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Mechanical thinning and prescribed fire benefit bumble bees and butterflies in a northern California conifer forest

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ABSTRACT

Land managers across western North America are increasingly treating forests with mechanical thinning and prescribed fire to reduce stand density, with the aims of reducing wildfire risks and generating conditions that better align with historic forest structure. The effects of these treatments on invertebrates in forests is poorly understood, especially over longer time scales. We tested for effects of three forest treatments on butterfly and bumble bee abundance and species richness in a ponderosa pine and white fir forest in northern California, USA, that was treated systematically two decades prior to our surveys. The forest treatments included: mechanical thinning that selected for large diameter trees, thinning for a more pine dominated stand, thinning for pine dominance combined with prescribed fire, and control areas without any treatments. The most substantial difference in vegetation structure stemming from the past treatments was reduced forest overstory and greater flowering plant richness in all treatments relative to control. Butterfly and bumble bee richness was greater in all treatment types relative to control, though not always significantly so. Butterfly abundance was significantly greater in all treatments relative to control, and bumble bee abundance was significantly greater in pine treatments relative to control. Bumble bee and butterfly richness and abundance were most strongly positively related to greater plant species richness. Overall, it appears that bumble bees and butterflies in our study area generally benefited from the changes in forest structure that were induced by each of the three treatments, and those benefits persisted for decades.

1. Introduction

Across much of the western U.S., historical fire suppression and selective logging of large trees have yielded unnaturally dense stands of relatively small trees (Battaglia et al., 2018; Merriam et al., 2022). These conditions are likely deleterious for many wildlife species (Furnas et al., 2022; Roberts et al., 2021), and, combined with a warming climate and frequent drought, also increase fire risk (Miller and Safford, 2012; Steel et al., 2015). In some locations, the resulting fire regime may even threaten the persistence of the forests themselves, as climate change may be rendering some post-fire landscapes inhospitable to forest regeneration (Coop et al., 2020). In response, land managers across the western US are striving to address the increasing risk of high-severity wildfire by increasing the 'pace and scale' (North et al., 2021) of forest treatments intended to reduce the risk of severe wildfire and restore at least some attributes of pre-suppression forest structure and composition (Stephens et al., 2023). Recent research is helping to elucidate effects of forest treatments on vertebrates (Basile et al., 2019; Fontaine and Kennedy, 2012; Jones et al., 2022; Stephens et al., 2012) but far less is known about how mechanical thinning and prescribed fire affect populations of insect pollinators like bumble bees (Mola et al., 2021) and butterflies, despite the important roles they play in ecosystems, and the increasing realization that many insect pollinators are declining (Cameron et al., 2011; Lebuhn et al., 2013; Soroye et al., 2020).

However, recently some work on insect pollinators and habitat management on western public lands has addressed the effect of forest restoration on pollinator networks (Davies et al., 2023) and how forest cover, composition, and age influence pollinators (Ulyshen et al., 2024). Much of this work has focused on riparian corridors (Cole et al., 2020), meadows (Baumann et al., 2021; Mola et al., 2020), or other more open habitats (Loffland et al., 2017; Tarbill et al., 2023) where pollinator abundance and diversity tend to be higher. But forests also provide

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important resources for many pollinators (Hanula et al., 2016; Mola et al., 2021; Ulyshen et al., 2023), and the great majority of the forested western landscape is xeric, not mesic, so even where upland forests may support fewer pollinators per land unit area than wetter or more open habitats, they likely support large segments of many pollinator populations that rely on them for foraging resources or nesting habitat (Gelles et al., 2022).

Forest treatments, such as thinning or prescribed fire, may affect pollinators by creating gaps in the canopy that promote increased diversity and biomass of herbaceous plants and shrubs in the understory (Kern et al., 2014; Webster and Halpern, 2010). They might also open travel corridors or increase permeability of forests to insects seeking particular habitats or resources, although at least one recent study indicates forests may not pose a barrier to movement (Mola et al., 2020). Recent studies of pollinator response to prescribed fire, wildfire, and forest treatment have generally reported positive or neutral effects of fire or forest thinning treatments on bees and butterflies (Mason et al., 2021; Gelles et al., 2022). Forest thinning and burning treatments have also resulted in greater butterfly richness and abundance, at least in the near term (Waltz and Covington, 2004). Unlike most other studies, which typically evaluate short-term forest treatment effects (3–5 years post-treatment), we aim to provide insights about long-term effects (20 years post-treatment) of forest treatments on pollinators and identify which species persist long after treatment application.

We studied the effects of forest treatments that were a combination of tree thinning and burning on bumble bees and butterflies in a northern California conifer forest. Both of these pollinator groups consist of relatively large-bodied insects that are comparatively easy to identify in the field without the need for microscopy or lethal sampling. Though they may not fully represent the needs of other insect pollinator groups, they can serve as ambassadors for invertebrate pollinators, as both groups are charismatic and of interest to the public. The two groups also have some interesting ecological differences. Bumble bees are largely habitat generalists and tend to use whatever flower resources are available in their region, though differences in tongue morphology can constrain each species' flower usage somewhat (Wood et al., 2021), and preferences for particular plant species tend to be supported in the literature (Cole et al., 2020; Loffland et al., 2017). However, while many butterfly species are similarly generalist in their foraging preferences, many are closely tied to a few (or even just one) plant species for reproduction (Habel et al., 2022).

Our study area encompassed randomly selected forest plots that were treated with three different mechanical thinning and prescribed fire protocols in a controlled, replicated study two decades before our pollinator surveys. We hypothesized that approximately 20 years post-treatment, treated plots would have greater abundance and diversity of bumble bees and butterflies than untreated plots because we assumed that plots with treatments would, at least in part, maintain some of the structural differences imparted by treatments (e.g., more open canopy, greater flowering plant richness in the understory).We did not make any *a priori* hypotheses about the relative effects of the three specific treatment protocols tested. Understanding the relatively long-term effects of forest treatments on two important groups of pollinators could aid in the design of forest treatments that are likely to become increasingly prevalent across western landscapes in the coming years.

2. Methods

2.1. Study area

The Goosenest Adaptive Management Area (GAMA) is a large-scale ecological research project established by the US Forest Service on Klamath National Forest in northeastern California to evaluate the efficacy of mechanical thinning and prescribed fire for generating late-successional forest conditions (Ritchie, 2005). At the time of our pollinator study, the vegetation within the study area was approximately 100-year old, second growth conifer forest, comprised predominantly of ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) (George et al., 2005) though wildfire suppression and changes to local Karuk cultural burning practices (Halpern et al., 2022) since European settlement has substantially shifted the dominance from pine to fir. Elevations range from 1500 to 1645 m above sea level and there is relatively little topographic relief (George et al., 2005). Over the recent 15-year period (2006–2020) the annual minimum temperature averaged 3.9 °C and the maximum temperature averaged 19.9 °C, with average precipitation of 51.1 cm per year (data from https://ncei.noaa.gov/access/us-climate-normals for the nearest station of Weed, CA). Spring 15-yr averages for min and max temperature were 2.8 C and 18.6 C and 13.3 cm average precipitation, and summer averages were 11.8 C and 32.2 C and 3.6 cm precipitation (data also from NCEI).

