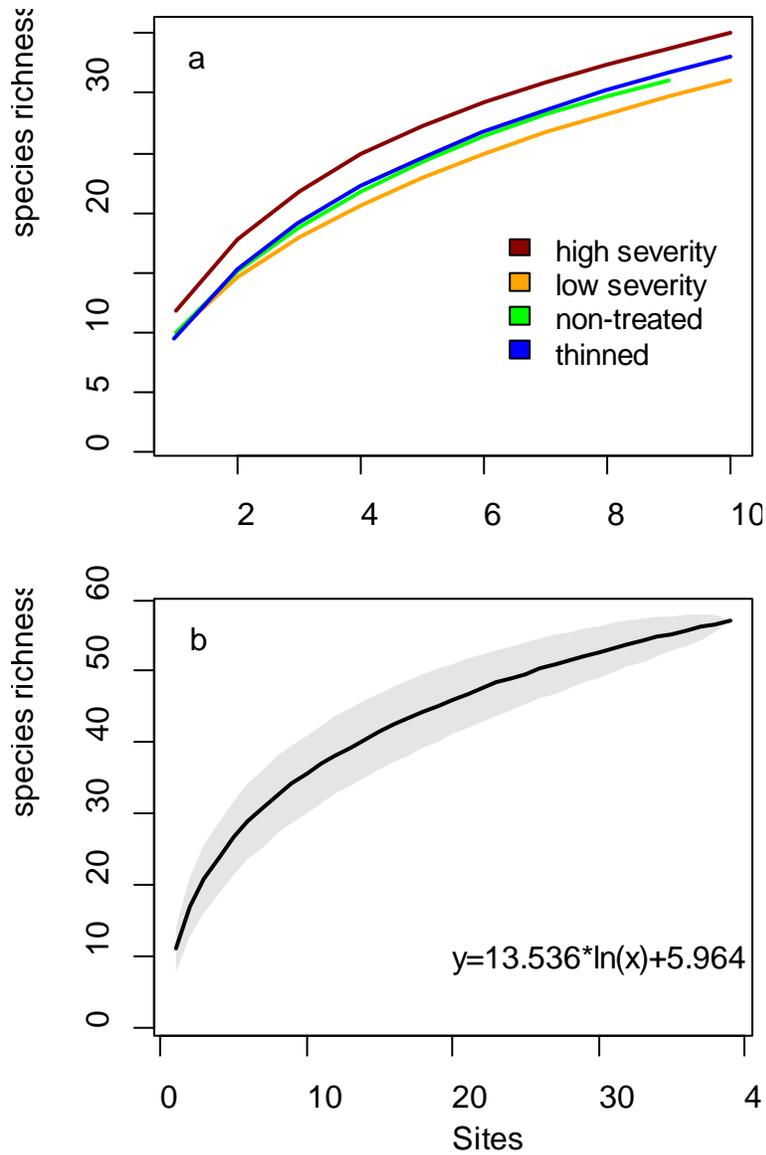
Figure 2. Rarefaction analysis comparing accumulation of species richness as a function of the number of sites sampled (a) across multiple disturbance types and (b) across the entire collection. The function in (b) provides an empirical solution for expected species richness (y term) as a function of the number of sites sampled (x term).
