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Research

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Changes in the Summer Wild Bee Community Following a Bark Beetle Outbreak in a Douglas-fir Forest

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Abstract

The status of wild bees has received increased interest following recent estimates of large-scale declines in their abundances across the United States. However, basic information is limited regarding the factors affecting wild bee communities in temperate coniferous forest ecosystems. To assess the early responses of bees to bark beetle disturbance, we sampled the bee community of a Douglas-fir, *Pseudotsuga menziesii* (Mirb.), forest in western Idaho, United States during a Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Curculionidae), outbreak beginning in summer 2016. We resampled the area in summer 2018 following reductions in forest canopy cover resulting from mortality of dominant and codominant Douglas-fir. Overall, results from rarefaction analyses indicated significant increases in bee diversity (Shannon's *H*) in 2018 compared to 2016. Results from ANOVA also showed significant increases in bee abundance and diversity in 2018 compared to 2016. Poisson regression analyses revealed percent tree mortality from Douglas-fir beetle was positively correlated with increases in total bee abundance and species richness, where community response variables displayed a cubic trend with percent tree mortality. Percent reduction in canopy cover from 2016 to 2018 was also correlated with bee species richness and diversity. These findings suggest that wild bee communities may benefit from changes in forest structure following bark beetle outbreaks.

Key words: bee conservation, forest ecology, pollinators, Scolytinae

Forests cover over one-third of land area in North America (The World Bank 2016) and provide forage and habitat resources for many wild and native pollinators, including bees (Hymenoptera: Apiformes) (Hanula et al. 2016) which are considered the predominant group of insect pollinators in many ecosystems (Potts et al. 2010; Winfree 2010). The status of wild bees has received increased interest following recent estimates of large-scale declines in their abundances across the United States (Winfree et al. 2009; Koh et al. 2016). However, basic information is limited regarding the factors affecting wild bee communities in temperate coniferous forest ecosystems (Rivers et al. 2018), where the community compositions have rarely been described (Reese et al. 2018, Rhoades et al. 2018). Insect pollinators are generally more abundant in habitats with relatively greater amounts of floral resources, and bees are the only pollinator group that feeds exclusively on nectar and pollen throughout their entire life cycle (Michener 2007, Brown and Paxton 2009, Winfree 2010, Rivers et al. 2018). In temperate forest ecosystems, areas with canopy openings and lower tree densities which allow for adequate temperatures and sunlight to promote growth of flowering plants are therefore associated with relatively greater abundances of bees (Winfree et al. 2007, Taki et al. 2013, Roberts et al. 2017, Rivers et al. 2018). Furthermore, temperature and light availability, which may increase in forest stands following reductions in tree cover, are positively correlated with foraging frequency and duration of certain bee species (Fye 1972, Polatto et al. 2014).

Alterations to forest structure resulting from management practices or natural disturbance events can create forest stand conditions favorable toward the habitat and floral resource requirements that support wild bee populations (Hanula et al. 2016). For instance, recent studies have detected relatively greater abundances and species richness of wild bees where silvicultural thinning and gap creation that reduced stand densities and canopy cover have occurred (Romey et al. 2007, Taki et al. 2010, Proctor et al. 2012, Hanula et al. 2015). Similarly, wildfire is thought to create more favorable habitat for bees due to suppression of the shrub layer and increases in herbaceous plant growth in burned areas (Potts et al. 2003, Waltz and Cuvington 2004, Grundel et al. 2010, Taylor and Catling 2011), and increased bee species richness and abundance have been observed following high-severity wildfire in temperate coniferous forest (Galbraith et al. 2019). However, studies investigating interactions between biotic forms of natural disturbances, such as bark beetle outbreaks, and wild bee communities in temperate coniferous forests are sparse in general (e.g., Muller et al. 2008) and have yet to be reported in North America.

Native bark beetles (Coleoptera: Curculionidae, Scolytinae), which evolved within the temperate forest ecosystems of western North America, act as key agents of biotic disturbance (Bentz et al. 2010, Fettig et al. 2019). Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is attributed to the most insect-related mortality of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in North America (Furniss and Carolin 1977). Populations typically occur at low densities due to limited availability of optimal host material (recently dead or stressed Douglas-firs), but often increase following other forest disturbance events (e.g., wildfires, windstorms, or defoliation events) that create large amounts of susceptible host trees (Furniss and Carolin 1977). Under these conditions, Douglas-fir beetle populations may reach high enough densities to successfully colonize and kill large numbers of healthy trees across a landscape for several years. The gradual creation of forest canopy gaps and overall reduction in canopy cover due to mortality of large trees resulting from Douglas-fir beetle outbreaks may create favorable habitat and microclimates for herbaceous plants and their associated pollinators (Anderson et al. 1969, Franklin et al. 2002, Roberts 2004, Swanson et al. 2011). The present study tested the hypothesis that Douglas-fir beetle-caused tree mortality and the subsequent changes in forest structure effected changes in the associated wild bee community in areas with significant levels of beetle activity. To test this, we sampled the bee community of a Douglas-fir forest in western Idaho, United States during a Douglas-fir beetle outbreak beginning in summer 2016. The area was sampled again during summer 2018 to determine changes in bee diversity and community composition and evaluate relationships between bee diversity and the structural attributes of their forest habitat.

Materials and Methods

Study Site and Plot Description

The study was conducted along the ridge of Boise Mountain, Boise National Forest, Idaho (43.708°N, 116.092°W; 1,700–1,900 m elevation) where Douglas-fir is the dominant tree species interspersed with ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. The suppression of wildfires since the mid-twentieth century has caused plant communities to change from predominantly open forests with grass understories to higher shrub and tree densities in certain areas (Steele and Geier-Hayes 1989). In stands with relatively closed canopies (canopy cover ≥70%), the understory is dominated by mallow ninebark, *Physocarpus malvaceus* Greene, saskatoon, *Almelanchier alnifolia* Nutt, and bittercherry, *Prunus emarginata* (Dougl. ex Hook) Eaton. In stands with reduced canopies, common flowering plants include horsemint, *Agastache urticifolia*, Oregon grape, *Berberis* spp., mountain snowberry, *Symphiocarpmus oreophilus*, bitterbrush, *Purshia* spp., and *Spirea* spp. (Steele and Geier-Hayes 1989).

