RESEARCH ARTICLE

Both Landsat- and LiDAR-derived measures predict forest bee response to large-scale wildfire

Sara M. Galbraith[1], Jonathon J. Valente[2], Christopher J. Dunn[2] & James W. Rivers[2]

[1]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA
[2]Department of Forest Engineering, Resources, and Management, Oregon State University, Corvallis, Oregon, USA
Center for Environment Management of Military Lands, Colorado State University, Fort Collins, Colorado, USA
U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, Alabama, USA

Abstract

Large-scale disturbances such as wildfire can have profound impacts on the composition, structure, and functioning of ecosystems. Bees are critical pollinators in natural settings and often respond positively to wildfires, particularly in forests where wildfire leads to more open conditions and increased floral resources. The use of Light Detection and Ranging (LiDAR) provides opportunities for quantifying habitat features across large spatial scales and is increasingly available to scientists and land managers for post-fire habitat assessment. We evaluated the extent to which LiDAR-derived forest structure measurements can predict forest bee communities after a large, mixed-severity fire. We hypothesized that LiDAR measurements linked to post-fire forest structure would improve our ability to predict bee abundance and species richness when compared to satellite-based maps of burn severity. To test this hypothesis, we sampled wild bee communities within the Douglas Fire Complex in southwestern Oregon, USA. We then used LiDAR and Landsat data to quantify forest structure and burn severity, respectively, across bee sampling locations. We found that the LiDAR forest structure model was the best predictor of abundance, whereas the Landsat burn severity model had better predictive ability for species richness. Furthermore, the Landsat burn severity model was better at predicting the presence and species richness of bumble bees (*Bombus spp.*), an ecologically distinct and economically important group within the Pacific Northwest. We posit that the divergent responses of the two modeling approaches are due to distinct responses by bee taxa to variation in forest structure as mediated by wildfire, with bumble bees in particular depending on closed-canopy forest for some portions of their life cycle. Our study demonstrates that LiDAR data can provide information regarding the drivers of bee abundance in post-wildfire conifer forest, and that both remote sensing approaches are useful for predicting components of wild bee diversity after large-scale wildfire.

Introduction

Insect pollinators play an indispensable role in natural and managed ecosystems by pollinating > 85% of the world's wild flowering plants (Ollerton et al., 2011) and 35% of agricultural crops (Klein et al., 2007), as well as

providing more than US$260 billion in ecosystem services annually (Porto et al., 2020). Despite their importance, long-term pollinator population declines (Goulson et al., 2015) and ongoing challenges to pollinator health (Lopez-Uribe et al., 2020; Potts et al., 2010) have led to widespread concerns about the integrity of natural

ecosystems and global food security (Allen-Wardell et al., 1998; Biesmeijer et al., 2006; Potts et al., 2016). In turn, this has led to heightened interest in evaluating the response of pollinators to natural and anthropogenic disturbances, especially beyond the agricultural settings in which most pollinator research has been traditionally conducted. Although a growing body of work has found a wide range of managed forests support pollinator populations (Heil & Burkle, 2018; Rivers et al., 2018b; Rivers & Betts, 2021; Roberts et al., 2017; Taki et al., 2013; Ulyshen et al., 2023), our understanding of how pollinators respond to natural disturbances within managed forest landscapes is nascent and many important questions remain outstanding (Rivers et al., 2018a).

Bees are considered to be the most important pollinator group in most terrestrial systems (Willmer et al., 2017), and there is mounting evidence that many species of wild bee populations respond positively to disturbances occurring within forest ecosystems (Bogusch et al., 2015; Burkle et al., 2019; Galbraith et al., 2019a; Roberts et al., 2017; Taki et al., 2013; Zitomer et al., 2023), including wildfires (Carbone et al., 2019; Galbraith et al., 2019a; Mason Jr et al., 2021). Bees play a critical role in the post-fire structuring of such systems because the pollination services they provide ultimately support the broader ecological community, and thus, there is heightened interest in understanding their response to large-scale wildfire (Rivers et al., 2018a). Results from this growing body of work have demonstrated that characteristics of wildfire, such as burn severity, are often important predictors of bee community composition (Galbraith et al., 2019a; Mason Jr et al., 2021; Ponisio et al., 2016; Ulyshen et al., 2022).

Burn severity is a measure for fire's effects on the ecosystem, where high-severity fire removes more fuel and transfers more heat than low-severity fire (Keeley, 2009). Although burn severity appears to be a key driver of forest bee response to wildfire, few investigations have measured the impacts of burn severity on this group (Mason Jr et al., 2021). Of the limited studies on this topic, several have provided evidence for a positive relationship between bee diversity and burn severity, proposing this relationship is driven by the greater availability of floral resources in response to a wildfire-induced reduction in tree canopy, particularly within forests of the western United States (Galbraith et al., 2019a; Gelles et al., 2022). However, the response of local bee communities to burn severity is likely to depend on environmental conditions, such as the local fire regime (Koltz et al., 2018) and functional traits represented by the local bee and flower communities (Brown et al., 2017). For example, moderate severity fires in Mediterranean pine forests decreased canopy cover enough to promote floral

abundance and augment bee diversity, whereas severe burns actually reduced critical habitat elements required by the local bee community (Lazarina et al., 2019). Like many studies on bees in large-scale forest ecosystems, however, that study lacked habitat data needed to rigorously test such hypotheses (Lazarina et al., 2019). Understanding which habitat variables drive bee response to burn severity across different systems requires better tools for measuring habitat at fine resolutions and broad spatial scales.

Remote sensing offers an increasing array of tools for measuring these variables. The rapid increase in remote sensing technology has improved the accessibility and quality of data used for modeling how organisms are influenced by environmental factors at large spatial scales (Nagendra, 2001; Randin et al., 2020), yet bees and other arthropods are disproportionately underrepresented in such studies (Galbraith et al., 2015; Leyequien et al., 2007; Newton et al., 2009). Of the existing insect research that has employed remotely sensed data, the great majority of this work has relied on passive remote sensing tools, most often using satellite imagery to categorize land cover types (Willcox et al., 2018). These tools often produce coarse spatial data with insufficient resolution for capturing relevant changes to insect habitat (Willcox et al., 2018). Studies examining bee response to wildfire, for example, have typically used derived measures that represent an index of ecological change due to wildfire (Rhodes et al., 2022), such as the amount of burned area or an index of burn severity. These indices do not account for forest structure characteristics that may be driving bee response to burn severity (e.g., tree height and basal area) at the resolution needed to make predictions about habitat quality.

Active remote sensing tools can provide opportunities for an improved understanding of the fine-scale habitat changes that are needed to understand the response of small organisms, including insects, to disturbances (Galbraith et al., 2015; Rhodes et al., 2022). One tool in particular, Light Detecting and Ranging (LiDAR), holds promise over remotely sensed maps measuring burn severity because it provides information on vertical structural components and produces data at a much finer spatial resolution. Previous studies have associated LiDAR-derived variables with arthropod assemblages, finding that beetle body size (Müller & Brandl, 2009), beetle species occurrence (Bombi et al., 2019; Work et al., 2011), butterfly species distributions (de Vries et al., 2021), and spider occurrence (Vierling et al., 2011) could be mapped with varying degrees of accuracy within mature forests. However, only a single study to date has examined the relationship between bees and LiDAR-derived variables (Traylor et al., 2022); that study found that tree

composition—but not LiDAR-derived forest structure measurements—was linked to bee communities in southeastern US forest sites, perhaps due to a limited range of structural variation that was examined. However, bee diversity did show a negative relationship to in situ measurements of tree basal area (Traylor et al., 2022), highlighting the promise this technique holds for understanding how forest bees are influenced by stand structural components that are expected to be altered by large-scale wildfire.