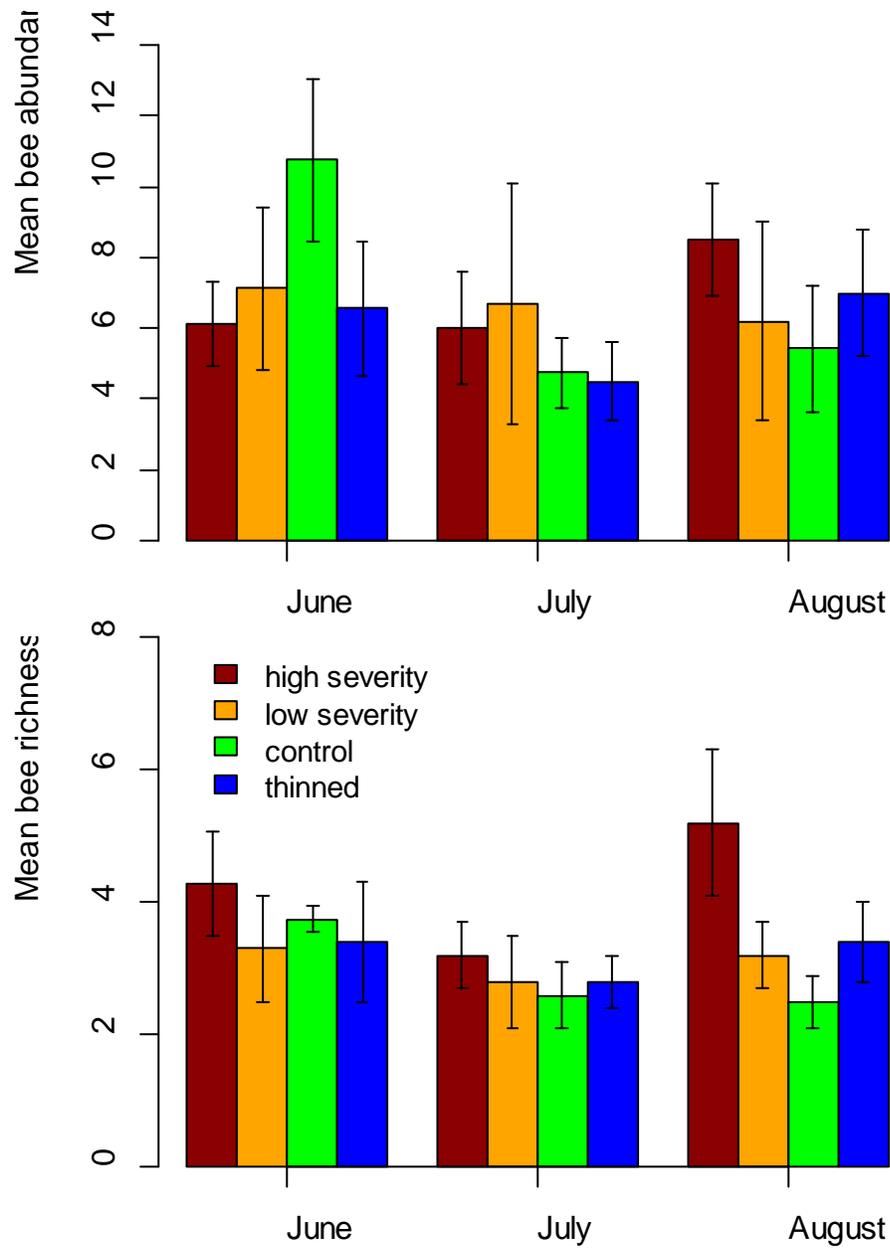
Figure 3. The effects of a disturbance type × collection period interaction on mean native bee abundance and species richness. Bars show plus or minus one standard error.