We selected plot locations based on aerial and ground surveys from 2015 that indicated Douglas-fir beetle was causing noticeable tree mortality within surrounding stands (i.e., >10 trees or >4.6 m^2 of basal area killed by Douglas-fir beetle per ha within the last 2 yr). All trees on the plots were confirmed free of active Douglas-fir beetle infestation prior to plot establishment. We manipulated the distribution of Douglas-fir beetle and subsequent rates of Douglas-fir beetle-induced tree mortality on eighteen 0.4-ha square plots using commercial formulations of the Douglas-fir beetle anti-aggregation pheromone 3-methylcyclohex-2-en-1-one (MCH) to evaluate a novel formulation (Foote et al. 2020). Treatments included 1) MCH bubble capsules (Synergy Shield MCH, Product #3311, Synergy Semiochemicals Corp., Burnaby, BC, Canada) applied at 30 per plot containing ~500 mg of MCH (released at ~5 mg/d @ 20°C), spaced on approximately a 12 m × 12 m grid; 2) SPLAT MCH (ISCA Technologies Inc., Riverside, CA) applied at 15 g (10.0% MCH by weight) per plot using 15 dollops (release rate 63 mg/d @ 26°C) spaced on a 13 m by 21 m grid; and 3) untreated plots where no MCH was applied to trees. Six plots were randomly assigned to each treatment group. The bubble capsule treatment was based on the established operational recommendations (Ross et al. 2015) and the SPLAT MCH treatment was based on manufacturer recommendations. MCH release devices were attached to the north side of the tree bole at approximately 1.4 m height. One 16-unit multiple-funnel trap (Lindgren 1983) baited with the Douglas-Fir Beetle Lure (Product #3187, Synergy Semiochemicals Corp.) was placed near plot center to provide Douglas-fir beetle attraction to all plots. Lures included frontalin (released at ~2.5 mg/d @ 20°C), seudenol (released at 1.5 mg/d @ 20°C), reconstituted Douglas-fir turpentine (released at ~150 mg/d @ 20°C), and ethanol (released at ~10 mg/d @ 20°C).

Bee Sampling

We sampled for bees in July 2016 (year of beetle colonization and prior to needle fall) and again in 2018 (post needle fall following Douglas-fir beetle-induced tree death) using pan traps and following methods from previous studies that sampled bee populations in forest habitats (e.g., Campbell and Hanula 2007, Westphal et al. 2008, Hanula et al. 2015). Pan traps used were 96-ml polystyrene bowls painted yellow and filled to ~75% capacity with deionized water with <1 ml dissolved liquid dish detergent to reduce surface tension. In each plot, traps were placed at approximately 10.5 m and 21 m radiating from plot center in each cardinal direction (eight traps per plot) and were stabilized using 0.1 × 5.5 cm wooden dowels. Pan traps were operational on calm, sunny days for 48-h intervals in 2016 (14–16 and 27–29 July) and 2018 (11–16 July 2018). The 2018 collection periods were chosen to match the roughly 450–550 accumulated degree-days (baseline 10°C) of the July 2016 sampling period (when peak floral bloom was observed). The same plots and trap locations were used in both years.

All bee specimens captured were stored in 70% ethanol until processed, pinned, and identified. Bees were identified to species or morphospecies using appropriate keys (Hurd and Michener 1955; Mitchell 1962, 1980; LaBerge 1989; Michener 2000; Gibbs 2010; Williams et al. 2014) and other pictorial guides (discoverlife.org). Voucher specimen identifications were verified by Lincoln Best (Oregon Bee Atlas Project, Oregon State University). Reference specimens were deposited in the Oregon State University Arthropod Collection, Corvallis, OR (Foote 2019; Accession: OSAC_AC_2018_12_27-01-001).

Overstory Sampling

We used variable radius plots to sample stand basal area, the amount of a cross-sectional area occupied by tree boles at breast height (1.36

m), for all trees >20 cm diameter at breast height (DBH), located at plot center and approximately 25 m from plot center in each cardinal direction in June 2016. We recorded the DBH of each individual tree measured in these variable radius plots also. We determined percent canopy cover (the proportion of sky hemisphere obscured by vegetation when viewed from a single point) from the mean of nine spherical densitometer readings (one measurement at each bee sampling location and plot center) for each plot using methods described by Lemmon (1956). We measured canopy cover in July 2017 (prior to needle fall following Douglas-fir beetle-induced tree death) and again in July 2018 (post needle fall following Douglas-fir beetle-induced tree death). In July 2018, we determined percent tree mortality per plot by visually inspecting each tree for presence (dead) or absence (alive) of crown fade.

Floral and Nesting Resource Sampling

We sampled understory vegetation along four 21-m transects in each cardinal direction from plot center using the line-point intercept method (Godínez-Alvarez et al. 2009). Sampling points were established at 3-m intervals for seven points along each transect (28 points per plot). At each point, we identified all flowering plants intersecting the vertical plane over the transect line using Hitchcock and Cronquist (2018). We also quantified potential aboveground bee nesting resources using methods adapted from Grundel et al. (2010) along the same transects. We quantified the total amount of dead wood >2.5 cm in diameter using the line-point intercept method, and tallied all standing dead trees (snags) ≥20 cm for each plot. An individual piece of dead wood or snag was considered one aboveground nesting unit. We determined percent organic content via ignition loss from a composite of nine soil cores per plot (one at each bee trapping location and plot center), using a handheld soil sampler (30 cm depth, 2.54 cm in diameter). We also measured forest floor (i.e., O-horizon) depth at each bee trapping location and plot center.

Statistical Analyses

Differences in mean numbers of bees, genera richness, and species diversity per plot between July 2016 and July 2018 were analyzed separately using ANOVA. We used the Shapiro/Wilk test and homogeneity of variance (HOV) test to determine whether bee diversity indices were normally distributed and exhibited equal variance (Hanula et al. 2015, Roberts et al. 2017). Data were not normally distributed. Therefore, we used the square root function ($\sqrt{[x + 0.01]}$) to transform the data prior to analyses. All statistical tests incorporated a type I error rate of $\alpha = 0.05$ for assessing significance and were performed using JMP 13 software (JMP, Version 13. SAS Institute Inc., Cary, NC, 1989–2019).

We constructed sample-based rarefaction curves using the iNEXT package (Colwell et al. 2012; Chao et al. 2014, Hsieh et al. 2016) for 2016 and 2018 trap collections after summing species captures per plot. We determined point estimates for species richness ($q = 0$), Shannon diversity ($q = 1$, the exponential of Shannon entropy), and Simpson diversity ($q = 2$, the inverse of Simpson concentration). We extrapolated all rarefaction curves, predicted diversity values, and associated 95% confidence intervals out to 1,000 sampling units for each collection year. Significant ($\alpha = 0.05$) differences in projected diversity values between collection years were determined based on lack of overlap between 95% confidence intervals (see Hanula et al. 2015).