In the 1990s, twenty 40.5-ha forest treatment units were established within GAMA, with five of the units assigned to each of four treatments: removal of non-pine species to encourage pine dominance (Pine), removal of non-pine species in addition to the use of prescribed fire (Pine with Fire), mechanical treatment intended to shift the forest composition towards large-diameter trees regardless of species (Big Tree), and no treatment, where the forest was left to continue on it established course (Control). Mechanical treatments were applied to all but the Control units in 1998, 1999, and 2000. Pine and Pine with Fire treatments were established with the aim of yielding a minimum of 80 % residual basal area comprised of ponderosa pine (Ritchie, 2005). Small diameter trees (<30.5 cm Diameter at Breast Height [DBH]) were cut while dominant and codominant pine trees with > 30.5 cm DBH were left standing and 15 % of each unit was left with small group selections ranging from 0.2 to 1.2 ha each. Soils in these groups were ripped and planted with a density of 875 trees per ha using 2–0 bare root ponderosa pine planting stock (grown 2 years from seed in the same soil bed [the 2], not transplanted to another soil bed [the 0]). Pine with fire treatment units were thinned following the procedure outlined above and were burned repeatedly in fall 2001 and 2010. Fine details of forest treatments can be found in Ritchie (2005). The Big Tree treatment aimed to thin units without regard to tree species composition, implemented in a manner similar to the pine treatment, but without the emphasis on retaining only pine species. A complex protocol for cutting trees was applied to trees < 76.2 cm DBH, while trees that were > 76.2 cm DBH were thinned to retain the largest dominant and codominant trees at a 5.5- to 7.6-m spacing. Although these treatments were designed toward meeting a variety of objectives besides fire resilience, they share many characteristics with prescriptions currently being planned or implemented throughout the region for the primary goals of reducing fire risk and restoring ecosystem function (North et al., 2021). Treatments significantly reduced stand density and increased mean residual tree size relative to the control while the Pine with Fire treatment marginally increased ponderosa pine relative density; Ritchie (2020) provides the most current published summaries of vegetation responses to the treatments.

2.2. Sampling locations

For bumble bee sampling, each of the 20 treatment plots was gridded with nine points spaced 200 m apart and at least 100 m from the plot edge, yielding a total of 180 individual survey points. Sampling points were a subset of pre-established forest sampling points established on a systematic grid as part of the GAMA research area and were clearly marked with permanent grid point markers (Ritchie, 2005). Due to a combination of dense vegetation in some areas that precluded the use of a sampling net, and a wildfire that led to the evacuation of the entire study area late in our field season, we were unable to survey 25 of the intended 180 sampling points for bumble bees. Of the 165 points that were surveyed, 44 were in Big Tree, 45 in Control, 43 in Pine, and 33 in Pine with Fire treatment (Fig. 1). For butterfly sampling, we established 60 walking transects that were on average 400 m in length, though

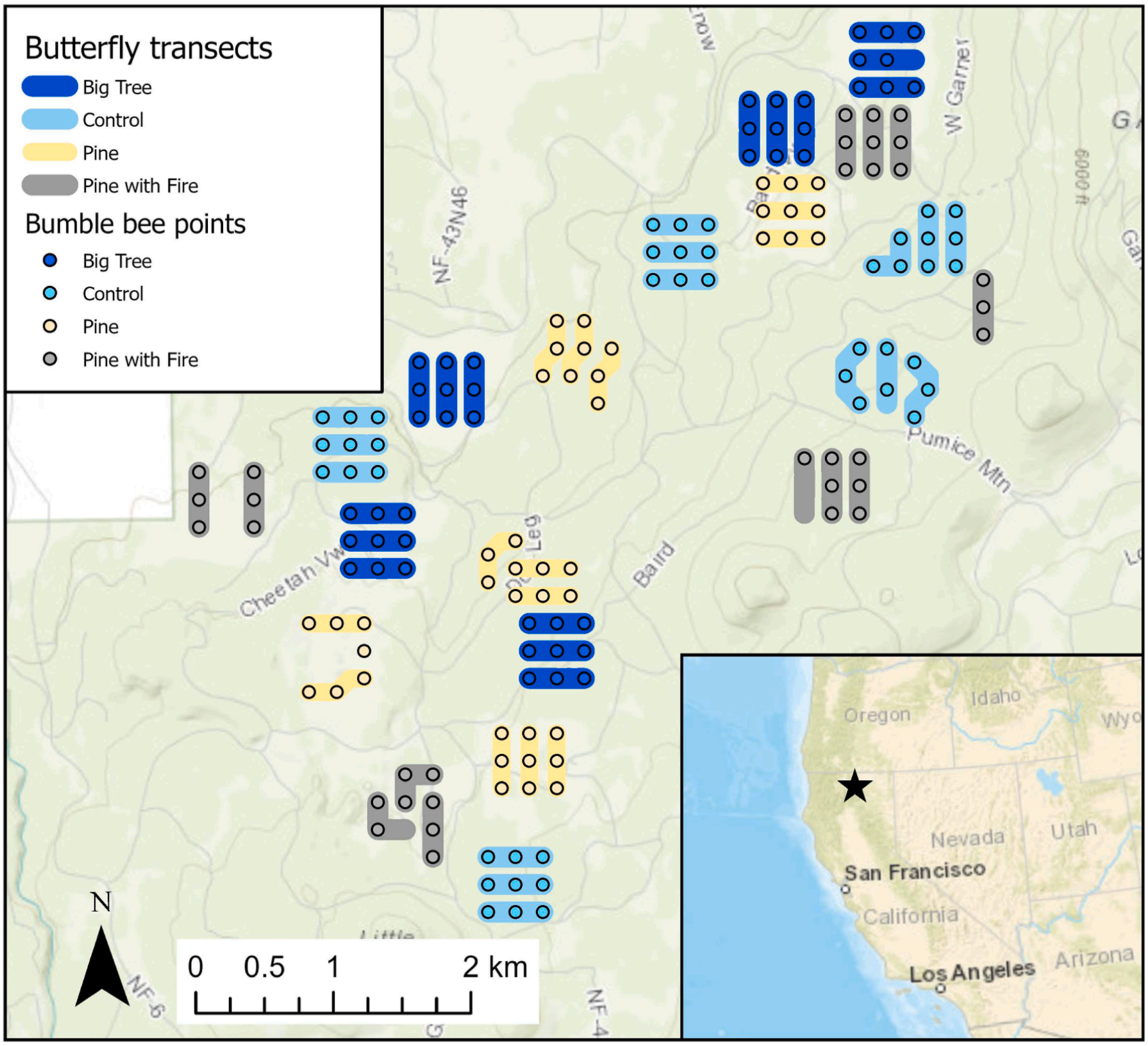

Fig. 1. Butterfly transects (colored lines) and bumble bee sampling points (colored circles) within the Goosenest Adaptive Management Area in northern California (see inset). Only sampled transects and points are presented.

length varied slightly depending on the transect path. The majority of transects (87 %) were 400 m in length, and the remainder ranged from 441 to 483 m. The butterfly sampling transects were oriented to intersect with established bumble bee sampling locations (Fig. 1) and each treatment plot had 3 transects within it. As with the bumble bee surveys, a portion of the intended transects were not sampled, resulting in a total of 15 transects sampled in Big Tree, 15 in Control, 14 in Pine, and 11 in Pine with Fire.

2.3. *Bumble bee surveys*

Bumble bees were surveyed once at each sampling point, between June 2 and July 10, 2021, using non-lethal capture methods that are described in Loffland et al. (2017). As a brief overview, sampling points were surveyed during relatively warm periods of the day (0900–1700) when bees are generally most active. A surveyor searched for and captured all bumble bees within a 20-m radius of the sampling point during a 16 min search period. Observed bumble bees were captured with a sweep net, at which time the 16 min search period was paused while the bee was placed into a vial and put inside a cooler filled with ice, immediately after which the search period resumed. After 16 min of active searching elapsed, the observer photographed and identified chilled bumble bees to species in the field, and then released the bees at the survey location after they warmed in the sun. Photographs were later reviewed to verify any challenging bumble bee identifications.

Following the bee survey, the surveyor performed a rapid vegetation survey at the sampling point. The surveyor visually estimated the total overstory, mid-layer percent cover (the cover provided by all trees and shrubs <4 m in height, which could exceed 100 % because due to multi-layer plant cover), forb cover, herbaceous cover, and shrub cover. Additionally, surveyors attempted to identify all flowering plant species within the 20-m sampling radius, though identification to species was not always achieved (1.3 % of all plant observations were not to species). Our term, “flowering plant species”, refers to number of unique plant species that were actively in bloom during the survey visit. We later summarized this data to generate an index of plant richness, by tallying the total number of unique species (genus or family when species was not determined) at a given point.