In this study, we investigated the use of LiDAR-derived forest structure variables to predict bee abundance and bee species richness in a highly heterogeneous post-wildfire conifer forest landscape. We hypothesized that models using LiDAR-derived measures of post-fire forest structure (hereafter; LiDAR forest structure models) would have better predictive ability for bee abundance and species richness relative to a commonly used Landsat-derived burn severity model (hereafter; Landsat burn severity model), the Relative differenced Normalized Burn Ratio (RdNBR; Miller & Thode, 2007, Miller et al., 2009). We also hypothesized that bumble bees (*Bombus* spp.), an ecologically and economically important group that has been relatively well studied in post-fire habitats (e.g., Mola & Williams, 2018; Simanonok & Burkle, 2020), would respond differently than the bee community as a whole because they are large-bodied and colonial-nesting (i.e., eusocial) and are therefore expected to forage over greater distances than other forest bee species in the community (Osborne et al., 2008). Although our previous work found a link between burn severity and bee abundance and species richness, we posited that the relationship was likely driven by increased floral resources in areas where high-severity wildfire removed more of the forest canopy relative to less severely burned sites (Galbraith et al., 2019a). As such, we expected that a model characterizing the structure of the forest after wildfire would provide an improved characterization of bee suitability relative to burn severity, and thus, a post-fire forest structure model using three-dimensional LiDAR data would better predict bee abundance and species richness patterns than a burn severity model from Landsat data. However, bumble bees show strong growth in colony size in post-wildfire settings (Mola et al., 2020a) and several species in this group use forests throughout their life cycle (Mola et al., 2020b; Mola et al., 2021). These findings led us to predict that the response of bumble bees to wildfire would be less influenced by forest structure, and more influenced by burn severity.

Understanding bee responses to wildfire has become particularly timely and relevant to conservation efforts given the increase in the extent and severity of wildfire in the western United States in recent decades (Dennison et al., 2014;

Westerling et al., 2006), and projections that this trend will continue well into the next century despite limitations on forest fuels (Abatzoglou et al., 2021; Flannigan et al., 2013). Thus, an improved understanding of the specific habitat changes that drive the influence of wildfire on bee communities is needed to enhance conservation of bees, both as elements of biodiversity and for the ecosystem services they provide within and beyond forest ecosystems (Hanula et al., 2016; Rivers et al., 2018a; Ulyshen et al., 2023). By exploring novel applications of tools such as LiDAR to improve our understanding of the relationship between pollinators and wildfire, we will expand our ability to continue testing these relationships in diverse forest systems.

Materials and Methods

We conducted this study in the > 19 000 hectare Douglas Fire Complex, which burned during July–August of 2013 in the Klamath Mountains of the Klamath–Siskiyou ecoregion of southwestern Oregon. This area is characterized by a frequent, mixed severity fire regime (Taylor & Skinner, 1998) and is dominated by conifer tree species such as Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and Jeffrey pine (*Pinus jeffreyi*), as well as containing some hardwood species (e.g., tanoak [*Lithocarpus densiflorus*], madrone [*Arbutus menziesii*]). The Douglas Complex fires resulted in a mosaic of burn severity in the mixed conifer landscape (Zald & Dunn, 2018) across multiple landownerships; we focused our study in forests managed by the U.S. Bureau of Land Management (BLM) within the burn perimeter, which consisted largely of even-aged Douglas-fir stands prior to the fire, with some snags and live trees remaining after harvest.

Site selection

We randomly selected sampling locations within the burn perimeter to represent the full burn severity gradient of the Douglas Complex. We chose locations by randomly generating points within the burn perimeter that centered on stands encompassing a minimum 6.5 hectares of forest burned within the same burn severity category (with RdNBR of < 235, 235–649, and > 649 representing low, moderate, and high severity categories, respectively; Reilly et al., 2017). In addition, we selected points that were a minimum 1 km from other points within the same burn severity category to reduce spatial autocorrelation of bee communities.

Bee and habitat sampling

We collected bees at $n = 34$ sites during four sampling rounds during May–September 2016 and 2017. We spaced

sampling rounds by 3–4 weeks to cover the flight seasons of the regional bee community without having undue negative impacts on foundress queen bumble bees (*Bombus* spp.) that are most abundant in late spring. Our earliest sampling round (mid-May) coincided with bloom of early-season plants used by bees in post-fire areas (e.g., *Vaccinium ovatum*, *Berberis nervosa*), and our final sampling round coincided with declining bloom of the regional forb community.

During each sampling round and on each stand, we passively sampled bee communities using two blue vane traps (BVTs) with no killing agent or preservative. All sampling methods introduce trade-offs (Prendergast et al., 2020), so we selected this sampling method because BVTs are attractive to diverse bee taxa in forested ecosystems (Rhoades et al., 2018; Rivers et al., 2018b; Rivers & Betts, 2021). In addition, using BVTs allowed us to standardize sampling across a range of sites that exhibited differences in vegetation of the understory and canopy. For each sampling site, we hung a trap each on two separate 1.8 m tall posts. To avoid placement bias, the first trap was placed 10 m from the site center along a randomly selected azimuth and the second trap was placed 10 m from the center in the opposite direction. We avoided placing traps in dense vegetation patches to standardize visibility for bees as much as possible. We placed BVTs on t-posts located 10 m from the center of the stand where they remained in place for 48 h, after which we collected trap contents. Bees were identified to species or, if species-level keys or named reference specimens were unavailable, to morphospecies by L. R. Best and A. R. Moldenke from Oregon State University. A reference collection is held at the Oregon State Arthropod Collection (Galbraith et al., 2019c). Additional information about site selection, bee sampling, bee identification, and the bee community can be found in Galbraith et al. (2019a, 2019b).

Remote sensing data

Burn severity was quantified using the Relative differenced Normalized Burn Ratio (RdNBR), a satellite imagery-based metric of pre- to post-fire change (Miller et al., 2009). Cloud-free pre-fire (July 2013) and post-fire (July 2014) images were sourced from the Landsat 8 Operational Land Imager. As described in Zald and Dunn (2018), normalized burn ratio (NBR), which combines near-infrared and mid-infrared bands of Landsat imagery, was calculated for pre- and post-fire images, then RdNBR calculated as:

$$RdNBR = \frac{RdNBR_{Pre-fire} - RdNBR_{Post-fire}}{\sqrt{Absolute\ value\left(\frac{RdNBR_{pre-fire}}{1000}\right)}}$$

We selected stands that spanned the burn severity gradient based on relationships between RdNBR and basal area mortality (Reilly et al., 2017; Fig. 1), therefore accounting for differences in both pre-fire and post-fire vegetation cover (Miller et al., 2009). The 34 selected stands fell into four burn severity categories: low ($n = 10$; RdNBR mean = 103.53, SD = 46.78), medium–low ($n = 7$; RdNBR mean = 326.48, SD = 37.07), medium–high ($n = 8$; RdNBR mean = 548.56, SD = 48.73), and high ($n = 9$; RdNBR mean = 851.46, SD = 140.21).

The post-fire LiDAR dataset was collected by Quantum Spatial Inc. (now NV5) in the same fire complex, but during late summer 2017. This collection period coincided with field bee sampling. Unlike the LANDSAT data, which correlate with burn severity and therefore required sampling as close to the date of the wildfire as possible, it was desirable to have LiDAR data collected as close as possible to the timing of bee sampling to reflect the forest habitat conditions at that time. We selected LiDAR-derived variables from metrics developed by Hoe et al. (2018), as these variables represent a full suite of post-wildfire habitat elements. All metrics from point clouds were processed using the FUSION software (v. 4.40, http://forsys.cfr.washington.edu/fusion/fusion_overview.html) at a 900 m² scale consistent with Landsat data and then analyzed all remote sensing data layers, including visual interpretation of the point clouds, in Esri ArcMap 10.7.1 (Hoe et al., 2018). We then used available literature to select a subset of 10 LiDAR variables that were most relevant to pollinator habitat by describing forest structure after wildfire (Table 1).