We used a forward model selection approach to evaluate which forest habitat variables were valid for entry into explanatory models for variation in bee abundance, richness, and diversity across the study site. Variables considered for entry in the model included total basal area, canopy cover, shrub cover, herbaceous plant cover and richness, aboveground nesting resource abundance, O-horizon depth, and soil organic matter content. We performed Poisson regression analyses to determine any correlations between the observed changes in bee abundance, richness, and diversity versus percent tree mortality within plots, fitting each dependent variable separately. We then used forward model selection methods to find explanatory models that best accounted for the variation in changes in bee abundance, richness, and diversity within plots between years. Variables considered for entry in the model included percent tree mortality, change in canopy cover, basal area, canopy cover, shrub cover, herbaceous plant cover and richness, aboveground nesting resource abundance, O-horizon depth, and soil organic matter content. All statistical tests incorporated a type I error rate of $\alpha = 0.05$ for assessing significance and were performed using JMP 13 software.

Results

Forest Stand Characteristics

Plots had a mean basal area of 21.7 ± 2.5 m^2/ha, with a mean tree DBH of 46.1 ± 2.8 cm in 2016. On average, 52.4% of Douglas-fir trees were killed by Douglas-fir beetle, ranging from 15% to 91% across the study site. Mean percent canopy cover (82.8%) decreased on average by 22.0% in 2018 following needle fall, ranging from a 44.3% decrease to a 1.8% increase in overall cover. Mean percent shrub cover (45.6 ± 5.1%) and herbaceous ground cover (19.4 ± 2.8%) was predominantly (>90%) comprised of *P. malvaceus* Greene, *A. alnifolia* Nutt, *P. emarginata* (Dougl. ex Hook) Eaton, *Galium aparine* L., *A. urticifolia* (Bentz.) Kuntze, *Berberis*, and *Spirea* spp. Mean aboveground nesting resource abundance (the total amount of woody debris > 2.5 cm in diameter along sampling transects plus all snags within plot boundaries) was 34 ± 4.3 units per plot. Mean forest floor depth was 63.6 ± 4.9 mm, and mean soil organic matter content was 13 ± 0.7%. Individual plot attributes are summarized in Table 1.

Trap Collections

We collected a total of 514 bees from 18 genera representing 57 species/morphospecies (Table 2). *Lasioglossum* (*Dialictus*) spp., *Osmia proxima* Cresson, *Hoplitis fulgida* (Cresson), *Ceratina acantha* Provancher, *Hylaeus verticalis* (Cresson), and *Bombus bifarius* Cresson were the most common species. We collected a total of 148 bees (12 genera, 27 species) in July 2016 compared to 366 bees (13 genera, 38 species) in July 2018. The most common genera in 2016 were *Lasioglossum* (51.4% of captures), *Ceratina* (15.5%), *Hoplitis* (12.8%), and *Bombus* (6.9%). The most common genera collected in July 2018 were *Lasioglossum* (30.3%), *Osmia* (23.2%), *Ceratina* (12.3%), and *Hoplitis* (8.5%).

Relationships Between Habitat Attributes and Bee Diversity

The best model for describing the variance in overall bee abundance included herbaceous ground cover (HC), aboveground nesting resource abundance (NR), and soil organic matter content (OM) as explanatory variables ($F_{4,13} = 5.8$; $P = 0.009$; $R^2 = 0.55$), where bee abundance was positively correlated with HC and NR, and negatively correlated with OM (Table 3). A one-unit increase in HC and NR would equate to an average increase of 8.5 and 1.8 bees per plot, respectively. A one-percent increase in OM would equate to an average decrease in bee abundance by 1.3 individuals per plot.

Table 1. Attributes for 0.4-ha plots where bee abundance and diversity were measured before and after a *Dendroctonus pseudotsugae* outbreak on Boise National Forest, Idaho in 2016 and 2018

Plot	BA (m^2/ha)	Mean DBH (cm)[a]	% Tree mortality[b]	% Canopy cover (2016)	% Canopy cover (2018)	% Shrub cover	% Floral cover	Floral spp. richness	Nesting resource abundance	O-Horizon depth (cm)	% OM content
6	33.4	46.8	15.1	92.8	92.6	25	25.0	6	39	63.5	0.16
7	43.5	47.5	17.9	96.9	86.1	21	19.1	5	28	89.5	0.20
4	24.3	49.2	24.5	86.5	67.8	86	2.4	2	25	70.8	0.13
16	3.7	44.4	25.0	83.9	50.2	21	21.4	6	28	79.0	0.13
3	16.5	52.0	30.6	86.2	64.7	46	22.6	7	21	88.3	0.13
14	2.8	50.0	33.3	82.3	47.6	39	17.9	5	57	37.0	0.09
12	20.2	56.2	43.2	91.1	89.7	43	11.9	5	39	40.8	0.10
18	29.8	57.1	46.2	91.1	57.4	25	32.1	7	57	50.8	0.09
11	21.5	53.8	51.1	91.8	51.1	39	6.0	2	28	78.5	0.14
8	23.8	37.2	57.7	83.7	85.2	61	17.9	6	39	57.8	0.11
10	28.9	41.1	61.9	80.4	55.9	50	14.3	6	28	56.8	0.13
5	15.6	49.4	64.7	74.9	65.8	75	2.4	2	39	94.5	0.17
9	17.4	38.5	65.8	76.5	73.5	89	4.8	2	46	68.8	0.16
17	25.7	41.9	71.4	77.7	59.3	43	31.0	7	25	78.5	0.15
13	38.9	12.7	77.7	91.8	79.2	29	16.7	6	57	66.5	0.10
15	12.4	60.6	77.8	65.5	37.8	64	25.0	10	28	61.8	0.09
1	17.4	47.0	89.5	76.7	65.3	21	40.5	8	4	50.8	0.12
2	14.7	43.5	90.6	59.8	39.4	43	38.1	9	28	12.0	0.12

Plots are listed in order of increasing tree mortality.

[a] DBH, diameter at breast height (1.37 m).

[b] Based on presence (dead) or absence (live) of crown fade.

Bee species richness was best explained by a model including shrub cover (SC), O-horizon depth (OD), and NR as explanatory variables ($F_{4,13}$ = 7.1; P = 0.004; R^2 = 0.60), where bee species richness was positively correlated with NR, and negatively correlated with SC and OD (Table 3). A one-unit increase in NR would equate to an average increase of 5.6 species per plot. A one-unit increase in SC or OD would equate to an average decrease of 0.5 and 2.2 species per plot, respectively. Bee diversity (Shannon's H) was best described by a model including HC and percent canopy cover (CC) as explanatory variables ($F_{3,14}$ = 8.1; P = 0.004; R^2 = 0.52), where HC was positively correlated with bee diversity, and CC was negatively correlated with bee diversity (Table 3). A one-unit increase in CC would equate to an average decrease in Shannon diversity by 0.1 units per plot. A one-unit increase in HC would equate to an average increase in Shannon diversity measure by 1.8 units per plot.