2.4. *Butterfly surveys*

Butterfly survey transects were each surveyed once between June 3 and July 10, 2021, between 0900 and 1700, and were not completed if there was rain, temperatures below 45 °F, or wind > 40.2 km/h. Transects consisted of 4 approximately 100 m long segments that comprised a continuous ∼400 m transect. Segments of a transect were surveyed sequentially in a single bout. The observer walked the transect at a steady pace of ∼35 m per min, recording the number of butterflies of each species seen within 2.5 m of either side of the transect line. Species identifications were assigned confidence scores of: > 90 % certainty, 51–89 % certainty, and < 50 % certainty. Butterflies were captured and examined briefly for identification when a species could not be reliably identified by sight and the butterfly could easily be captured without an extended pursuit away from the transect. Voucher specimens of butterfly species not already known to occur at the site were collected after the official transect survey was complete and were deposited at the U.C. Davis Bohart Museum of Entomology.

Surveyors attempted to identify all flowering forbs and shrubs to species as they walked each segment of the survey transect, though in some cases plants could not be identified to species. We later summarized the species richness of flowering forbs and shrubs at the transect level by tallying the unique number of plant species (or genus and family when species could not be determined) identified across all segments for a given transect.

2.5. *Vegetation analysis*

We tested for a significant effect of treatment on the 8 vegetation measures detailed below, using the R language, version 4.4.0 (R Core Team 2024), that were included in either the bumble bee or butterfly richness and abundance modeling. We used a GLMM model from the R package glmmTMB (Brooks et al., 2017), with a Gaussian error distribution for all vegetation metrics except for richness metrics which were modeled with a Poisson error distribution, and used a single categorical effect of treatment and random Plot effect to control for spatial autocorrelation.

We used the vegetation survey data to determine the four most frequently encountered forb and shrub species per treatment type. We tabulated the total number of times a forb or shrub species was detected across all vegetation survey points (for a maximum of 1 detection per species per point), without consideration of plot coverage for that species. In instances where a species was detected at the same number of points, then multiple plant species were listed (e.g., species A and B both were the 3rd most detected plant species). The purpose of these summaries was to understand how treatment type may have influenced plant species composition.

2.6. *Bumble bee and butterfly data analysis*

We summarized the total number of bumble bees captured across all sampling points, but because we sampled fewer than the intended number of points in some treatments, we also generated an index of bumble bee abundance per point (i.e., number of bumble bees captures divided by number of points surveyed in a given treatment type). We also summarized bumble bee richness at the sampling point level. We summarized the total number of butterflies observed across all sampling transects, but because we sampled fewer than the intended number of transects in some treatments, we also generated an index of abundance per transect. Unlike the bumble bee methods, we summarized butterfly richness at the transect level, a larger spatial area of approximately 2000 m^2 of area versus 1256 m^2 of area for each bumble bee survey circle. We only included butterfly detections where the observer was highly confident in the identification (confidence >90 %).

We tested for an effect of treatment on point-level species richness using a generalized linear mixed model (GLMM) for bumble bees and butterflies, modeled with a Poisson error distribution for the count data, and included a combination of: a random effect of Plot (for the point-level and transect-level data), an intercept-only zero-inflation parameter, and a spatial position variable that followed a Matérn covariance structure by using the glmmTMB package in R. If a given model structure provided the best model fit and non-significant spatial autocorrelation in the residuals, then we reported results from that model. If multiple model forms made spatial autocorrelation non-significant we used the model with the fewest terms (e.g., we chose a model with only the Treatment term, over a model with the Treatment + random Plot effect if both sufficiently accounted for spatial autocorrelation). A transect length term was included in the butterfly richness model to account for differences in transect length.

We selected 6 vegetation measures to test as predictors of bumble bee richness at the point level, including: forb cover, herbaceous cover, midlayer cover, overstory cover, shrub cover, and flowering plant richness. Flowering plant richness was the count of unique flowering plant species detected at a sampling point during the bumble bee survey. A small number of plants could not be identified to species (1.3 % of all plant observations) and we treated these plant identifications as a unique species in the richness counts, so even though our measure of “plant richness” is not strictly the count of unique plant species, we refer to it as “plant richness” in the remainder of the manuscript. We built models that contained only a single vegetation term per model (e.g., a single model with forb cover only, another model with shrub cover only, etc.) to avoid overparameterizing each model. As with the treatment effect models, we fit multiple GLMMs with the same terms that were detailed in the species richness model building process.

Unlike the bumble bee sampling, which took place at individual points, the butterfly sampling was transect based, with most transects (91 %) intersecting three collocated bumble bee sampling points. To assess possible predictors of butterfly richness at the transect level, we selected 6 vegetation measures derived from habitat description at the collocated bumble bee points (forb cover, herbaceous cover, midlayer cover, overstory cover, shrub cover, and flowering plant richness), and two metrics derived from vegetation description along the length of the butterfly transects (transect shrub richness and transect forb richness). For the metrics derived from the collocated bumble bee sampling points, we took the mean of vegetation values from all of the collocated bumble bee points that intersected with each transect. The remaining metrics, transect forb richness and transect shrub richness, were respectively, the count of unique blooming forb and shrub plant species encountered over the entirety of the transect. We built models that contained only a single vegetation term per model (e.g., a single model with forb cover only, another model with shrub cover only, etc.) to avoid overparameterizing each model. As with the treatment effect models, we fit multiple GLMMs with the same terms that were detailed in the species richness model building process. We used the same GLMM model structure as the richness analysis to test for the effect of treatment and vegetation (using the same 8 vegetation covariates listed above) on the abundance of all butterflies (i.e., counts of butterflies of all species were pooled at the transect level). A transect length term was included in the butterfly richness model to account for differences in transect length, but not in the butterfly abundance model because butterfly abundance data were filtered to only include transects with length = 400 m (>87 % of transects) due to poor model fit when a variety of transects length were present. This resulted in a sample size of 48 transects for the butterfly abudance models (Control N = 13, Big Tree N = 15, Pine N = 9, Pine with Fire N = 11). Unlike the bumble bee surveys, we had a fairly rich pool of butterfly species, but an insufficient number of detections to model abundance for most species.

All richness and abundance models for bumble bees and butterflies were checked for model fit using the DHARMa package in R (Hartig, 2018) and for significant autocorrelation using the “testSpatialAutocorrelation” function within the DHARMa package. We reported the AIC (Akaike Information Criterion) for each model and ranked them according to this metric model quality, with the lowest AIC value indicating the most explanatory value and parsimoniousness.

3. Results

3.1. *Effects of forest treatments on vegetation*

Six of 8 vegetation measures had at least one treatment type that differed significantly from the control type (Fig. 2). Overstory, midlayer

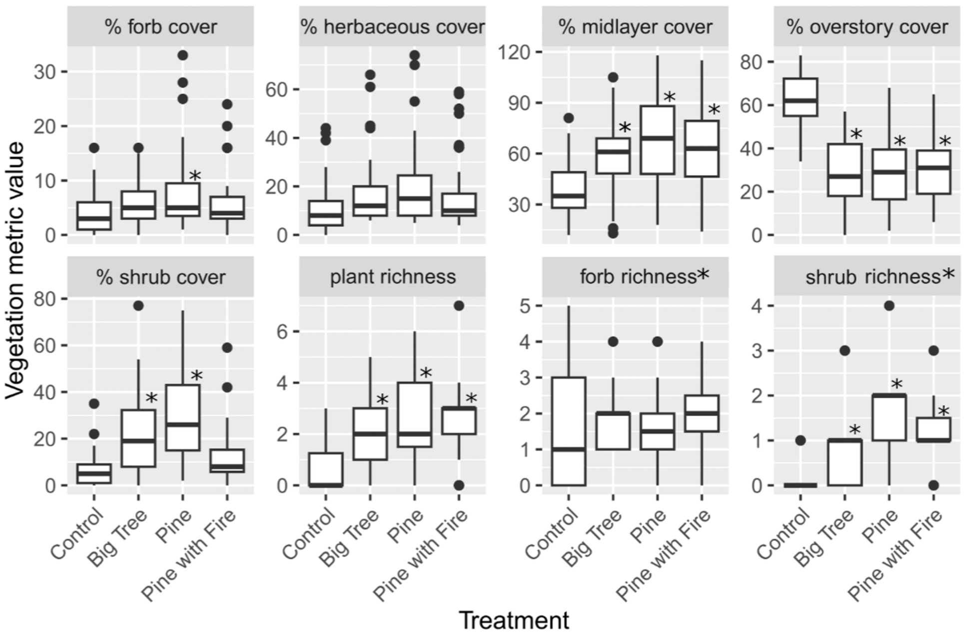

Fig. 2. Boxplots of six vegetation values summarized at the sampling point level and two vegetation values at the butterfly sampling transect level (panels with an asterisk next to the heading) for each treatment type. The y-axes are scaled for each vegetation metric. Boxes with an asterisk are significantly different from the Control values in the same panel. Plant, forb, and shrub richness panels represent the total number of unique flowering plants, forbs, or shrubs observed. One outlier with a value of 190 % for shrub cover (reflecting overlapping shrub layers) was removed from the plot for ease of presentation.

cover, and flowering plant richness had the most consistent response across treatments, with all non-Control types exhibiting higher (midlayer cover, flowering plant richness) or lower (overstory cover) average values than Controls. The Pine treatment type had the highest values for flowering plant richness and all percent cover metrics except overstory cover. Of the transect level measures of vegetation, only shrub richness was significantly greater in treatment areas vs the Control.