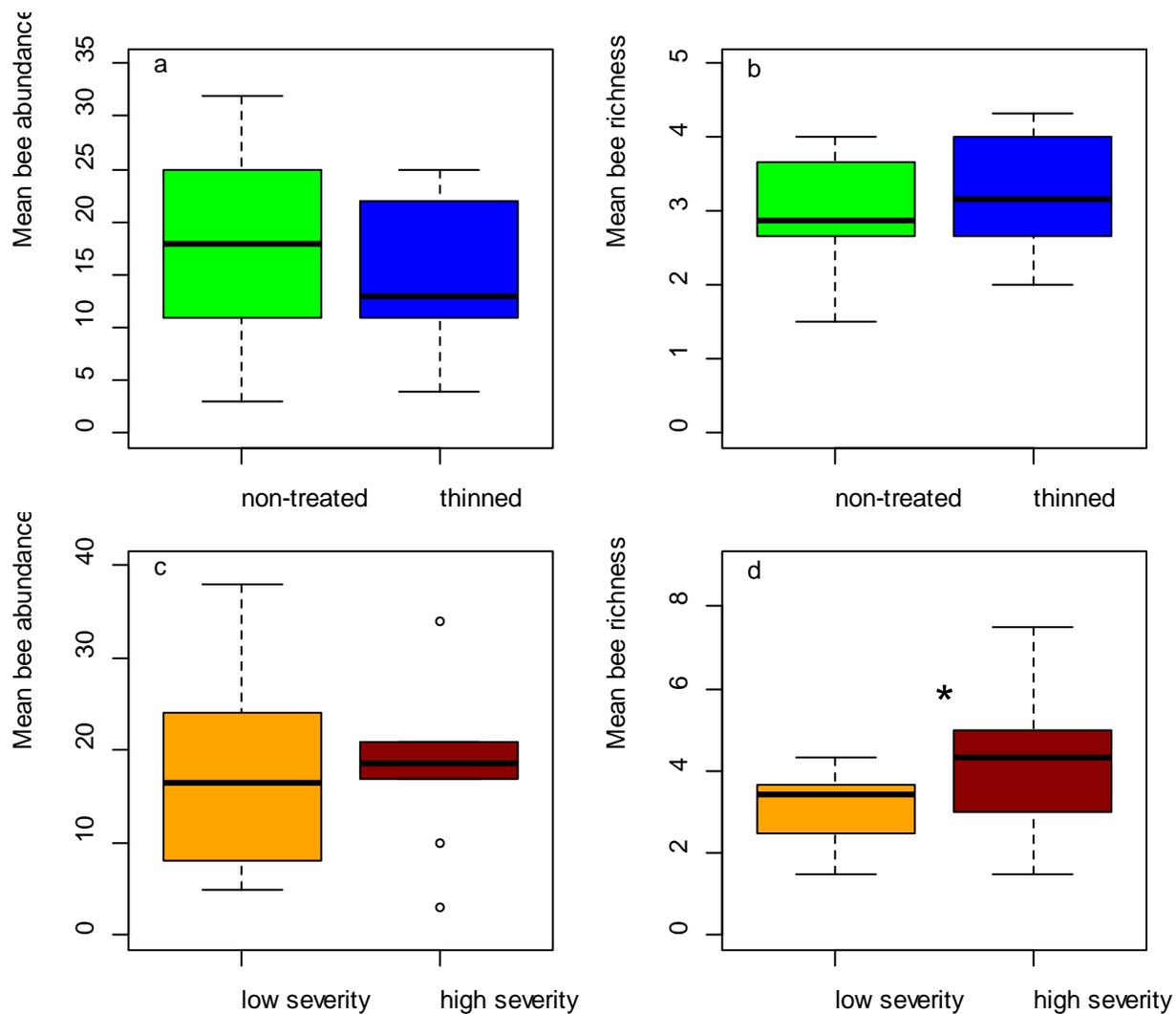
Figure 4. The distribution of bee abundance and species richness compared between (a, b) non-treated and thinned stands, and (c, d) stands exposed to high- and low-severity wildfire. Asterisk denotes a significant difference ($\alpha=0.05$) between sample means.