Changes in Bee Abundance and Diversity Between 2016 and 2018

Results from rarefaction estimated our sampling intensity captured 93.4% of the theoretical maximum diversity of the 2016 bee community that could be estimated by yellow pan trap sampling, and at 98.4% of the theoretical maximum diversity of the 2018 bee community using the same methodology (Table 4). Site-level species richness of the 2016 bee community was estimated at 59.4 (± 28.1) and 61.3 (± 16.0) for the 2018 bee community (Fig. 1; Table 4). Species richness did not significantly differ between collection years, determined by overlapping 95% confidence bands between the 2016 and 2018 rarefaction curves (Fig. 1). Site-level Shannon diversity was estimated at 18.0 (± 2.8) in 2016 compared to 23.3 (± 2.0) in 2018 (Fig. 2; Table 4). Shannon diversity significantly differed between collection years based on the lack of overlapping 95% confidence bands between the 2016 and 2018 rarefaction curves (Fig. 2). Site-level Simpson diversity was estimated at 9.2 (± 1.9) in 2016, and at 12.3 (± 1.2) in 2018 (Fig. 3; Table 4). The increase in Simpson diversity from 2016 to 2018 was not significant at the α = 0.05 level (Fig. 3).

Results from ANOVA show significant increases in bee abundance ($F_{2,15}$ = 14.4; P = 0.001), bee genera richness ($F_{2,15}$ = 13.8; P = 0.002), and bee diversity ($F_{2,15}$ = 11.9; P = 0.003) from 2016 to 2018 (Table 5). Percent tree mortality from Douglas-fir beetle herbivory was significantly correlated with increases in bee abundance (df = 3, 14; χ^2 = 14.4; P = 0.015; R^2 = 0.37), bee species richness (top: df = 3, 14; χ^2 = 35.7; P < 0.0001; R^2 = 0.54), but not bee diversity (top: df = 3, 14; χ^2 = 7.9; P = 0.064; R^2 = 0.22) (Fig. 4). Correlations between community response variables and percent tree mortality exhibited a cubic pattern, with the direction of correlation differing with level of tree mortality (Fig. 4). Specifically, there was a positive trend between bee abundance and bee richness versus percent tree mortality when mortality rates were less than ~35% as well as above ~60%. A negative trend was observed for these variables when tree mortality was 35–60% (Fig. 4, top and middle). The opposite pattern was observed between bee diversity and percent tree mortality, where diversity decreased within plots with tree mortality rates above 80% (Fig. 4, bottom). The best model for predicting change in bee abundance from 2016 to 2018 ($F_{4,13}$ = 11.0; P = 0.006; R^2 = 0.63) included herbaceous plant ground cover (HC), percent tree mortality (% M), and 2018 percent reduction in canopy cover (ΔCC) as positive explanatory variables (Table 6). A one-unit increase in % M, HC, and ΔCC was estimated to increase bee abundance by an average of 7.2, 35.5, and 3.5 individuals per plot, respectively. The best model for describing changes in bee species richness ($F_{5,12}$ = 8.9; P = 0.0011; R^2 = 0.62) included 2017 canopy cover (CC), % M, and ΔCC as positive explanatory variables, as well as SC as a negative explanatory variable (Table 6). A one-unit increase in CC, ΔCC, and % M was estimated to increase bee species richness by an average 1.4, 8.5, and 1.4 taxa per plot, respectively. A one-unit increase in

Table 2. List of bee species collected during a study of the responses of wild bee communities to bark beetle disturbance in a Douglas-fir forest, Boise National Forest, Idaho, 2016 and 2018

Family	Species	Abundance		Total
		2016	2018	
Andrenidae		2	12	14
	Andrena helianthi	0	1	1
	Andrena latifrons	1	0	1
	Andrena nivalis	0	4	4
	Andrena pallidifovea	1	1	2
	Andrena thaspii	0	1	1
	Andrena sp. 1	0	5	5
Apidae		35	61	96
	Anthophora terminalis	0	2	2
	Anthophora urbana	1	0	1
	Bombus bifarius	8	7	15
	Bombus flavifrons	2	0	2
	Bombus mixtus	0	3	3
	Ceratina ancantha	16	22	38
	Ceratina nanula	5	16	21
	Ceratina neomexicana	1	7	8
	Diadasia diminuta	0	2	2
	Diadasia enavata	0	2	2
	Eucera speciosa	1	0	1
	Nomada sp. 1	1	0	1
Colletidae		3	30	33
	Colletes sp. 1	0	1	1
	Hylaeus sp. 1	1	10	11
	Hylaeus sp. 2	1	1	2
	Hylaeus sp. 3	1	18	19
Halictidae		62	97	159
	Halictus confusus	1	0	1
	Halictus ligatus	2	6	8
	Lasioglossum (*Dialictus*) sp. 1	6	11	17
	Lasioglossum (*Dialictus*) sp. 2	3	9	12
	Lasioglossum (*Dialictus*) sp. 3	8	12	20
	Lasioglossum (*Evylaeus*) sp. 1	11	9	20
	Lasioglossum (*Evylaeus*) sp. 2	1	3	4
	Lasioglossum olympiae	3	13	16
	Lasioglossum pacificum	2	0	2
	Lasioglossum paraforbesii	12	29	41
	Lasioglossum sisymbrii	13	4	17
	Sphecodes sp. 1	0	1	1
Megachilidae		17	141	158
	Anthidium mormonum	1	9	10
	Anthidium sp. 1	0	1	1
	Anthidium utahense	0	4	4
	Ashmeadiella timberlakei	0	7	7
	Chelostoma minutum	4	8	12
	Hoplitis albifrons	0	4	4
	Hoplitis fulgida	2	5	7
	Hoplitis louisae	3	18	21
	Hoplitis orthognatha	0	23	23
	Hoplitis producta	0	3	3
	Hoplitis sp. 1	4	0	4
	Hoplitis sp. 2	0	4	4
	Megachile frigida	0	1	1
	Osmia aglaia	0	1	1
	Osmia bucephala	0	20	20
	Osmia caerulescens	1	0	1
	Osmia coloradensis	0	1	1
	Osmia dakotensis	1	4	5
	Osmia proxima	0	3	3
	Osmia similima	1	23	24
	Osmia sp. 1	0	2	2
	Osmia sp. 2	0	2	2

Table 2. Continued

Family	Species	Abundance		Total
		2016	2018	
	Osmia vandykei	0	2	2
Totals	57	148	366	514

Species denoted as sp. 1, 2, etc. refer to distinguishable morphospecies.

Table 3. Results from multiple regression model selection used to assess relationships between forest habitat attributes and bee abundance and diversity, Boise National Forest, Idaho

Response (Y)	Regression
Abundance	$\sqrt{(Y)} = 4.14 + 0.92\,(HC) + 0.21\,(NR) - 0.16\,(OM)$
Richness	$\sqrt{(Y)} = 7.8 - 0.03\,(SC) - 0.14\,(OD) + 1.49\,(NR)$
Diversity	$\sqrt{(Y)} = 1.8 - 0.03\,(CC) + 0.45\,(HC)$

CC = % Canopy cover 2016; SC = % Shrub cover; NR = aboveground nesting resource abundance; HC = % Herbaceous ground cover; OM = % Soil organic matter content (15–30 cm); OD = O-Horizon depth.