Only one of the four most frequently detected forb species was shared across all treatment types, *Monardella odoratissima*. This species also was the most frequently detected species in all treatments. Two of the top four forb species in the Control treatment, *M. odoratissima* and *Penstemon gracilentus,* were shared with other treatment types (Table A1). Species frequency ranks were not the same across treatments. Only one of the four most frequently detected shrub species was shared across all treatment types, *Ericameria bloomeri* (Table A2). Only one of the more frequently detected shrub species in the Big Tree treatment was shared with the Control treatment type, while the Pine and Pine with Fire treatments had more species overlap with Control.

3.2. Bumble bees

We captured 212 individual bumble bees of 6 species across all treatment and control plots within the study area (Table 1). *Bombus vancouverensis nearcticus* was captured far more frequently than any other bumble bee species, accounting for 145 (68 %) of all captures. Generally, bumble bees were most abundant in the Pine treatment type when we accounted for sampling differences (Table 1). Two species, *B. melanopygus* and *B. mixtus* had equal or greater abundances in treatments other than the Pine treatment, but both species were very rarely captured during surveys. The two species with substantial numbers of captures, *B. vancouverensis nearcticus* and *B. vosnesenskii*, were both least frequently captured on the Control plots (0.13 and 0 bumble bees/point, respectively) and most commonly captured on the Pine plots (2.16 and 0.7 bumble bees/point, respectively).

We observed a total of 6 bumble bee species in the Pine treatment, 5 species in each of the Big Tree and Pine with Fire treatments, and 2 species in Control. All treatment types had a plurality of points with no bumble species detected (Fig. 3) and the Control plots very rarely had bumble bee detections.

At the sampling point level, all treatments types had significantly greater bumble bee species richness relative to the Control (Table 2). The treatment model with the lowest spatial autocorrelation (Moran's I observed = 0.01, expected = −0.01, p-value > 0.05) was a model with the Treatment term, spatial term, and a zero-inflated Poisson distribution. Bumble bee species richness was significantly negatively related to overstory cover and positively related to an index of flowering plant richness and forb cover at the point level, but not significantly influenced by 3 other vegetation covariates (Table 3, Fig. 4). All models

Table 1

Total number of bumble bee detections by treatment type, uncorrected for sampling differences (Number of captures) and corrected for sampling effort by dividing total number of detections by total number of points sampled (Captures per points sampled). Sampling effort is as follows: Control (N = 45), Big Tree (N = 44), Pine (N = 43), and Pine with Fire (N = 33).

	Number of captures				Captures per points sampled			
Species	Control	Big Tree	Pine	Pine with Fire	Control	Big Tree	Pine	Pine with Fire
B. vancouverensis nearcticus	6	26	93	20	0.13	0.59	2.16	0.61
B. flavidus	0	1	2	1	0	0.02	0.05	0.03
B. insularis	0	0	1	4	0	0	0.02	0.12
B. melanopygus	3	2	3	1	0.07	0.05	0.07	0.03
B. mixtus	0	2	1	0	0	0.05	0.02	0
B. vosnesenskii	0	13	30	3	0	0.3	0.7	0.09
Total	**9**	**44**	**130**	**29**	**0.2**	**1.01**	**3.02**	**1.15**

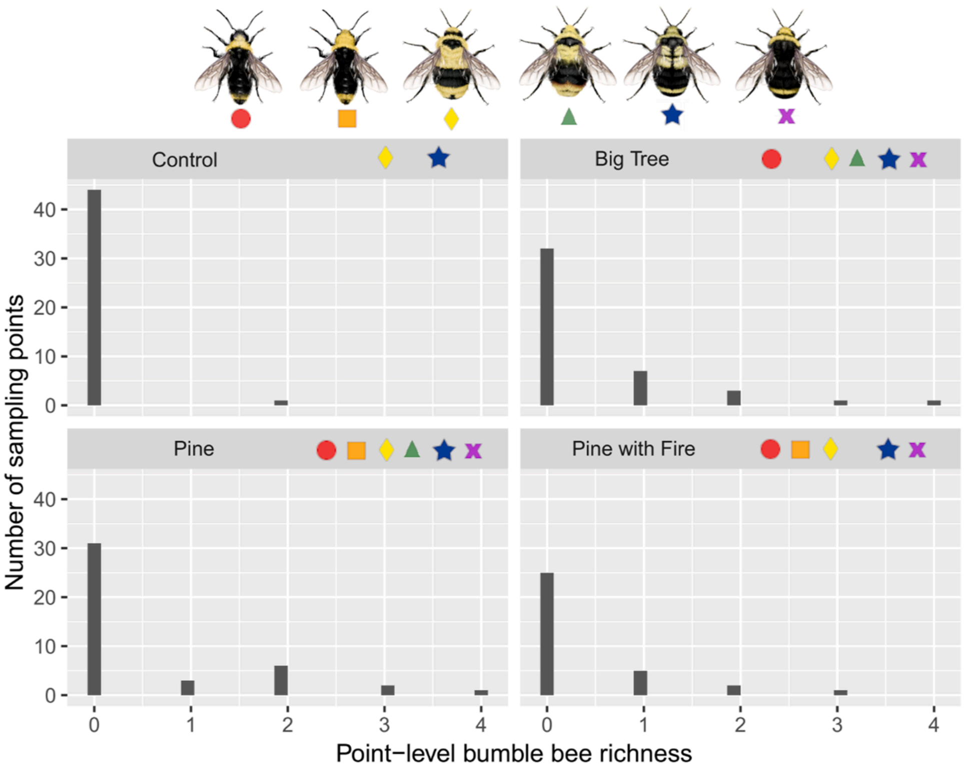

Fig. 3. Histogram of point-level bumble bee richness across all bumble bee sampling points in Control (N = 45), Big Tree (N = 44), Pine (N = 43), and Pine with Fire (N = 33). Bee species symbols are as follows from left to right, red circle – *Bombus flavidus*, orange square – *B. insularis*, yellow diamond – *B. melanopygus*, green triangle – *B. mixtus*, blue star – *B. vancouverensis nearcticus*, purple X – *B. vosnesenskii*. Symbols to right of treatment name indicate which species were detected at least once in a given treatment.

Table 2
Effect of treatment type on bumble bee and butterfly richness and abundance at the sampling point level. Predicted values are derived from their respective models. Number in parentheses represent 95 % confidence intervals. Treatments with values that were significantly different ($p < 0.05$) from the Control are marked with an asterisk. Models that had significant spatial autocorrelation in the final model are reported with "Y" in the last column.

Model type	Control	Big Tree	Pine	Pine with Fire	Significant spatial autocorrelation
Bumble bee richness	0.06 (0.01, 0.44)	0.54 * (0.15, 1.95)	0.59 * (0.15, 2.28)	0.45 * (0.12, 1.74)	N ($p > 0.05$)
Bumble bee abundance	0.13 (0.01, 1.67)	1.32 (0.25, 7.03)	2.87 * (0.55, 14.94)	0.57 (0.08, 4.36)	Y ($p < 0.01$)
Butterfly richness	0.96 (0.55, 1.68)	3.13 * (2.34, 4.20)	2.44 * (1.60, 3.73)	3.18 * (2.27, 4.46)	N ($p = 0.35$)
Butterfly abundance	2.84 (1.51, 5.37)	6.67 * (4.37, 10.19)	5.82 (3.05, 11.12)	7.06 * (4.54, 10.98)	N ($p = 0.15$)

except for the overstory and the intercept-only model had significant spatial autocorrelation, but the effect appeared to be marginal for at least two of these models. Overstory cover and flowering plant richness were significantly negatively correlated (Pearson's R = −0.37, $p < 0.001$).