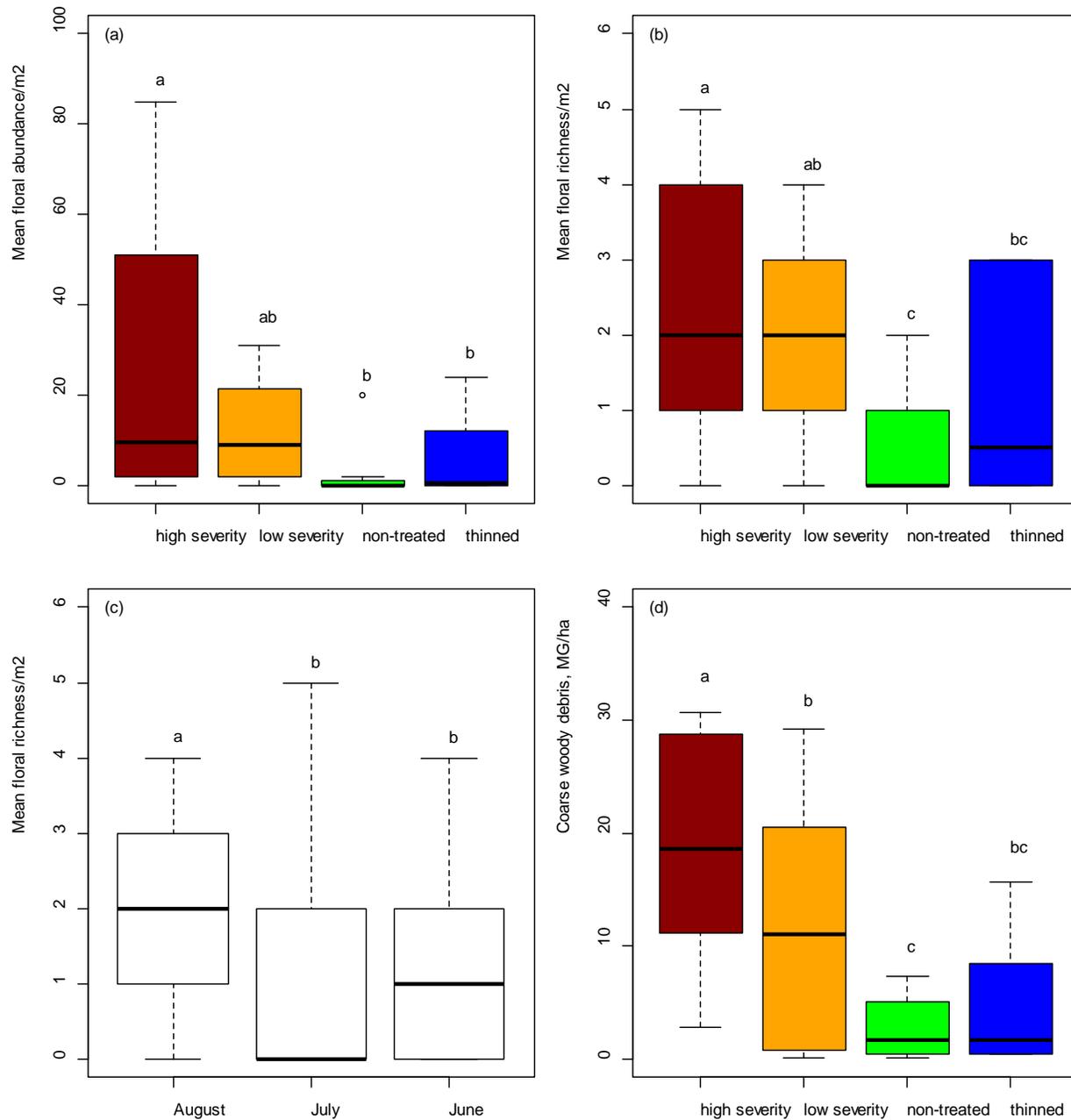
Figure 5. The distribution of (a) mean floral abundance and (b) mean floral richness in response to disturbance type, as well as (c) response of mean floral richness to sampling period (date). (d) the distribution of coarse woody debris surface loadings in response to disturbance type. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

31