Data analysis

No single scale is likely to be relevant to the diversity of bee species in our landscape (Galbraith et al., 2019b), as bee body size is strongly correlated with bee foraging range (Greenleaf et al., 2007). As such, we measured each of the 11 landscape variables under consideration (Table 1) around our sampled stands using five concentric circles with radii of 50, 100, 250, 500, and 1000 m. We centered each circle on a midpoint between the two BVT sampling locations (i.e. the stand center) and the radii were selected based on the typical foraging ranges of wild bees of a range of body sizes (Zurbuchen et al., 2010). We then condensed this multiscale information for each variable into a single covariate using principal components analyses (PCA; prcomp function in R (v. 3.6.3; R Core Team, 2022)). The first principal component accounted for most of the cross-scale variance for each variable (mean = 69% [SD = 5.04], range: 63–78%; Table 2) and was used to represent the variable in all subsequent analyses. We did this for three reasons: First, it
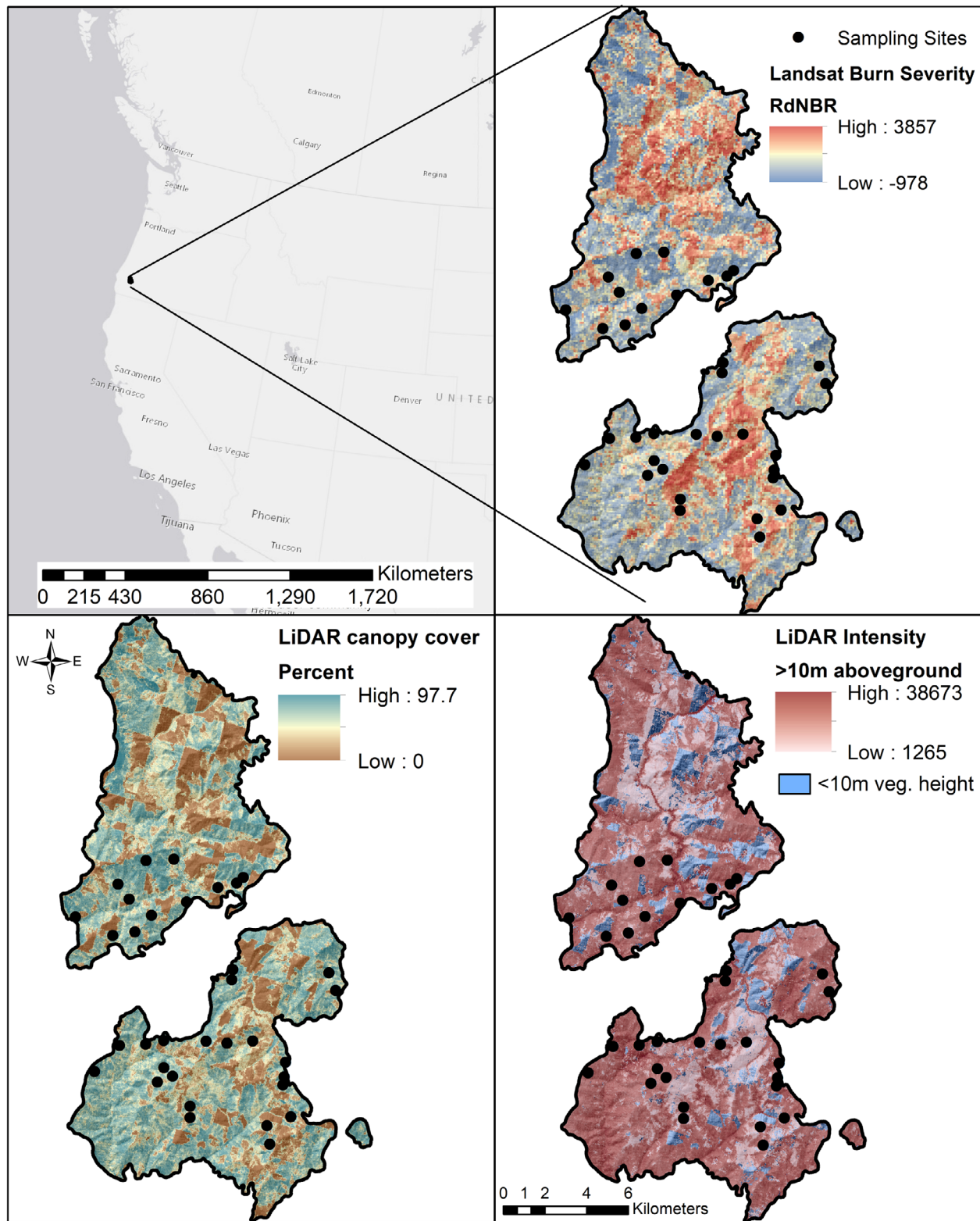
Figure 1. Map of the Douglas Complex Fire in southwestern Oregon, United States where the study took place. The panels show the context of the burn area within the pacific northwestern United States (upper left); and the sampling sites overlaid with the Landsat burn severity data (upper right), LiDAR canopy cover data (lower left), and LiDAR intensity data (lower right).

Table 1. Description of the remotely sensed variables used in the study with justification from previous research on native bees within conifer forest.

Sensor	Variable(s)	Description	Relevance to bee habitat use
Landsat	Relativized differenced Normalized Burn Ratio (RdNBR)	Two-dimensional burn severity metric calculated from the change in pre- and post-fire surface reflectance of the near and infrared spectrum	Burn severity is correlated with bee diversity in forest ecosystems (Galbraith et al., 2019a; Lazarina et al., 2019)
LiDAR	Basal area mortality (BAM)	Three-dimensional burn severity metric calculated from the change in proportion of dead stems after the fire	Burn severity is correlated with bee diversity in forest ecosystems (Galbraith et al., 2019a; Lazarina et al., 2019)
LiDAR	Post-wildfire mean tree height (Htmean)	Mean vegetation height	Proxy for stand age/basal area, which is negatively related to bee diversity (Rhoades et al., 2018)
LiDAR	Post-wildfire cover (Cover)	Based on returns >2 m	Cover includes any returns from anything at this height of the forest, such as vegetated canopy and snags. Canopy cover is negatively related to bee diversity (Grundel et al., 2010; Hanula et al., 2015; Hanula et al., 2016; Rubene et al., 2015)
LiDAR	Post-wildfire understory reflectance (CRS1)	Mean reflectance below canopy (<2 m)	High values indicate a dense vegetation layer with high infrared reflectance (e.g., green understory vegetation) (Hoe et al., 2018). Vegetation in the understory influences bee abundance and diversity (Campbell et al., 2007)
LiDAR	Post-wildfire canopy reflectance (CRS3)	Mean reflectance at canopy level (>10 m)	High values indicate a dense vegetation layer with high infrared reflectance (e.g., green vegetation in the sub-canopy or canopy) (Hoe et al., 2018). Canopy cover is negatively related to bee diversity (Grundel et al., 2010; Hanula et al., 2015; Hanula et al., 2016; Rubene et al., 2015)
LiDAR	Post-wildfire mean intensity (IntMean)	Mean intensity value for all returns	Foliar reflectance can improve upon classifications (Silveyra Gonzalez et al., 2018), and therefore may discriminate between vegetation and surfaces that predict bee abundance and richness.
LiDAR	Post-wildfire mean intensity value—understory (Int1)	Mean intensity value for returns <2 m	Foliar reflectance can improve upon classifications (Silveyra Gonzalez et al., 2018), and therefore may discriminate between understory vegetation and surfaces that predict bee abundance and richness
LiDAR	Post-wildfire mean intensity value—canopy (Int3)	Mean intensity value for returns >10 m	Foliar reflectance can improve upon classifications (Silveyra Gonzalez et al., 2018), and therefore may discriminate between canopy vegetation and surfaces that predict bee abundance and richness. Forests support distinct bee species across strata (Urban-Mead et al., 2021)
LiDAR	Post-wildfire return proportions—understory (RP1)	Based on returns <2 m	Improves upon burn severity estimates (Hoe et al., 2018) and a measure of vertical complexity in herb/shrub layer. Vegetation in the understory influences bee abundance and diversity (Campbell et al., 2007)
LiDAR	Post-wildfire return proportions—canopy (RP3)	Based on returns >10 m	Improves upon burn severity estimates (Hoe et al., 2018) and a measure of vertical complexity. Shown to be important for some butterfly species (de Vries et al., 2021)

minimized correlation among potential covariates, which tended to be high among identical variables measured at different scales; second, it reduced the total number of covariates being considered for our models while still accounting for most of the heterogeneity across scales of biological relevance; and third, it ensured that our covariates contained information that was ecologically relevant to all species included in our analysis, regardless of the

Table 2. The variable loadings and proportion of variance explained by the first principal component for each covariate.