Only one treatment type, Pine ($p < 0.05$), had significantly greater bumble bee abundance relative to the Control, however spatial autocorrelation was significant in the model residuals (Moran's I observed = 0.04, expected = −0.01, p-value < 0.01). A zero-inflated Poisson and a random Plot effect provided the best model fit for the Treatment effect model, but could not resolve the spatial relatedness. Average predicted bumble bee abundance was significantly greater at Pine treatment points relative to Control points and Big Tree and Pine with Fire treatments had greater abundance, but did not significantly differ from the Control (Table 2). Bumble bee abundance was significantly positively related to flowering plant richness, forb cover, shrub cover, and herbaceous cover (Table 4, Fig. 5). However, spatial autocorrelation was present to varying extents in all abundance models, which may increase the likelihood of a significant covariate effect. The midlayer cover model had poor fit and we excluded this model's results.

Bumble bee abundance reached its greatest levels at the highest forb and shrub cover values (Fig. 5) but also increased over the range of flowering plant richness and herbaceous cover values. Of these four covariates, there was strong correlation only between forb cover and herbaceous cover (Pearson's R = 0.63), which suggests that high shrub cover and high flowering plant richness were not mutually exclusive at our study area.

3.3. Butterflies

Across all sampled transects, we detected 267 butterflies of 19 species and 5 higher-level taxa (Table 5). The most frequently detected species by far was *Nymphalis californica*, followed by detections of "Blues" (butterflies that could only be identified to the Lycaenidae family), *Celastrina echo*, and butterflies that could only be identified to the *Speyeria* genus. The remaining species had very few detections. Most species were detected most frequently in non-control plots. This includes *N. californica*, which was detected most frequently in the Big Tree treatment, but second most frequently in the Control plots.

At the transect level, two of three treatments types had significantly greater butterfly species richness relative to the Control (Table 2, Fig. 6). We selected a GLMM model for treatment that included only Treatment type and transect length as covariates, along with a Poisson error distribution because this provided the best model fit and non-significant

Table 3

Effect of vegetation covariates on bumble bee species richness at the sampling point level. Effects are reported for models that had the lowest spatial autocorrelation with the exception of the intercept only model. None of the Midlayer cover and Shrub cover models had non-significant spatial autocorrelation. Y or N in the ZIP column indicates if a model included used a zero-inflated Poisson distribution, or a Poisson distribution. SE represents standard error. Rows with an asterisk beside the covariate effect denote a significant effect ($p < 0.05$). A “Y” in the significant spatial autocorrelation column indicates models with autocorrelation ($p < 0.05$). Covariate effects are reported on the log scale. Models are presented in increasing order of Akaike Information Criterion (AIC) scores.

AIC	ZIP	Covariate	Intercept ± SE	Covariate effect ± SE	Significant spatial autocorrelation
234.6	N	Overstory cover + Spatial	−1.00 ± 0.61	−0.03 * ± 0.01	N (p = 0.47)
240.4	Y	Forb cover	−0.53 ± 0.35	0.06 * ± 0.02	Y (p = 0.04)
241.3	Y	Flowering plant richness	−0.75 ± 0.40	0.28 * ± 0.10	Y (p = 0.02)
247.5	Y	Shrub cover	0.45 ± 0.26	−0.01 ± 0.01	Y (p < 0.01)
251.4	N	Intercept + Plot	−1.75 ± 0.40	NA	N (p = 0.10)
252.7	N	Midlayer cover + Plot	−1.49 ± 0.49	0.00 ± 0.01	Y (p = 0.04)
280.0	Y	Herbaceous cover	0.01 ± 0.30	0.01 ± 0.01	Y (p = 0.01)

spatial autocorrelation (Moran’s I test, observed = 0.01, expected = −0.02, p-value = 0.35). Predicted richness in Big Tree and Pine with Fire treatments was more than 3 times greater than on Control transects (Table 2).

Five of eight vegetation covariates had a significant effect on butterfly richness (Table 6); four had positive effects on butterfly species richness associated with greater covariate values, and one, overstory cover, had a negative effect. The three models with the lowest AIC scores were, in ascending order: herbaceous cover, overstory cover, and the flowering plant richness.

Five of eight vegetation covariates had a significant effect on butterfly abundance at the transect level (Table 6) and of those, forb cover and transect forb richness had marginally significant spatial autocorrelation. Again, as with the butterfly richness models, we found increasing values of all significant vegetation covariates to have a positive effect on abundance with the exception of overstory cover. The three models with the lowest AIC values in ascending order were: flowering plant richness, overstory cover, and forb cover. We used a model that included a random Plot effect and zero-inflated Poisson distribution for the estimation of Treatment effect because it provided the best fit and resulted in non-significant spatial autocorrelation (Moran’s I observed = 0.03, expected = −0.02, p-value = 0.15). Butterfly abundance (all species pooled) was significantly greater in the Big Tree and Pine with Fire treatments relative to Control (Table 2).

Responses to four vegetation covariate values were similar for both butterfly abundance and richness (Fig. 7). We present the predicted responses for these three vegetation values because they were significant

Table 4

Effect of vegetation covariate on bumble bee abundance pooled across all species at the sampling point level. SE represents standard error. Rows with an asterisk beside the covariate effect denote a significant effect ($p < 0.05$). Effects are reported on the log scale. Y or N in the ZIP column indicates if a model included used a zero-inflated Poisson distribution, or a Poisson distribution. Models are presented in increasing order of Akaike Information Criterion (AIC) scores. A “Y” in the significant spatial autocorrelation column indicates models with autocorrelation ($p < 0.05$).

AIC	ZIP	Covariate	Intercept ± SE	Covariate effect ± SE	Significant spatial autocorrelation
336.0	Y	Plant rich + Spatial	−2.35 ± 0.92	0.34 * ± 0.14	Y (p < 0.01)
371.0	Y	Forb + Plot	−0.38 ± 0.54	0.05 * ± 0.01	Y (p = 0.03)
390.0	Y	Shrub + Plot	−0.68 ± 0.62	0.02 * ± 0.01	Y (p = 0.04)
392.2	Y	Herb + Plot	−0.27 ± 0.57	0.01 * ± 0.00	Y (p = 0.02)
395.0	Y	Intercept + Plot	−0.19 ± 0.58	NA	Y (p < 0.01)
396.5	Y	Overstory + Plot	0.00 ± 0.62	0.00 ± 0.01	Y (p = 0.04)

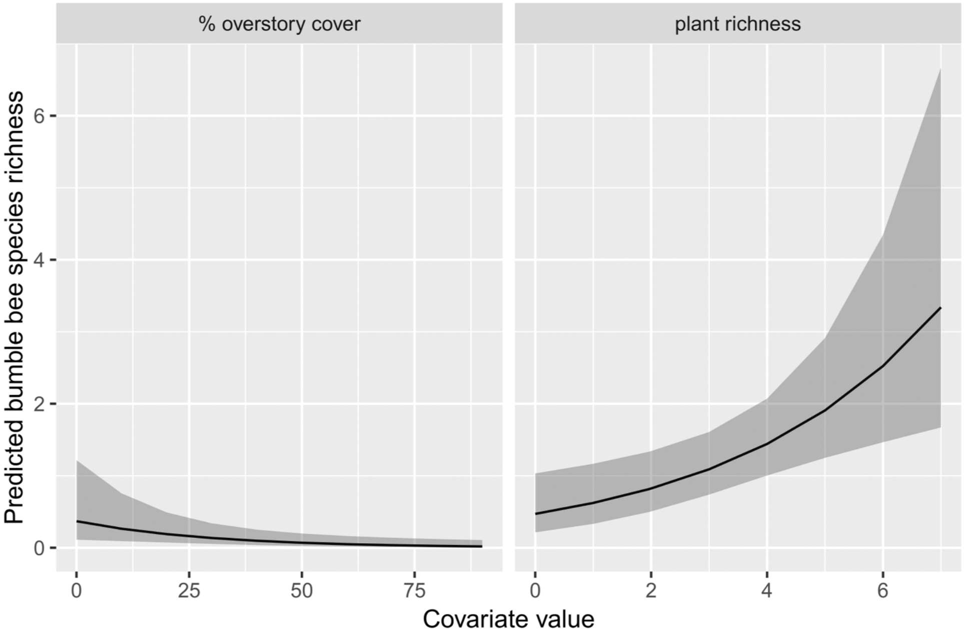

Fig. 4. Predicted bumble bee richness in relation to flowering plant richness (x-axis left panel) and overstory cover (x-axis right panel) at the sampling point level. Solid black line represents the mean predicted value and shading represents the 95 % confidence intervals.