Table 4. Results from rarefaction analyses used to estimate overall sampling coverage, species richness, Shannon diversity, Simpson diversity of bees during 2016 and 2018 on Boise National Forest, Idaho

Diversity index	Year			
	2016		2018	
	Pt. estimate	± SE	Pt. estimate	± SE
Sampling coverage	93.7	3.3	98.5	0.5
Species richness	59.4	28.1	61.3	16.0
Shannon diversity	18.0a	2.8	23.29b	2.0
Simpson diversity	9.2	1.9	12.3	1.2

Point estimates followed by different letters within a column indicate no overlap of confidence intervals at the $\alpha = 0.05$ confidence level.

SC was estimated to decrease bee species richness by an average of 2.7 species per plot. Finally, the best model for predicting changes in bee diversity ($F_{3,14} = 10.965$; $P = 0.0012$; $R^2 = 0.60$) included HC and ΔCC explanatory variables (Table 6). A one-unit increase in HC was estimated to increase Shannon diversity by an average of 4.9 units per plot, while a one-unit decrease in CC was estimated to also decrease Shannon diversity by 1.0 unit per plot.

Discussion

Relationships Between Forest Habitat Attributes and Bee Diversity

In the present study, bee diversity was correlated with herbaceous cover and canopy cover (Table 3). Floral resource availability was generally highest in plots with reduced canopies (Table 1) and showed a significant positive relationship with bee abundance and diversity (Table 3). These results support earlier studies that have investigated the relationships between bee community composition and forest habitat structure. In general, forest habitats with relatively open canopies are expected to promote the growth of herbaceous plants on the forest floor that are utilized by the resident bee community (Anderson et al. 1969, Roberts 2004). Nesting resource availability and quality may also affect local bee community assemblages (Cane 1991; Potts et al. 2003, 2005; Grundel et al. 2010). For forest-associated bee communities, the availability of potential nesting cavities, soil quality, and the amount of exposed bare ground are considered primary factors that influence their community structure (Potts et al. 2005, Grundel et al. 2010). In this study, the quantity and quality of both above- and belowground nesting resources were correlated with bee species richness. Soil organic matter content, a factor negatively associated with soil draining capacity (Cane 1991, Potts et al. 2005, Cane and Tempedino 2001), was negatively correlated with bee richness (Table 3). Bee species richness was positively correlated with dead woody vegetation abundance (Table 3), where downed woody material or standing dead trees (snags) may be utilized as aboveground nesting locations for certain species. These results further suggest that nesting resource quantity and quality are likely determinants of bee community composition in a given area, and that soil quality and dead woody vegetation availability may be among the primary factors that determine forest habitat suitability for bees.

Changes in Bee Abundance and Diversity Following Douglas-fir Beetle-Induced Tree Mortality

Previous studies have shown that forest stands with reduced canopies as a result of forest management practices (e.g., Romey et al. 2007, Taki et al. 2010, Proctor et al. 2012, Rubene et al. 2015) and fire (Nyoka 2010) generally have greater bee abundance and species richness relative to nearby untreated or undisturbed areas. The present study incorporated two sampling efforts over a 3-yr period to detect any changes in summer bee abundance or diversity following bark beetle disturbance. Following Douglas-fir beetle-induced tree mortality, there were significant increases in bee abundance, and diversity (Table 4), where plots with higher levels of tree mortality were correlated with greater increases in bee abundance and bee species richness (Fig. 1). Reduction in canopy cover following tree mortality was positively correlated with overall bee abundance and diversity (Table 5). Results from rarefaction analyses indicate that the sampling methodology used in this study detected >90% of the theoretical maximum diversity of bees that could be captured across the entire study site (Table 6) by using yellow pan traps. With data extrapolated out to greater sampling intensities, the resulting rarefaction curves indicate that species richness between the 2016 and 2018 bee communities would not differ (Fig. 1; Table 6). It is logical that species richness would remain relatively constant across this landscape over relatively short time periods, as the addition of new species following disturbance may be predominantly attributed to novel species immigrating into the recently disturbed landscape from surrounding areas. However, at smaller spatial scales changes in diversity and species evenness may occur more rapidly, such as over the course of the 3-yr

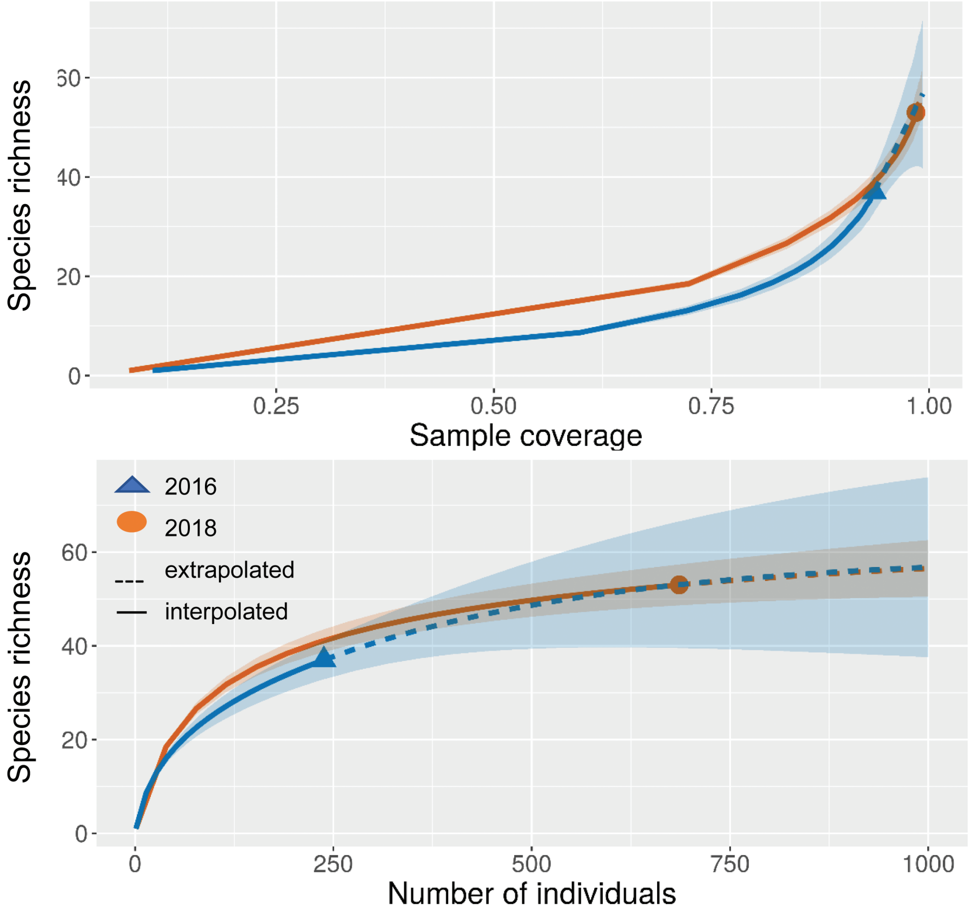

Fig. 1. Results from rarefaction estimating differences in bee species richness between 2016 and 2018, following a *Dendroctonus pseudotsugae* outbreak in Boise National Forest, Idaho. Species and relative abundances were extrapolated out to 100% theoretical sampling intensities (top) and are represented at theoretical sample sizes of 1,000 (bottom). The associated 95% confidence bands of the interpolated and extrapolated data are also represented.