Covariate	Variable loadings					Variance explained (proportion)
	50 m	100 m	250 m	500 m	1000 m	
Cover	0.52	0.53	0.55	0.34	0.15	0.63
CRS1	0.50	0.51	0.53	0.39	0.24	0.66
CRS3	0.49	0.50	0.52	0.43	0.24	0.69
Int1	0.47	0.47	0.51	0.43	0.35	0.74
Int3	0.46	0.47	0.50	0.45	0.35	0.77
IntMean	0.48	0.49	0.52	0.40	0.32	0.69
RP1	0.52	0.53	0.55	0.34	0.15	0.63
RP3	0.51	0.51	0.53	0.40	0.20	0.67
BAM	0.46	0.45	0.48	0.44	0.39	0.78
Htmean	0.51	0.52	0.52	0.42	0.16	0.68
RdNBR	0.50	0.50	0.52	0.43	0.23	0.69

We measured each of 11 covariates at five different spatial scales then condensed them using variable-specific principal components analyses. We then chose the first principal component to use in our analysis exploring the impacts of Landsat and LiDAR variables on bee communities.

scale at which they perceive landscape structure. To further minimize the potential for multi-collinearity in our models, we also examined Pearson's correlation among the 10 LiDAR principal components prior to model building. We found that Cover was highly correlated ($|r| > 0.74$) with all covariates except Int3 and BAM, and that the latter two were highly correlated ($r = -0.79$) with one another. We thus selected Cover and Int3 to use as the variables in LiDAR models because they represented most of the variability in the original 10 covariates of interest.

We compared the performance of Landsat- and LiDAR-derived variables on four response variables: bee abundance, bee species richness, presence of *Bombus* spp., and species richness of *Bombus* spp. Initially, we planned to examine abundance of all *Bombus* species, but we were unable to identify a probability distribution that reasonably represented this response variable; thus, we simplified abundance to a presence/absence measure. Preliminary data exploration indicated substantial heterogeneity in number of bees trapped among sampling rounds, so we conducted analyses at the plot-by-sampling round level. We used generalized linear mixed models in all analyses that assumed a negative binomial response distribution (bee abundance and species richness), a Poisson distribution (*Bombus* richness), or a Bernoulli distribution (*Bombus* presence/absence). All models included categorical effects of year and sampling round. We also included a random effect to account for the effect of sampling in the same sites over multiple years. For the abundance analyses, we modeled individuals captured per trap by

including an offset for number of sampling traps on the stand (i.e., 1 or 2), as a small subset of traps were rendered inoperable by marauding American black bears (*Ursus americanus*). In richness and presence/absence models, we included number of traps as a categorical covariate to account for heterogeneity in sampling effort. We fitted all models using the lme4 package (Bates et al., 2015) in R.

Preliminary examination of the data indicated a clear linear relationship between all response variables and the LiDAR Cover variable. Either a linear or quadratic relationship with Int3 and RdNBR seemed plausible. We thus fit four Landsat models and four LiDAR models. The Landsat models included linear and quadratic RdNBR effects with and without an interaction with sampling round. The LiDAR models all included a linear Cover effect along with linear and quadratic Int3 effects, with and without interactions between sampling round and both LiDAR covariates. In each analysis, we compared all eight candidate models using Akaike's information criterion corrected for small sample size (AIC$_c$). We evaluated the fit of the top model for each of the four response variables by testing the dataset for zero inflation and by testing the scaled residuals for normality, overdispersion, outliers, and heteroscedasticity across predicted values using the DHARMa package (v. 0.4.3; Hartig, 2021) in R version 4.2.0 (R Core Team, 2022). We then calculated the AIC$_c$ weight (i.e., the weight of evidence the model is the best of the candidate set) of each ith model as

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{8} \exp(-0.5\Delta_r)}$$

where $_i$ represents the difference in AIC$_c$ between model i and the top ranked model (Burnham & Anderson, 2002). Finally, we compared the relative importance of Landsat-derived vs. LiDAR-derived variables for explaining each response variable by summing these weights across models containing the relevant variables (Burnham & Anderson, 2002). All data and code are available as supplementary materials.

Results

We collected samples at $n = 33$ stands in 2016 and $n = 34$ stands in 2017, and our sampling documented a relatively high diversity of bee species in recently burned conifer forest. Across both years, we trapped 3130 specimens representing 99 species/morphospecies, 23 genera, and 5 families (Table S1). The most abundant genus we detected was *Halictus* (4 species, 36.5% of total

individuals captured) followed by *Bombus* (11 species, 20.7%), *Lasioglossum* (16 species/morphospecies, 19.6%), and *Xylocopa* (1 species, 7.3%; Table S1). Only two bee species—*Apis mellifera* and *Osmia bicornis*—were classified as non-native. Because those two species accounted for a small number of individuals (<6%) and because we found little difference between models evaluating the response of all bee species relative to those evaluating native bee species alone, we retained both species in our final analyses. During the course of our study, 24 *Lasioglossum* specimens were damaged during trapping to the point where they could not be identified to morphospecies (Table S1); therefore, these individuals were included in descriptive measures and models quantifying bee abundance, but they were removed from descriptions and models of bee species richness.

We found that the LiDAR-based forest structure variables were better than the Landsat-based RdNBR variable for explaining total bee abundance. For this response variable, the LiDAR model containing linear Cover and Int3 effects with sampling round interactions had the greatest support (AIC$_c$ weight = 0.52; Table 3). All models containing RdNBR had little support as indicated by AIC$_c$ values > 2. Indeed, when assessed over all candidate models, the relative importance of forest structure metrics for explaining total and native bee abundance was more than three times greater than that of RdNBR (Fig. 2). Conversely, RdNBR was substantially more useful for explaining *Bombus* presence/absence than the forest structure variables. Among the eight models we considered, only the quadratic RdNBR model had substantial support (AIC$_c$ weight = 0.83; Table 3), whereas all models

Table 3. A comparison of candidate models used to evaluate the effects of Landsat and LiDAR variables on four bee community metrics: total abundance, total abundance and richness, and presence/absence and richness of *Bombus* species.