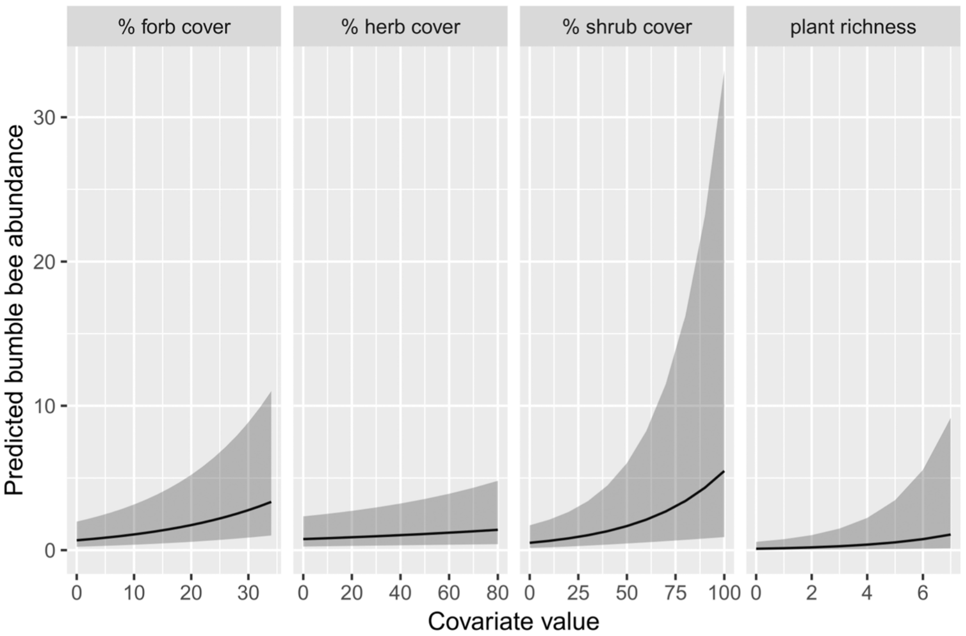

Fig. 5. Predicted relationship between total bumble bee abundance at the point level and four measures of vegetation cover. Solid black line represents the mean predicted value and shading represents the 95 % confidence intervals. Confidence intervals also include error from a Plot-level random effect.

Table 5

Total number of butterfly detections by treatment type, uncorrected for sampling differences (Number of detections) and corrected for sampling effort by dividing total number of detections by total number of transects sampled per treatment type (Detections per transects sampled). (Control, N = 15 transects sampled; Big Tree, N = 15; Pine with Fire, N = 11; Pine, N = 14).

	Number of detections				Detections per transects sampled			
Species	Control	Big Tree	Pine	Pine with Fire	Control	Big Tree	Pine	Pine with Fire
Nymphalis californica	29	35	11	8	1.93	2.33	0.79	0.73
Blues (Lycaenidae family)	0	16	18	10	0.00	1.07	1.29	0.91
Celastrina echo	1	15	6	15	0.07	1.00	0.43	1.36
Speyeria sp.	4	6	8	16	0.27	0.40	0.57	1.45
Papilio eurymedon	0	7	3	4	0.00	0.47	0.21	0.36
Oeneis neyadensis nevadensis	1	3	4	1	0.07	0.20	0.29	0.09
Adelpha californica	0	1	3	2	0.00	0.07	0.21	0.18
Speyeria coronis snyderi	0	2	3	1	0.00	0.13	0.21	0.09
Coenonympha tullia eryngii	1	2	1	1	0.07	0.13	0.07	0.09
Speyeria zerene	2	2	1	0	0.13	0.13	0.07	0.00
Lycaena heteronea ssp.	0	0	1	2	0.00	0.00	0.07	0.18
Speyeria egleis mattooni	0	1	1	1	0.00	0.07	0.07	0.09
Speyeria hydaspe	1	0	1	1	0.07	0.00	0.07	0.09
Callophrys augustinus iroides	0	1	1	0	0.00	0.07	0.07	0.00
Callophrys gryneus	0	1	1	0	0.00	0.07	0.07	0.00
Pyrgus ruralis ruralis	0	0	1	1	0.00	0.00	0.07	0.09
Satyrium saepium	0	0	0	2	0.00	0.00	0.00	0.18
Butterfly (Lepidoptera order)	0	0	0	1	0.00	0.00	0.00	0.09
Limenitis lorquini	0	1	0	0	0.00	0.07	0.00	0.00
Hesperiidae sp.	0	0	0	1	0.00	0.00	0.00	0.09
Polygonia satyrus nearnarsyas	0	1	0	0	0.00	0.07	0.00	0.00
Polygonia sp.	0	0	0	1	0.00	0.00	0.00	0.09
Papilio rutulus	0	1	0	0	0.00	0.07	0.00	0.00
Satyrium behrii behrii	0	0	0	1	0.00	0.00	0.00	0.09
Total	**39**	**95**	**64**	**69**	**2.60**	**6.33**	**4.57**	**6.27**

effects in both the richness and abundance models. Butterfly richness increased most rapidly with forb cover, increasing from 1.9 species at 0 % forb cover to 4.9 species at 18 % forb cover. Butterfly abundance also increased most rapidly for forb cover, increasing from 4.0 individual butterflies at 0 % forb cover to 11.1 individuals at 18 % forb cover. All three of the plotted vegetation covariates have strong correlation to each other. Flowering plant richness is significantly correlated with both forb and overstory cover (Pearson's R: 0.43 and −0.47 respectively).

4. Discussion

The forest treatments applied in our study area had substantial effects on the richness and abundance of bumble bees and butterflies approximately 20 years after treatment. We found greater richness (though sometimes not significant) of both taxa within treated plots. Bumble bee abundance was significantly greater in Pine treatment relative to Control. Butterfly abundance was significantly greater in all treatments relative to Control. We note that in some instances, mostly the bumble bee models, spatial autocorrelation in model residuals

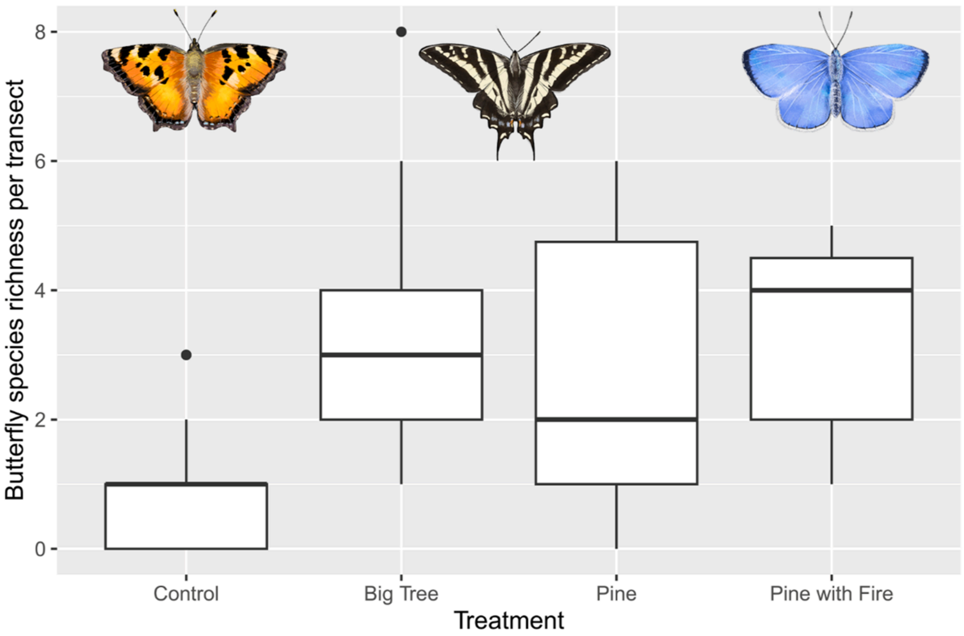

Fig. 6. Transect-level butterfly species richness in response to forest treatments. Center bold horizontal line represents median richness, top and bottom of box the first and third quartiles, respectively. Three of the five most common butterfly species are presented atop the plot and are from left to right as follows: *Nymphalis californica*, *Papilio eurymedon, and Celastrina echo*.