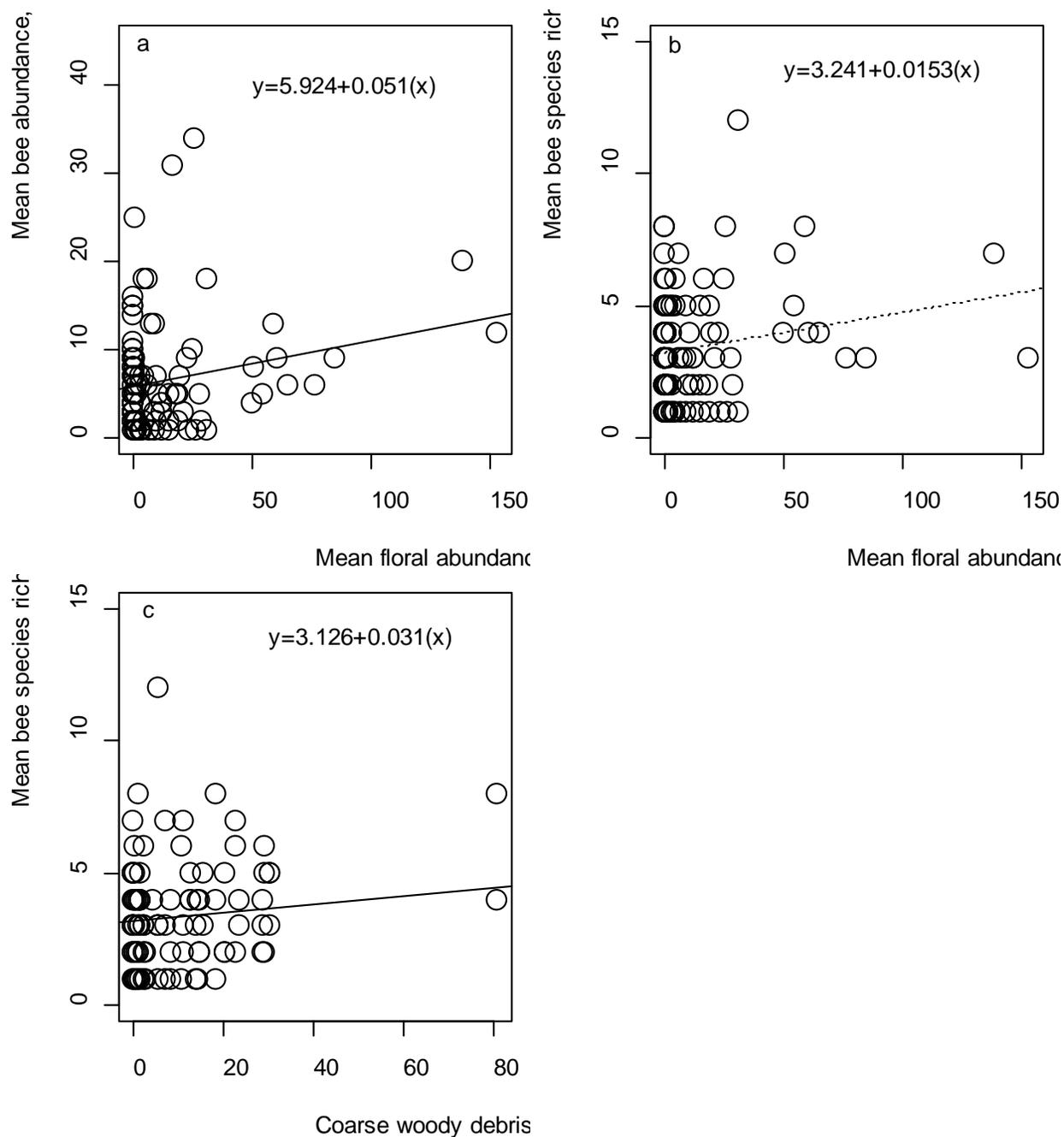
Figure 6. Linear regression analyses showing the relationship between (a) bee abundance and floral abundance, (b) bee species richness and floral abundance, and (c) bee species richness and coarse woody debris loadings. Solid lines indicate regressions significant at the α=0.05 level and the dashed line indicates significance at the α=0.10 level.