sampling period in this study. Additional results from rarefaction estimate Shannon diversity to significantly increase following Douglas-fir beetle-induced tree mortality (Fig. 2; Table 6). Simpson diversity was also predicted to be greater in 2018 compared to 2016. However, this predicted difference was not significant at the 95% confidence level (Fig. 3; Table 6). The addition of relatively rare bee species that were only observed in 2018 may have caused greater increases in Shannon diversity between years when compared to the observed increases in Simpson diversity. Specifically, Shannon diversity gives equal value to the incidence of each species within a reference sample regardless of their relative abundance (Hsieh et al. 2016). This differs from how Simpson diversity is determined, which assigns relatively small value to extremely rare species when approximating the diversity of a given assemblage (Hsieh et al. 2016). Overall, these results are generally consistent with those of related studies comparing the arthropod communities in forests disturbed by bark beetles to other community assemblages in nearby undisturbed areas. For example, gaps in the forest canopy created by tree mortality attributed to European spruce beetle, *Ips typographus* L., had greater arthropod abundance and species richness compared to nearby areas with closed canopies in the Bavarian Forest National Park, Germany (Müller et al. 2008, Lehnert et al. 2013). Results from the current study present the first description of a relationship between a bark beetle outbreak and the resident bee community in North America, suggesting that bark beetle disturbance may be a mechanism by which forest structure is altered to promote wild bee diversity.

Results from this study indicate that the short-term changes in bee diversity following a bark beetle outbreak may vary with changes in disturbance intensity, where increases in bee diversity may be highest in areas with relatively moderate rates of tree mortality (Fig. 1). This relationship is similar to changes in biodiversity predicted under the intermediate disturbance hypothesis (IDH), which postulates that diversity of competing species will be maximized following disturbance events at intermediate frequencies and/or intensities (Molino and Sabatier 2001, Svensson et al. 2012). In Mediterranean pine forests, bee, wasp, and sawfly communities have exhibited unimodal relationships with wildfire severity following disturbance, which supports the IDH (Lazarina et al. 2019). However, in a Douglas-fir landscape in the Pacific Northwest (Oregon), bee abundance and species richness showed a logarithmic response to wildfire severity (Galbraith et al. 2019). There, overall bee abundance and species richness were highest during mid-summer and within the most severely burned areas, leading the authors to conclude that community responses were likely correlated with the highest increases in flowering plants and boring insect exit holes used by cavity-nesting bees in these areas. The effects of other high-intensity forest disturbances on bee diversity can also contradict the IDH. For example, increased herbaceous groundcover, light, and temperature following complete removal of the canopy in clear-cut stands can cause higher rates of bee activity within these disturbed areas compared to nearby intact forest (Romey et al. 2007; Hanula et al. 2015, 2016). In the present study, tree mortality only explained roughly 20% of the variation observed within changes in bee diversity

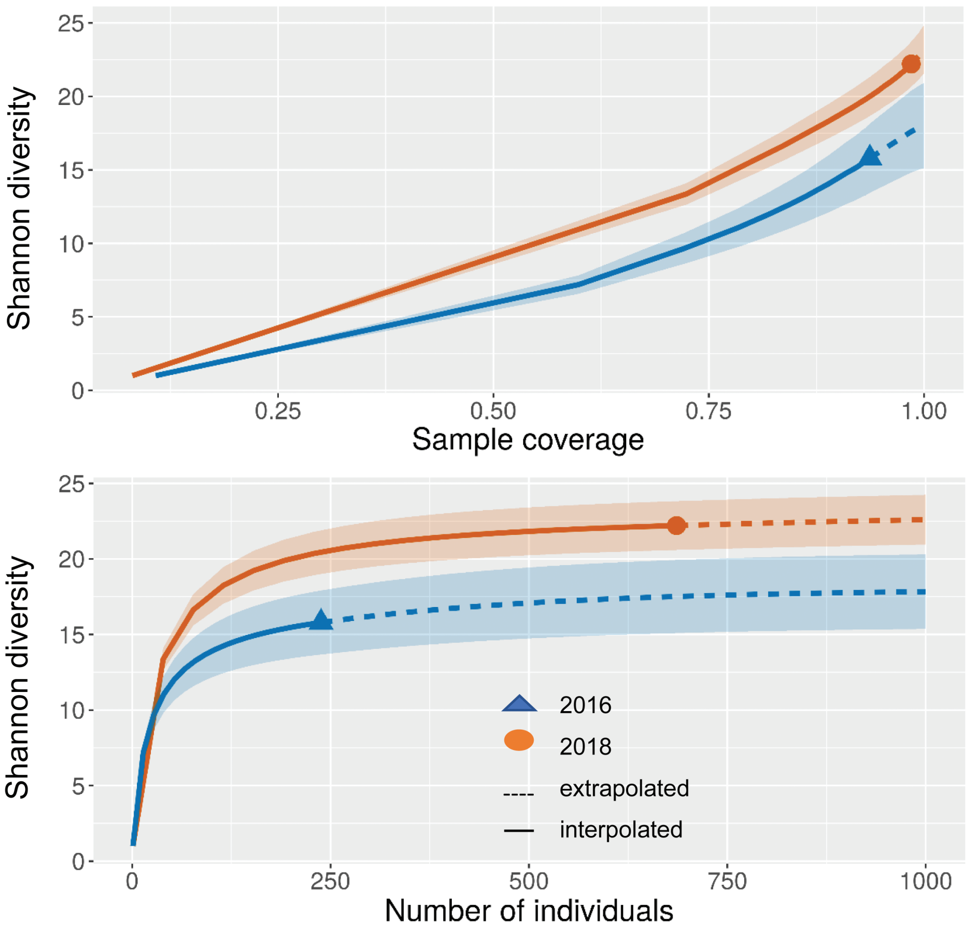

Fig. 2. Results from rarefaction estimating differences in Shannon diversity between 2016 and 2018 bee communities, following a *Dendroctonus pseudotsugae* outbreak in Boise National Forest, Idaho. Species and relative abundances were extrapolated out to 100% theoretical sampling intensities (top) and are represented at theoretical sample sizes of 1,000 (bottom) individuals. The associated 95% confidence bands of the interpolated and extrapolated data are also represented.

from 2016 to 2018. However, herbaceous groundcover exhibited a significant positive relationship with both bee abundance and species diversity across the site during both collection years (Tables 3 and 5) similar to observations reported by Galbraith et al. (2019). Overall, the combined results from studies discussed here suggest the IDH is a relatively simplistic model for estimating disturbance–diversity relationships (Fox 2013), and that bee community responses to natural forest disturbance will vary by forest and disturbance type as well as disturbance intensity.