Table 6
Effect of vegetation covariates on butterfly species richness and abundance (denoted in the model type column) at the transect level. Models that used a zero-inflated Poisson distribution with intercept only are given a "Y" under the ZIP column. Models that had significant spatial autocorrelation in the residuals have the p-value of a Moran's I test reported in the Spatial Effect column. Models that had a random plot effect included have "+ Plot" added to the Covariate name. Models are presented in increasing order of Akaike Information Criterion (AIC) scores. A "Y" in the significant spatial autocorrelation column indicates models with autocorrelation ($p < 0.05$).

Model Type	AIC	ZIP	Covariate	Intercept ± SE	Transect length effect ± SE	Covariate effect ± SE	Significant spatial autocorrelation
Richness	211.5	Y	Herbaceous cover	1.27 ± 2.20	0.00 ± 0.01	0.03 * ± 0.01	N ($p > 0.05$)
Richness	213.2	Y	Overstory cover	2.06 ± 2.20	0.00 ± 0.01	−0.01 * ± 0.01	N ($p > 0.05$)
Richness	217.5	N	Flowering plant richness	1.17 ± 2.09	0.00 ± 0.01	0.19 * ± 0.07	N ($p > 0.05$)
Richness	217.9	Y	Forb cover	3.42 ± 2.58	"−0.01 ± 0.01	0.05 * ± 0.02	N ($p > 0.05$)
Richness	220.5	Y	Midlayer cover	1.81 ± 1.93	0.00 ± 0.00	0.01 * ± 0.00	N ($p > 0.05$)
Richness	220.6	Y	Transect shrub richness	2.43 ± 2.93	0.00 ± 0.01	0.20 ± 0.11	N ($p > 0.05$)
Richness	222.3	Y	Shrub cover	1.82 ± 1.90	0.00 ± 0.00	0.01 ± 0.00	N ($p > 0.05$)
Richness	223.4	Y	Intercept	2.43 ± 2.22	0.00 ± 0.01	NA	N ($p > 0.05$)
Richness	224.9	Y	Transect forb richness	1.98 ± 2.06	0.00 ± 0.01	0.06 ± 0.08	N ($p > 0.05$)
Abundance	289.3	N	Flowering plant richness + Plot	0.81 ± 0.21	NA	0.35 * ± 0.07	N ($p > 0.05$)
Abundance	297.6	Y	Overstory + Plot	2.38 ± 0.23	NA	−0.02 * ± 0.01	N ($p > 0.05$)
Abundance	301.1	Y	Forb + Plot	1.38 ± 0.20	NA	0.06 * ± 0.02	Y ($p = 0.04$)
Abundance	305.7	Y	Herb + Plot	1.60 ± 0.20	NA	0.01 ± 0.01	N ($p > 0.05$)
Abundance	306.0	Y	Shrub + Plot	1.64 ± 0.17	NA	0.00 ± 0.00	N ($p > 0.05$)
Abundance	306.1	Y	Midlayer + Plot	1.65 ± 0.24	NA	0.00 ± 0.00	Y ($p = 0.03$)
Abundance	307.6	N	Transect shrub rich + Plot	1.37 ± 0.16	NA	0.23 * ± 0.09	N ($p > 0.05$)
Abundance	311.3	N	Transect forb rich + Plot	1.33 ± 0.22	NA	0.11 * ± 0.08	N ($p > 0.05$)
Abundance	311.4	N	Intercept + Plot	1.54 ± 0.17	NA	NA	Y ($p = 0.02$)

indicates some risk of overemphasizing the magnitude and significance of effects. Nevertheless, it appears that forest management actions designed to restore more natural forest structure and composition can also help maintain or improve invertebrate pollinator diversity and abundance.

4.1. *Vegetation structure results*

The differences that we observed in bumble bee and butterfly diversity and abundance corresponded to the differences in vegetation structure and plant community composition that resulted from the forest treatments implemented two decades prior. Some of the more substantial changes in vegetation structure were reduced forest overstory and greater flowering plant richness in all treatment types relative to Control, with greatest effects observed in the Pine treatment type. Understory plant species richness has similarly been shown to increase after thinning treatments elsewhere in dry conifer forests (Dodson et al., 2008). In our study, shrub cover was significantly greater relative to Control in Pine and Big Tree treatments, but not Pine with Fire treatments, presumably because periodic prescribed fire treatments slowed shrub establishment or removed shrubs that had established. Shrub cover often slightly declines after initial thinning and burning treatment due to mechanical disturbance of established shrubs, then increases 5–10 years following treatment (Korb et al., 2020).

4.2. *Bumble bee and butterfly richness*

The greater bumble bee and butterfly richness we observed in thinned and or burned treatment areas is largely in agreement with previous studies of these insect groups in forests thinned by mechanical treatment

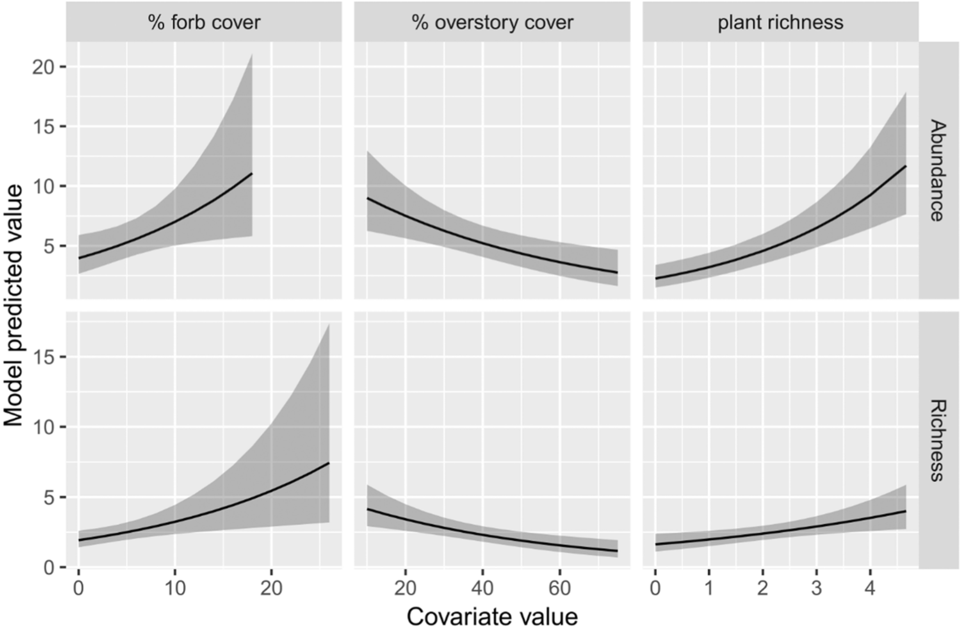

Fig. 7. Predicted butterfly abundance (upper panel row) and richness (lower panel row) in response to vegetation covariates (x-axis) that were significant for both abundance and richness. Solid black line denotes the predicted mean value and shaded region the 95 % confidence interval around the prediction. X-axes are scaled to the minimum and maximum of each observed covariate value. X-axis for abundance forb cover plot spans to values represented in the data subset used for abundance modeling. Y-axes are scaled are scaled for each row.