Response variable	Model	K	Log likelihood	AIC$_c$	ΔAIC$_c$	AIC$_c$ wt.	*Cum.* wt.
Bee abundance	Cover*Sample + Int3*Sample	15	−716.65	1465.50	0.00	0.52	0.52
	RdNBR^2	9	−724.76	1468.32	2.82	0.13	0.64
	Cover + Int3	9	−724.86	1468.52	3.02	0.11	0.76
	Cover*Sample + Int3^2*Sample	19	−713.68	1468.91	3.41	0.09	0.85
	RdNBR^2*Sample	15	−718.45	1469.09	3.59	0.09	0.94
	Cover + Int3^2	10	−724.46	1469.90	4.40	0.06	0.99
	RdNBR*Sample	11	−725.88	1474.94	9.44	0.00	1.00
	RdNBR	8	−731.22	1479.07	13.57	0.00	1.00
Bee richness	RdNBR^2*Sample	16	−511.45	1057.40	0.00	0.45	0.45
	RdNBR^2	10	−518.41	1057.81	0.41	0.37	0.82
	Cover*Sample + Int3*Sample	16	−512.86	1060.22	2.82	0.11	0.93
	Cover + Int3	10	−521.19	1063.38	5.97	0.02	0.95
	Cover + Int3^2	11	−520.49	1064.17	6.77	0.02	0.97
	Cover*Sample + Int3^2*Sample	20	−510.12	1064.18	6.78	0.02	0.98
	RdNBR*Sample	12	−519.49	1064.40	7.00	0.01	1.00
	RdNBR	9	−524.66	1068.12	10.71	0.00	1.00
Bombus presence	RdNBR^2	9	−129.91	278.62	0.00	0.83	0.83
	RdNBR	8	−133.11	282.85	4.23	0.10	0.93
	Cover + Int3	9	−132.75	284.30	5.68	0.05	0.97
	Cover + Int3^2	10	−132.57	286.13	7.51	0.02	0.99
	RdNBR*Collection	11	−133.07	289.33	10.71	0.00	1.00
	RdNBR^2*Collection	15	−129.26	290.72	12.11	0.00	1.00
	Cover*Collection + Int3*Collection	15	−131.97	296.15	17.53	0.00	1.00
	Cover*Collection + Int3^2*Collection	19	−130.33	302.22	23.60	0.00	1.00
Bombus richness	RdNBR^2	9	−260.93	540.66	0.00	0.47	0.47
	Cover + Int3	9	−261.70	542.20	1.54	0.22	0.69
	RdNBR^2*Sample	15	−255.57	543.34	2.68	0.12	0.82
	Cover + Int3^2	10	−261.52	544.04	3.38	0.09	0.91
	RdNBR	8	−263.88	544.41	3.75	0.07	0.98
	Cover*Sample + Int3*Sample	15	−257.87	547.94	7.28	0.01	0.99
	RdNBR*Sample	11	−262.81	548.80	8.14	0.01	1.00
	Cover*Sample + Int3^2*Sample	19	−255.43	552.41	11.75	0.00	1.00

For each model, we report the number of parameters (*K*), log likelihood, AIC$_c$, difference in AIC$_c$ compared to the top model (ΔAIC$_c$), weight of evidence in support of the model (AIC$_c$ wt.), and cumulative weight of the ranked models (*Cum.* wt.). Larger log likelihood values indicate better model fit, while smaller AIC$_c$ values indicate a more parsimonious fit.
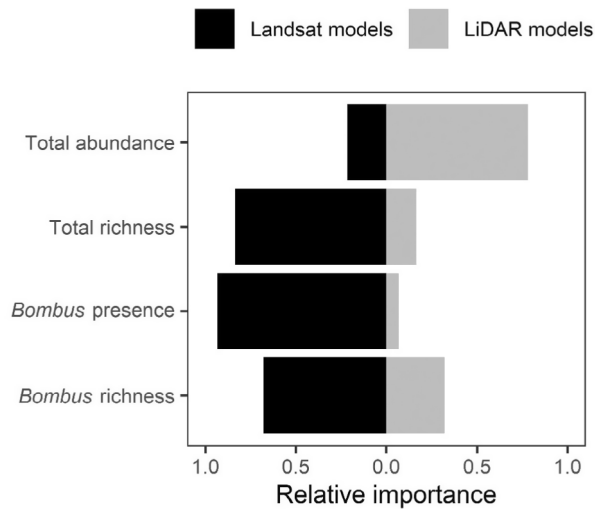
Figure 2. The relative importance of the Landsat burn severity and LiDAR forest composition models fit to explain four bee community metrics (bee abundance, bee species richness, *Bombus* presence, and *Bombus* richness). We calculated relative importance by summing the AIC_c weights of the four Landsat or four LiDAR models fit for each dataset. Weights of all eight models for a given response variable sum to one, so larger values indicate greater importance for the covariate group.

containing the forest structure metrics had limited support as indicated by AIC_c weights ≤ 0.05. When we summed these weights across models, the relative importance of RdNBR for explaining *Bombus* presence/absence was nearly 14 times greater than the importance of LiDAR-derived forest structure (Fig. 2).

Species richness results were more nuanced. Within both the total richness and *Bombus* richness model sets, a model containing a quadratic RdNBR effect had the greatest support; the top total richness model also included an interaction with sampling round (Table 3). Furthermore, the relative importance of RdNBR was five times greater than the importance of the forest structure variables for explaining total richness, and two times greater for explaining *Bombus* richness. No LiDAR forest structure models had substantial support for total richness, but the model including linear Cover and Int3 effects did have substantial support for *Bombus* richness with a AIC_c value of < 1.54.

The top abundance model indicated a strong decrease in bee abundance with increasing cover; this model also indicated the effects of Int3 varied among sampling rounds, but bee abundance was generally lowest at intermediate Int3 levels (Fig. 3A). Top models for the other three response variables exhibited similar patterns. Total bee richness, *Bombus* presence, and *Bombus* richness were lowest in stands with the lowest RdNBR values (i.e., at sites that burned the least severely), peaked at moderately

high levels of burn severity, and decreased again in stands experiencing the most severe fires (Fig. 3B–D).

Discussion

Our study found that LiDAR-derived forest metrics can improve our understanding of how bee communities respond to wildfire when used in conjunction with the Landsat-derived measures of burn severity that are commonly used to quantify post-fire landscapes. We hypothesized that LiDAR forest structure models would have better predictive ability for bee abundance and species richness relative to a Landsat burn severity model, and that bumble bees would exhibit a different responsive relative to the broader bee community because of their large foraging distances. We did find that abundance of the bee community was closely linked to forest structure; specifically, LiDAR-derived measures of cover > 2 m and the intensity of returns > 10 m. However, the best-fitting LiDAR forest structure model did not outperform the Landsat burn severity-only model in predicting the richness of the sampled bee community. Similarly, the Landsat burn severity model outperformed forest structure in predicting the presence and richness of *Bombus* in our study.