How bee populations respond to habitat disturbance depends on the life history and ecological attributes of each species, with the combined and interacting responses of all individuals in a disturbed area determining future community compositions (Potts et al. 2005, Williams et al. 2010, Haddad et al. 2008; Taki et al. 2013, Harrison et al. 2018). For example, traits including polylecty and high mobility can allow certain bee species to more readily colonize disturbed areas, where the resulting immigration of such species could alter future community compositions (Greenleaf et al. 2007, Williams et al. 2010). Differences in nesting behavior could also influence how populations will react to habitat disturbance. For forest-associated bee communities, local populations of wood-, cavity-, and stem-nesting species (e.g., *Ceratina* and *Osmia* species) may benefit more from newly available nesting resources (i.e., standing dead trees and downed woody debris, increased growth of herbaceous plants with pithy stems) following tree mortality events compared to populations of ground-nesting species (e.g., certain *Andrena* and *Lasioglossum* species) that require exposed bare soils with limited surrounding vegetation (Cane 1991). In this study, captures of *Ceratina* and *Osmia* bees were greater in 2018 compared to 2016, while the relative abundance of *Lasioglossum* bees decreased in 2018 (Table 2). While increases in floral cover likely benefit the majority of bee species located within newly disturbed areas by providing additional foraging resources, these potential increases in floral resources may also reduce the relative amount of exposed soil surface area available for ground-nesting species to construct their burrows. This increase in abundance of wood- and stem-nesting bees relative to ground-nesting species illustrates a possible mechanism for explaining the observed reductions in overall bee diversity sampled from plots with relatively higher levels of tree mortality. Species that are more responsive to increases in light availability following reductions in canopy cover could further alter forest community composition following disproportionate increases in their abundances relative to species less responsive to changes in light availability (Fye 1972, Polatto et al. 2014, Hanula et al. 2016). Related studies that also monitor light availability and temperature on the forest floor before and after a disturbance could provide a better understanding of how changes in these abiotic factors may influence bee community assemblages over time.

Future Research

Studies comparing bee community responses to different types of forest disturbance (i.e., abiotic vs biotic or anthropogenic) are few.

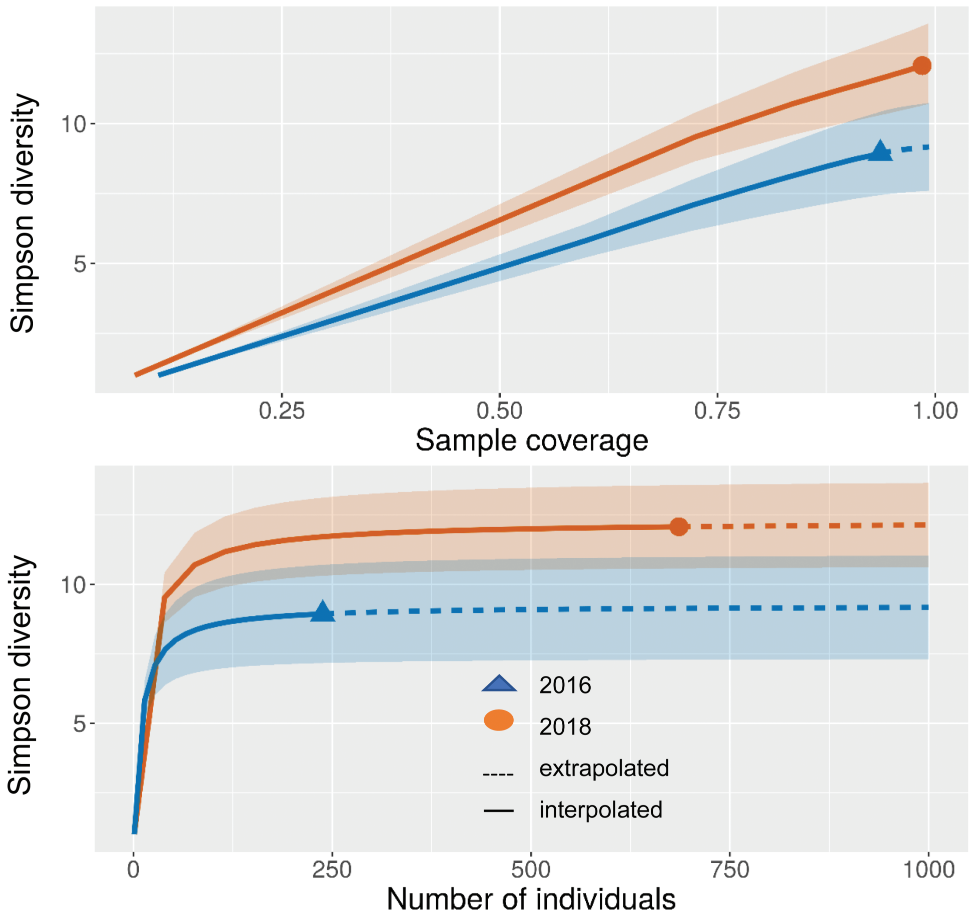

Fig. 3. Results from rarefaction estimating differences in Simpson diversity between 2016 and 2018 bee communities, following a *Dendroctonus pseudotsugae* outbreak in Boise National Forest, Idaho. Species and relative abundances were extrapolated out to 100% theoretical sampling intensities (top) and are represented at theoretical sample sizes of 1,000 (bottom) individuals. The associated 95% confidence bands of the interpolated and extrapolated data are also represented.

Table 5. Results from ANOVA testing for differences in bee abundance, bee genera, bee species richness, and bee diversity (Shannon's *H*) comparing 2016–2018 collections on Boise National Forest, Idaho

Year	Abundance		Genera richness		Diversity (Shannon's *H*)	
	Mean	SE	Mean	SE	Mean	SE
2016	8.7a	1.7	2.7a	0.4	7.3a	1.4
2018	21.0b	3.7	6.0b	0.7	18.3b	0.7

Means followed by different letters within a column are significantly different ($P > 0.05$).