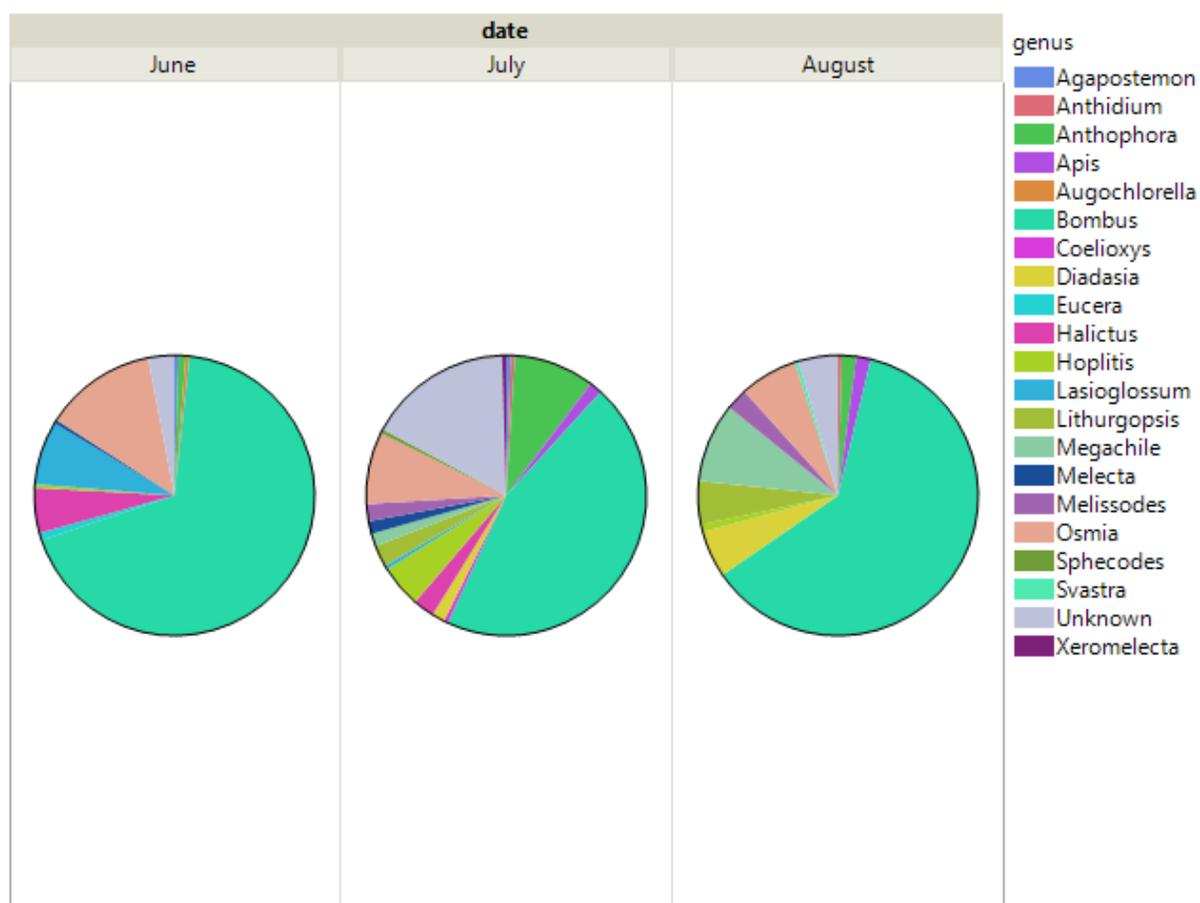
**Figure 7.** Community composition of bee genera relative to sample period.