The contrasting results we found when predicting measures of bee communities indicate divergent responses of different bee taxa to forest wildfire. Indeed, different bee species inhabiting the same communities can respond to habitat variables (e.g., floral abundance and diversity) at different spatial scales due to their diverse foraging ranges and distinct life-history traits (Bommarco et al., 2010; Williams et al., 2010). Thus, it is perhaps unsurprising that the abundance and richness of the sampled bee community would be predicted by a different set of measures. In our study area, a few species dominated the sampled bee community and they were much more abundant in severely burned, open stands (Galbraith et al., 2019a). However, for the genus *Bombus*, both presence and species richness were best predicted by the Landsat burn severity model, and they were greatest at the intermediate RdNBR principal component variable. Although species in this genus benefit from pulses of resources following wildfire (Burkle et al., 2019; Galbraith et al., 2019a, 2019b; Mola et al., 2020a), they are also able to travel through forests (Mola et al., 2020b; Mola et al., 2021) and therefore may prefer patchier, mixed-severity landscapes that provide an abundance of flowering plants and nesting substrates. In our study, the lowest values of the RdNBR principal component likely represented a landscape with too few floral resources for most of the bee community. However, the highest values of the variable might be limiting for groups such as *Bombus* because of
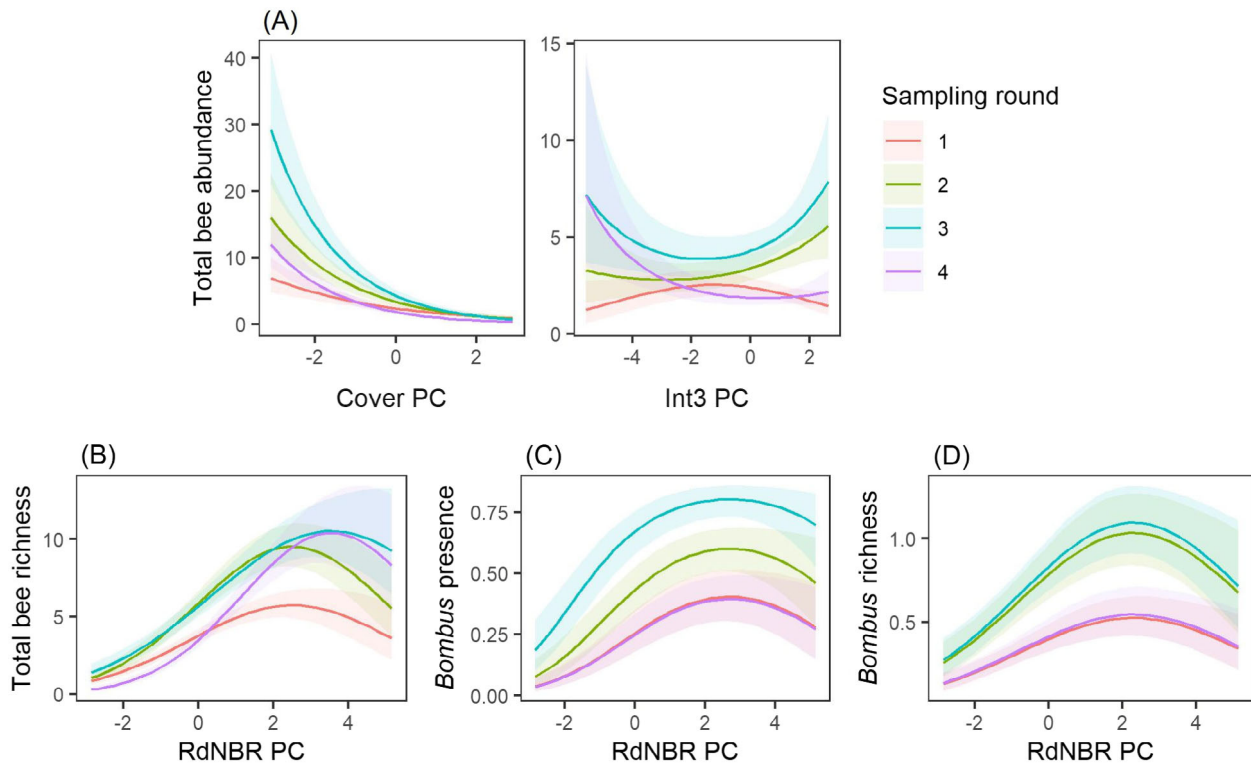
Figure 3. Relationships between remotely sensed variables and bee distributions based on the top model from each analysis. (A) Total bee abundance was best modeled using LiDAR-based covariates (Cover and Int3) whereas (B) total bee richness, (C) *Bombus* presence, and (D) *Bombus* richness were best modeled using the Landsat-based covariate RdNBR. We aggregated information for each covariate across multiple spatial scales using a principal components (PC) analysis prior to model building; values on the *x*-axes represent a gradient from low to high covariate values across scales.

reduced nutrition (Simanonok & Burkle, 2020) and nesting habitat (Liczner & Colla, 2019; Pugesek & Crone, 2021) within the landscape.

Our study provides novel insights into the way forest structure influences the bee communities, as we found that high-resolution, three-dimensional LiDAR variables (cover and intensity of returns in the canopy) outperformed burn severity for predicting bee abundance. Although we have shown in previous work that burn severity is strongly correlated with bee abundance (Galbraith et al., 2019a), LiDAR-derived measures of forest structure were a better measure of bee abundance in this study. Furthermore, bee richness, *Bombus* presence, and *Bombus* richness in this study exhibited a quadratic relationship with the RdNBR principal component variable and were slightly reduced at the highest values of the variable. We posit that these differences are likely due to the spatial scale of our inference: Our past work examined the influence of burn severity at the local scale (Galbraith et al., 2019a) whereas this investigation combined data from multiple spatial scales in each principal component variable. In using a new approach for addressing spatial

scale relative to our prior work in this system (Galbraith et al., 2019a; Galbraith et al., 2019b; Galbraith et al., 2021), we emphasize the importance of considering spatial scale when evaluating habitats for bee communities and interpreting results that represent species with diverse life histories and foraging ranges.

Landsat imagery has been made freely available over broad spatial and temporal scales, and it is an important tool for quantifying burn severity (Reilly et al., 2017). Our study provides further evidence that this approach can be used by land managers to predict the diversity of bee communities following wildfire, at least in regions where the relationship between bees and burn severity has been clearly established in the literature. However, to develop broader hypotheses about bees and burn severity, we must identify and measure the post-fire habitat variables that drive the relationship. Our findings highlight the unique opportunities provided by LiDAR data for exploring such variables.

One of such opportunities is investigating the relevance of previously unexplored LiDAR-derived variables to bee communities. Intensity returns > 10 m (Int3), in

combination with the Cover variable, was one of the most important measures for predicting bee abundance in our study. The intensity variable represents reflective properties of vegetation, and it relates to canopy openness and the spacing and foliage types within individual tree crowns (Moffiet et al., 2005). Bee abundance in our study was generally lowest at intermediate levels of intensity, and the relationship between bee abundance and intensity also depended on the season when bees were sampled. We hypothesize that the intensity variable may be indicating the temporal shift in bee resource use in these plots due to tree species composition. The presence of deciduous trees would lead to pulses of resources that change over time, so that the presence of these trees would be more important at certain points in the season. Because the foliage of deciduous trees differs from that of conifers, they would reflect different intensity returns in the remaining canopy after the fire. At other times in the season, bees might be more likely to respond to canopy openness rather than returns from these trees. Other studies have highlighted the importance of deciduous trees for pollinators (Ulyshen, 2011; Urban-Mead et al., 2021), so additional work is needed to evaluate the role of deciduous trees play in providing floral resources in post-fire forests, particularly in predominantly conifer forests of the western United States. In particular, such studies should consider sampling floral visitors within the canopy as well as the understory to assess whether the temporal availability of floral resources in deciduous trees may contribute to changes in bee communities across time (Ulyshen et al., 2023).

LiDAR presents new opportunities for understanding the role of insects within forest ecosystems because it can be used to measure critical forest structure variables at the scale needed for these studies. The cost and availability of LiDAR data are important considerations that may inhibit its widespread use for research and conservation, including investigations focused on forest pollinators. However, collecting field-based data can also be expensive at the spatial scales needed for landscape-scale management following large wildfires (Bombi et al., 2019; Pereira & Cooper, 2006), and there can be a large return on investment for obtaining LiDAR data if it can be leveraged to meet additional research objectives (Melville et al., 2015). Our study provides additional evidence that these datasets hold potential for answering a growing collection of questions focused on small invertebrates such as insect pollinators. As many governments and organizations make calls to protect pollinators (IPBES, 2016; Underwood et al., 2017; WHPHTF, 2015), remotely sensed data will continue to be essential for making conservation efforts possible at broad spatial scales and dynamic, heterogeneous landscapes.

References

Abatzoglou, J.T., Battisti, D.S., Williams, P.A., Hansen, W.D., Harvey, B.J. & Kolden, C.A. (2021) Projected increases in western US forest fire despite growing fuel constraints. *Communications Earth and Environment*, **2**, 227.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J. et al. (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12**(1), 8–17.

Bates, R., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**(1), 1–48.

Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T. et al. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science*, **313**(5785), 351–354.

Bogusch, P., Blažej, L., Trýzna, M. & Heneberg, P. (2015) Forgotten role of fires in central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). *European Journal of Forest Research*, **134**(1), 153–166.