Table 6. Results from multiple regression model selection used to assess relationships between habitat attributes and changes in bee abundance and bee diversity between 2016 and 2018, Boise National Forest, Idaho

Response (Y)	Regression
Δ Abundance	$\sqrt{(Y)} = 17.6 + 0.2\ (M) + 1.0\ (HC) + 0.1\ (\Delta CC)$
Δ Richness	$\sqrt{(Y)} = 6.8 + 0.1\ (M) + 0.1\ (\Delta CC) + 0.6\ (CC) - 0.2\ (SC)$
Δ Diversity	$\sqrt{(Y)} = 0.3 + 11.3\ (HC) + 4.6\ (\Delta CC)$

ΔCC = % Change in canopy cover from 2016 to 2018; CC = % Canopy cover 2016; HC = % Herbaceous ground cover; SC = % Shrub cover; NR = aboveground nesting resources abundance; M = % Tree mortality.

While forest management practices that revert stands to earlier successional stages may favor wild bees by providing a relative abundance of floral resources (Hanula et al. 2016), often the biological legacies (i.e., woody debris and standing dead trees) that can serve as nesting resources are lost (Foster and Tillman 2000, Grundel et al. 2010, Swanson et al. 2011). Similarly, fires may benefit bee communities by reducing the shrub layer and reallocating resources to their foraging resources (Potts et al. 2003, Waltz and Cuvington 2004, Grundel et al. 2010, Nyoka 2010, Taylor and Catling 2011), but may produce soil temperatures that exceed physiological thresholds of ground-nesting bees (Cane 2001, Grundel et al. 2010; Cane and Neff 2011). Furthermore, forest fires may kill and consume the floral and aboveground nesting resources of the resident bee community in the immediate term (Cane 2001). In contrast, bark beetle outbreaks do not have direct impacts on soil temperature or bee foraging resources (Morehouse et al. 2008, Edburg et al. 2012) and bark beetle-killed trees can remain standing for years unless removed by land managers.

Findings from this study indicate that bark beetle activity may indirectly produce beneficial changes in forest structure that promote

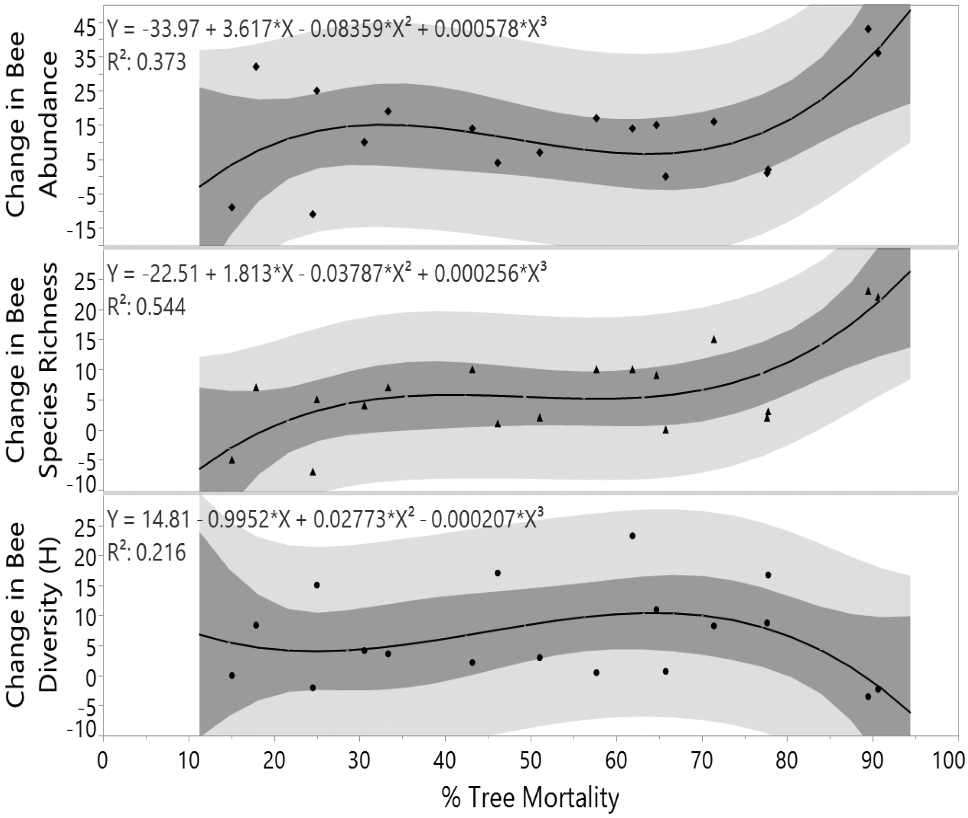

Fig. 4. Scatter plots illustrating cubic patterns of correlations between tree mortality attributed to *Dendroctonus pseudotsugae* and changes in bee abundance (top), bee species richness (middle), and bee diversity (bottom) between 2016 and 2018, Boise National Forest, Idaho. The associated 95% confidence (dark gray) and prediction (light gray) intervals are also represented.

bee abundance and diversity in disturbed areas. However, this study was limited to a single experimental site in Idaho where the bee community was sampled exclusively during periods of peak floral bloom during July 2016 and 2018. Furthermore, only yellow pan traps were used in this study which may have been less effective than other colors at capturing certain taxa (Droege et al. 2010). As increases in temperature and light availability following reductions in canopy cover can increase bee foraging activity in disturbed areas (Fye 1972, Polatto et al. 2014, Hanula et al. 2016), increases in the abundance and diversity of bees collected using passive trapping methods could be a result of increased trap visibility in areas where bees were more active, rather than diversity increasing due to increases in resource availability for the bee community following these reductions in canopy cover. This potential issue may occur in all studies where passive trapping methods are used to assess changes in bee communities following forest disturbance. Incorporating a variety of pan trap colors and other sampling techniques (e.g., aerial netting), while also identifying bee nesting locations within study sites can reduce the limitations of passive sampling methodologies. Therefore, these results may only apply to summer bee communities and thus provide only limited inference regarding relationships between bark beetles and forest-associated bees in general. This warrants future work that samples bee communities using a diversity of techniques, across additional locations and forest types throughout the year in order to provide a more thorough understanding of the effects of bark beetle disturbance on forest pollinator diversity. Overall, long-term monitoring programs of forest-associated bee communities within areas affected by recent or ongoing anthropogenic and natural disturbances are necessary to gain a better understanding of how their populations are impacted by certain management practices, wildfire, insect outbreaks, and climate change. Repeated monitoring of forest-associated bee populations within these early successional habitats for multiple years following tree death can provide valuable information on the general trends of how bee community assemblages change as forests move through successional stages, and guide future land management and bee conservation efforts.

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