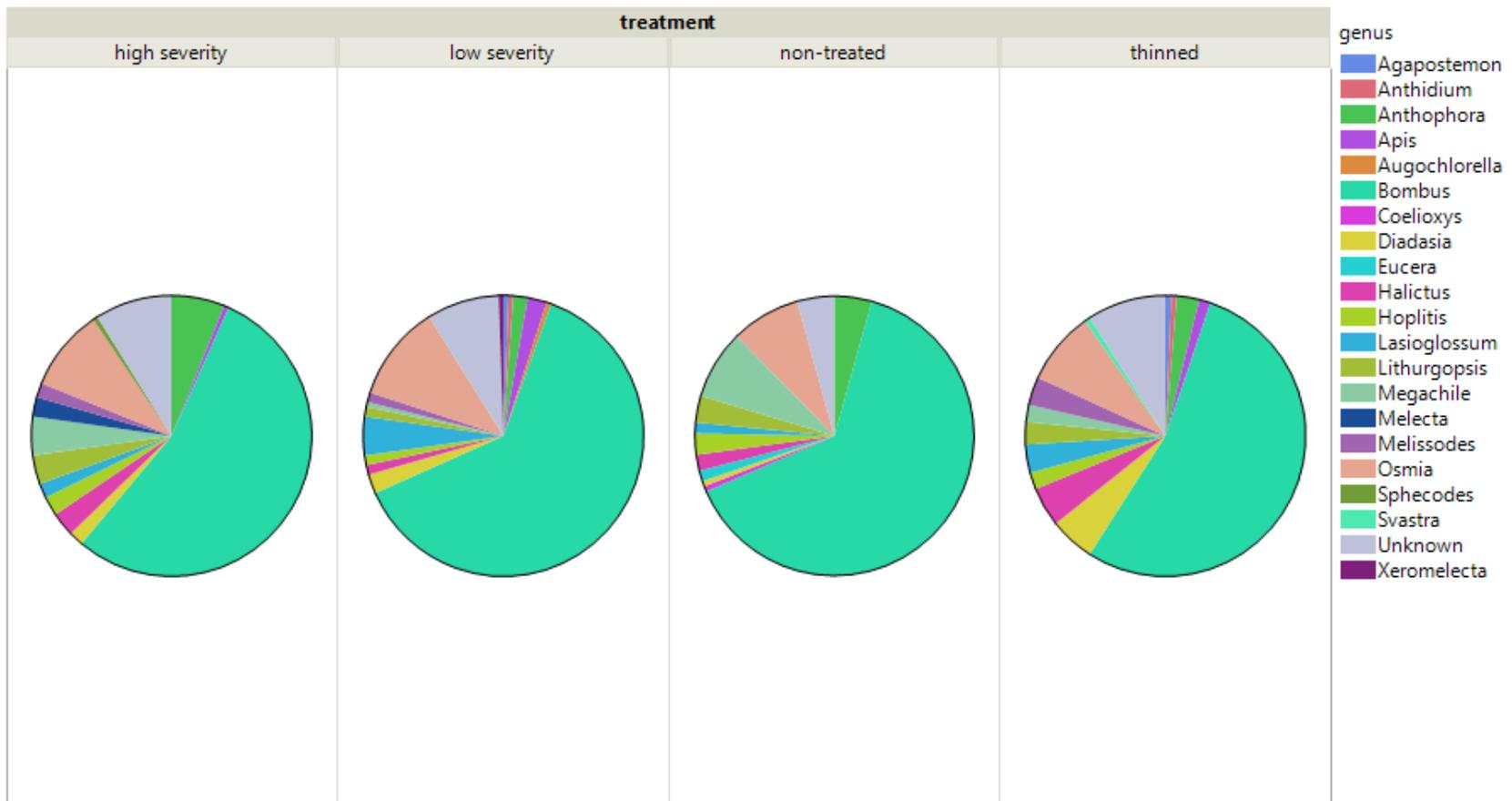
Figure 8. Community composition of bee genera relative to disturbance type.