Bombi, P., Gnetti, V., D'Andrea, E., De Cinti, B., Taglianti, A.V., Bologna, M.A. et al. (2019) Identifying priority sites for insect conservation in forest ecosystems at high resolution: the potential of LiDAR data. *Journal of Insect Conservation*, **23**, 689–698.

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P. et al. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, **277**(1690), 2075–2082.

Brown, J., York, A., Christie, F. & McCarthy, M. (2017) Effects of fire on pollinators and pollination. *Journal of Applied Ecology*, **54**(1), 313–322.

Burkle, L.A., Simanonok, M.P., Durney, J.S., Myers, J.A. & Belote, R.T. (2019) Wildfires influence abundance, diversity, and intraspecific and interspecific trait variation of native bees and flowering plants across burned and unburned landscapes. *Frontiers in Ecology and Evolution*, **7**, 252.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.

Campbell, J.W., Hanula, J.L. & Waldrop, T.A. (2007) Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. *Biological Conservation*, **134**(3), 393–404.

Carbone, L.M., Tavella, J., Pausas, J.G. & Aguilar, R. (2019) A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography*, **28**(10), 1487–1498.

Dennison, P.E., Brewer, S.C., Arnold, J.D. & Moritz, M.A. (2014) Large wildfire trends in the western United States, 1984-2011. *Geophysical Research Letters*, **41**(8), 2928–2933.

de Vries, J.P.R., Koma, Z., WallisDeVries, M.F. & Kissling, W.D. (2021) Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. *Diversity and Distributions*, **27**(7), 1251–1264.

Flannigan, M., Cantin, A.S., De Groot, W.J., Wotton, M., Newbery, A. & Gowman, L.M. (2013) Global wildland fire season severity in the 21st century. *Forest Ecology and Management*, **294**, 54–61.

Galbraith, S.M., Vierling, L.A. & Bosque-Pérez, N.A. (2015) Remote sensing and ecosystem services: current status and future opportunities for the study of bees and pollination-related services. *Current Forestry Reports*, **1**(4), 261–274.

Galbraith, S.M., Cane, J.H., Moldenke, A.R. & Rivers, J.W. (2019a) Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere*, **10**(4), e02668.

Galbraith, S.M., Cane, J.H., Moldenke, A.R. & Rivers, J.W. (2019b) Salvage logging reduces wild bee diversity, but not abundance, in severely burned mixed-conifer forest. *Forest Ecology and Management*, **453**, 117622.

Galbraith, S.M., Cane, J.H., Moldenke, A.R., Best, L.R. & Rivers, J.W. (2019c) Taxonomic voucher specimens for study of post-wildfire forest habitat in Douglas County, Oregon. *Catalog: Oregon State Arthropod Collection*, **3**(4), 1–12. Available from: https://doi.org/10.5399/osu/cat_osac.3.4.4618

Galbraith, S.M., Cane, J.H. & Rivers, J.W. (2021) Wildfire severity influences offspring sex ratio in a native solitary bee. *Oecologia*, **195**(1), 65–75.

Gelles, R.V., Davis, T.S. & Stevens-Rumann, C.S. (2022) Wildfire and forest thinning shift floral resources and nesting substrates to impact native bee biodiversity in ponderosa pine forests of Colorado front range. *Forest Ecology and Management*, **510**, 120087.

Goulson, D., Nicholls, E., Botías, C. & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**(6229), 1255957.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**(3), 589–596.

Grundel, R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E. & Pavlovic, N.B. (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, **20**(6), 1678–1692.

Hanula, J.L., Horn, S. & O'Brien, J.J. (2015) Have changing forests conditions contributed to pollinator decline in the southeastern United States? *Forest Ecology and Management*, **348**, 142–152.

Hanula, J.L., Ulyshen, M.D. & Horn, S. (2016) Conserving pollinators in North American forests: a review. *Natural Areas Journal*, **36**(4), 427–440.

Hartig, F. 2021. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.3. Available from: https://CRAN.R-project.org/package=DHARMa

Heil, L.J. & Burkle, L.A. (2018) Recent post-wildfire salvage logging benefits local and landscape floral and bee communities. *Forest Ecology and Management*, **424**, 267–275.

Hoe, M.S., Dunn, C.J. & Temesgen, H. (2018) Multitemporal LiDAR improves estimates of fire severity in forested landscapes. *International Journal of Wildland Fire*, **27**(9), 581–594.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). 2016. The assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. Available from: https://ipbes.net/assessment-reports/pollinators.

Keeley, J.E. (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire*, **18**(1), 116–126.

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**(1608), 303–313.

Koltz, A.M., Burkle, L.A., Pressler, Y., Dell, J.E., Vidal, M.C., Richards, L.A. et al. (2018) Global change and the importance of fire for the ecology and evolution of insects. *Current Opinion in Insect Science*, **29**, 110–116.

Lazarina, M., Devalez, J., Neokosmidis, L., Sgardelis, S.P., Kallimanis, A.S., Tscheulin, T. et al. (2019) Moderate fire severity is best for the diversity of most of the pollinator guilds in Mediterranean pine forests. *Ecology*, **100**(3), e02615.

Leyequien, E., Verrelst, J., Slot, M., Schaepman-Strub, G., Heitkönig, I.M. & Skidmore, A. (2007) Capturing the fugitive: applying remote sensing to terrestrial animal distribution and diversity. *International Journal of Applied Earth Observation and Geoinformation*, **9**(1), 1–20.

Liczner, A.R. & Colla, S.R. (2019) A systematic review of the nesting and overwintering habitat of bumble bees globally. *Journal of Insect Conservation*, **23**(5), 787–801.

Lopez-Uribe, M.M., Ricigliano, V.A. & Simone-Finstrom, M. (2020) Defining pollinator health: a holistic approach based on ecological, genetic, and physiological factors. *Annual Review of Animal Biosciences*, **8**, 269–294.

Mason, S.C., Jr., Shirey, V., Ponisio, L.C. & Gelhaus, J.K. (2021) Responses from bees, butterflies, and ground beetles to different fire and site characteristics: a global meta-analysis. *Biological Conservation*, **261**, 109265.

Melville, G., Stone, C. & Turner, R. (2015) Application of LiDAR data to maximise the efficiency of inventory plots in softwood plantations. *New Zealand Journal of Forestry Science*, **45**(1), 1–16.

Miller, J.D., Knapp, E.E., Key, C.H., Skinner, C.N., Isbell, C.J., Creasy, R.M. et al. (2009) Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment*, **113**(3), 645–656.

Miller, J.D. & Thode, A.E. (2007) Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of the Environment*, **109**(1), 66–80.

Moffiet, T., Mengersen, K., Witte, C., King, R. & Denham, R. (2005) Airborne laser scanning: exploratory data analysis indicates potential variables for classification of individual trees or forest stands according to species. *ISPRS Journal of Photogrammetry and Remote Sensing*, **59**(5), 289–309.

Mola, J.M. & Williams, N.M. (2018) Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. *Ecosphere*, **9**(1), e02056.

Mola, J.M., Miller, M.R., O'Rourke, S.M. & Williams, N.M. (2020a) Wildfire reveals transient changes to individual traits and population responses of a native bumble bee *Bombus vosnesenskii*. *Journal of Animal Ecology*, **89**(8), 1799–1810.

Mola, J.M., Miller, M.R., O'Rourke, S.M. & Williams, N.M. (2020b) Forests do not limit bumble bee foraging movements in a montane meadow complex. *Ecological Entomology*, **45**(5), 955–965.

Mola, J.M., Hemberger, J., Kochanski, J., Richardson, L.L. & Pearse, I.S. (2021) The importance of forests in bumble bee biology and conservation. *Bioscience*, **71**(12), 1234–1248.

Müller, J. & Brandl, R. (2009) Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology*, **46**(4), 897–905.

Nagendra, H. (2001) Using remote sensing to assess biodiversity. *International Journal of Remote Sensing*, **22**(12), 2377–2400.

Newton, A.C., Hill, R.A., Echeverría, C., Golicher, D., Rey Benayas, J.M., Cayuela, L. et al. (2009) Remote sensing and the future of landscape ecology. *Progress in Physical Geography*, **33**(4), 528–546.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**(3), 321–326.

Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D. et al. (2008) Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, **77**(2), 406–415.

Pereira, H.M. & Cooper, H.D. (2006) Towards the global monitoring of biodiversity change. *Trends in Ecology & Evolution*, **21**(3), 123–129.

Ponisio, L.C., Wilkin, K., M'Gonigle, L.K., Kulhanek, K., Cook, L., Thorp, R. et al. (2016) Pyrodiversity begets plant–pollinator community diversity. *Global Change Biology*, **22**(5), 1794–1808.

Porto, R.G., de Almeida, R.F., Cruz-Neto, O., Tabarelli, M., Viana, B.F., Peres, C.A. et al. (2020) Pollination ecosystem services: a comprehensive review of economic values, research funding and policy actions. *Food Security*, **12**(6), 1425–1442.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology and Evolution*, **25**(6), 345–353.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D. et al. (2016) Safeguarding pollinators and their values to human well-being. *Nature*, **540**(7632), 220–229.

Prendergast, K.S., Menz, M.H., Dixon, K.W. & Bateman, P.W. (2020) The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere*, **11**(5), e03076.

Pugesek, G. & Crone, E.E. (2021) Contrasting effects of land cover on nesting habitat use and reproductive output for bumble bees. *Ecosphere*, **12**(7), e03642.

R Core Team. 2022. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Randin, C.F., Ashcroft, M.B., Bolliger, J., Cavender-Bares, J., Coops, N.C., Dullinger, S. et al. (2020) Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment*, **239**, 111626.

Reilly, M.J., Dunn, C.J., Meigs, G.W., Spies, T.A., Kennedy, R.E., Bailey, J.D. et al. (2017) Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere*, **8**(3), e01695.

Rhoades, P.R., Davis, T.S., Tinkham, W.T. & Hoffman, C.M. (2018) Effects of seasonality, forest structure, and understory plant richness on bee community assemblage in a southern Rocky Mountain mixed conifer Forest. *Annals of the Entomological Society of America*, **111**(5), 278–284.

Rhodes, M.W., Bennie, J.J., Spalding, A., ffrench-Constant, R.H. & Maclean, I.M.D. (2022) Recent advances in the remote sensing of insects. *Biological Reviews*, **97**(1), 343–360.

Rivers, J.W. & Betts, M.G. (2021) Post-harvest bee diversity is high but declines rapidly with stand age in regenerating Douglas-fir forest. *Forest Science*, **67**(3), 275–285.

Rivers, J.W., Galbraith, S.M., Cane, J.H., Schultz, C.B., Ulyshen, M.D. & Kormann, U.G. (2018a) A review of research needs for pollinators in managed conifer forests. *Journal of Forestry*, **116**(6), 563–572.

Rivers, J.W., Mathis, C.L., Moldenke, A.R. & Betts, M.G. (2018b) Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. *GCB Bioenergy*, **10**(10), 766–781.

Roberts, H.P., King, D.I. & Milam, J. (2017) Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management*, **394**, 111–122.

Rubene, D., Schroeder, M. & Ranius, T. (2015) Diversity patterns of wild bees and wasps in managed boreal forests: effects of spatial structure, local habitat and surrounding landscape. *Biological Conservation*, **184**, 201–208.

Silveyra Gonzalez, R., Latifi, H., Weinacker, H., Dees, M., Koch, B. & Heurich, M. (2018) Integrating LiDAR and high-resolution imagery for object-based mapping of forest habitats in a heterogeneous temperate forest landscape. *International Journal of Remote Sensing*, **39**(23), 8859–8884.

Simanonok, M.P. & Burkle, L.A. (2020) High-severity wildfire limits available floral pollen quality and bumble bee nutrition compared to mixed-severity burns. *Oecologia*, **192**(2), 489–499.

Taki, H., Okochi, I., Okabe, K., Inoue, T., Goto, H., Matsumura, T. et al. (2013) Succession influences wild bees in a temperate forest landscape: the value of early successional stages in naturally regenerated and planted forests. *PLoS One*, **8**(2), e56678.

Taylor, A.H. & Skinner, C.N. (1998) Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *Forest Ecology and Management*, **111**(2–3), 285–301.

Traylor, C.R., Ulyshen, M.D., Wallace, D., Loudermilk, E.L., Ross, C.W., Hawley, C. et al. (2022) Compositional attributes of invaded forests drive the diversity of insect functional groups. *Global Ecology and Conservation*, **35**, e02092.

Ulyshen, M.D. (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, **261**(9), 1479–1489.

Ulyshen, M.D., Hiers, J.K., Pokswinksi, S.M. & Fair, C. (2022) Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. *Frontiers in Ecology and the Environment*, **20**(2), 78–83.

Ulyshen, M.D., Urban-Mead, K.R., Dorey, J.B. & Rivers, J.W. (2023) Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops. *Biological Reviews*, **91**, 796–812.

Underwood, E., Darwin, G. & Gerritsen, E. (2017) *Pollinator initiatives in EU Member States: success factors and gaps. Report for European Commission under contract for provision of technical support related to target 2 of the EU biodiversity strategy to 2020 – maintaining and restoring ecosystems and their services ENV.B.2/SER/2016/0018.* Brussels: Institute for European Environmental Policy.

Urban-Mead, K.R., Muñiz, P., Gillung, J., Espinoza, A., Fordyce, R., van Dyke, M. et al. (2021) Bees in the trees: diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management*, **482**, 118903.

Vierling, K.T., Bässler, C., Brandl, R., Vierling, L.A., Weiß, I. & Müller, J. (2011) Spinning a laser web: predicting spider distributions using LiDAR. *Ecological Applications*, **21**(2), 577–588.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase Western U.S. Forest wildfire activity. *Science*, **313**(5789), 940–943.

White House Pollinator Health Task Force (WHPHTF). (2015) *National Strategy to promote the health of honey bees and other pollinators*. Washington, D.C.: White House.

Willcox, B.K., Robson, A.J., Howlett, B.G. & Rader, R. (2018) Toward an integrated approach to crop production and pollination ecology through the application of remote sensing. *PeerJ*, **6**, e5806.

Williams, N.M., Crone, E.E., T'ai, H.R., Minckley, R.L., Packer, L. & Potts, S.G. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**(10), 2280–2291.

Willmer, P.G., Cunnold, H. & Ballantyne, G. (2017) Insights from measuring pollen deposition: quantifying the preeminence of bees as flower visitors and effective pollinators. *Arthropod-Plant Interactions*, **11**(3), 411–425.

Work, T.T., Onge, B.S. & Jacobs, J.M. (2011) Response of female beetles to LIDAR derived topographic variables in eastern boreal mixedwood forests (Coleoptera, Carabidae). *ZooKeys*, **147**, 623–639.

Zald, H.S. & Dunn, C.J. (2018) Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. *Ecological Applications*, **28**(4), 1068–1080.

Zitomer, R.A., Galbraith, S.M., Betts, M.G., Moldenke, A.R., Progar, R.A. & Rivers, J.W. (2023) Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests. *Ecological Applications*, **33**, e2855.

Zurbuchen, A., Cheesman, S., Klaiber, J., Muller, A., Hein, S. & Dorn, S. (2010) Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, **79**(3), 674–681.

Supporting Information

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

Table S1. Taxonomic diversity and abundance of wild bees captured via blue vane traps at $n = 34$ stands located within the Douglas Fire Complex during May–August 2016 and 2017.