(Roberts et al., 2017; Waltz and Covington, 2004) or wildfire (Mason et al., 2021; Roberts et al., 2017; Tarbill et al., 2023). In a study of bee richness and abundance in control, burned, thinned, or thinned and burned forests in hardwood forests in Illinois, bee diversity and abundance was found to be greatest in the thinned and burned treatments (Chase et al., 2023). Bee richness was demonstrated to be highest in forests one year after treatment with prescribed fire relative to three years post treatment, and untreated regions (Gelles et al., 2023). Similarly, a time-series study of bee richness and abundance relative to time-since clearcut forest harvest found that both richness and abundance declined with stand age (Zitomer et al., 2023). Likewise in our study, reduced overstory cover (more open stands) resulted in greater flowering plant richness, which supported a greater variety of bumble bee and butterfly species using understory plants. Indeed, some form of flowering plant richness and overstory were strong predictors of bee and butterfly richness. Richness of butterflies is often positively related to floral richness (Keele et al., 2023; Potts et al., 2009). Although we did not examine temporal trends in bumble bee and butterfly richness after forest treatment, other research has suggested bee abundance and richness in regenerating Douglas-fir forest may peak around five years after clearcutting and then decline in the following years as canopy cover increases and understory plant richness declines (Rivers and Betts, 2021). Therefore, it is notable that we still found a discernable difference in bumble bee and butterfly richness 20 years after treatment.

4.3. Bumble bee and butterfly abundance

Bumble bee abundance was significantly greater relative to Control only in the Pine treatment, but was non-significantly greater in the remaining treatments. Alternatively, butterfly abundance was significantly greater in all treatment types relative to Control. Bee abundance is positively associated with forest treatments that result in more open canopy (Gelles et al., 2023, Eckerter et al., 2022). Some studies have found no significant relationship between bee abundance and forest thinning combined with wildfire (Gelles et al., 2022). A meta-analysis of the effect of forest management on pollinators found that pollinator abundance (including bees and butterflies) was mostly positively or neutrally effected by prescribed fire, logging, and a combination of both fire and logging (Glenny et al., 2022) likely due to reduction in canopy cover which led to increased understory flowering plant richness. Indeed, in our study we found that flowering plant richness (for bumble bees) and flowering plant richness and flowering shrub richness (for butterflies) were among the most influential covariates on abundance. Interestingly, shrub cover alone had a non-significant effect on butterfly abundance, perhaps because this was a measure of shrub cover and not necessarily shrubs that were flowering at the time of the survey. Also, having a variety of flowering shrub types supported a greater variety of butterfly species and presumably a greater overall abundance of butterflies as a result.

4.4. Forests treatments may support recovery or stabilization of pollinator communities

Forest thinning has been shown to reduce wildfire risk (e.g., Loudermilk et al., 2014) and, when thinning is applied in stands that are artificially overstocked due to long-term fire suppression or other interventions, may provide other ecological benefits as well (Knapp et al., 2017). Our results demonstrating that mechanical thinning and prescribed fire treatments in a second-growth conifer forest of northern California had a positive effect on bumble bee and butterfly communities corroborate that management actions that thin forests can serve multiple management objectives. We note, however, that our sampling took place once during a season and did not span multiple years, so our results may not be representative of pollinator responses in a variety of temperature and precipitation scenarios. Additionally, because edges of treatment plots were sometimes in close proximity to one another in our study area (in one extreme case separated by 165 m, though in most cases >250 m) there may be some unmodeled landscape effects that partially confounded the local treatment effects. Pollinator communities are well known to be in decline across North America and throughout the world (Koh et al., 2016; Powney et al., 2019) due to a variety of factors including climate change (Soroye et al., 2020). However, one factor that can be more readily addressed at local and regional scales is the restoration of more open forests with gaps in the overstory that benefit flowering plants in the understory, and thus support the insect pollinators that both depend on them and play a vital role in propagating them. Assisted migration may present another avenue for sustaining pollinator populations in forests under climate change. Forestry research has focused on the assisted migration of overstory tree species (Pedlar et al., 2012), yet consideration of the broader plant community may be necessary to sustain other elements of ecosystem integrity and key pollinator species of concern (Sáenz-Romero et al., 2020).

Despite the clear benefits of forest treatments to pollinators in our study, we urge caution in generalizing our results to assume that all forms of forest thinning will be beneficial for pollinators. For instance, forest treatment that involves extensive shrub removal or even herbicide use to inhibit the regrowth of shrubs is unlikely to confer similar benefits to the treatments we investigated (Loffland et al., 2017). The Goosenest AMA only incorporated mechanical and prescribed fire treatments rather than using herbicides. In addition to reducing floral resources provided by shrubs, herbicide application may incidentally kill herbaceous flowering plants and lower non-shrub understory plant richness, with likely deleterious effects for many insect pollinators. Zhang and Finley (2024) partially attributed declines in understory plant diversity in ponderosa pine plantations treated with herbicide to an indirect effect of greater overstory tree cover, which could be mitigated through thinning treatments. It should be noted, however, that shrub removal is not always negative for pollinators, especially where invasive shrubs have become dominant and reduced the diversity and extent of the herbaceous understory community (Ulyshen et al., 2022).

4.5. Implications of treatment for other wildlife

While thinning and prescribed burning treatments may provide beneficial vegetative communities for bumble bees and butterflies, forests with more open canopy may be detrimental to other wildlife taxa that prefer closed-canopy, late-seral forest. For example, in thinned conifer forests of the western US, some bird species, such as Hermit Warbler (*Setophaga occidentalis*) and Swainson's Thrush (*Catharus ustulatus*), declined in the near term (<6 years) after treatments, but subsequently rebounded (15 years post-treatment), whereas species such as Hutton's Vireo (*Vireo huttoni*) remained less abundant in thinned areas versus controls in the long term (Cahall et al., 2013). Thinning and prescribed fire can also have a mix of both positive and negative effects on small mammals (Converse et al., 2006). Perhaps the best approach to maintain wildlife diversity on the landscape is by maintaining a heterogenous mix of vegetation structure and composition (Chaudhary et al., 2016; Fedrowitz et al., 2014) rather than managing towards a single metric, although later-seral attributes could remain priorities for retention and development where they have become rare due to human activities.

4.6. Management implications

Our study demonstrated that the three forest thinning treatments applied in our study area resulted in greater species richness and abundance of both bumble bees and butterflies – with the strength of the effect similar across all treatments. These changes appeared linked to reduced overstory cover and resulting increases in the diversity and cover of understory floral resources. We conclude that forest thinning in the manner described herein can be beneficial to the invertebrate pollinator community even while fulfilling more diverse management objectives, such as reducing fuel loads through thinning. Our work adds a longer-term perspective to the existing literature examining the effects of forest treatments on pollinator communities, and provides evidence that even 20 years post treatment pollinators still preferentially use treated forests. We encourage foresters and ecologists to include pollinator sampling in their management plans to better understand these important dynamics across a range of conditions and years since treatment.

CRediT authorship contribution statement

Cole Jerry S.: Writing – original draft, Methodology, Formal analysis. **Looney Christopher E.:** Writing – review & editing, Project administration, Conceptualization. **Loffland Helen L.:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Siegel Rodney B.:** Writing – original draft, Project administration, Funding acquisition, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1

Four of the most frequently detected forb species within each treatment type. Numbers in each row denote the first most frequently detected (1) to the fourth most frequently detected (4) forbs species per treatment. In instances where species were detected equally multiple rows received the same rank number

Forb species	Control	Big Tree	Pine	Pine with Fire
Monardella odoratissima	1	1	1	1
Clarkia rhomboidea		2		3
Kelloggia galioides		3	2	4
Cryptantha spp.		4		
Horkelia fusca				2

(*continued on next page*)

Table A1 (*continued*)

Forb species	Control	Big Tree	Pine	Pine with Fire
Penstemon gracilentus	2			3
Fragaria virginiana			3	3
Pedicularis semibarbata	3			
Hieracium albiflorum	4			
Fragaria spp.			3	
Hackelia californica			4	
Phlox diffusa			4	

Table A2
Four of the most frequently detected shrub species within each treatment type. Numbers in each row denote the first most frequently detected (1) to the fourth most frequently detected (4) forbs species per treatment. In instances where species were detected equally multiple rows received the same rank number

Shrub species	Control	Big Tree	Pine	Pine with Fire
Arctostaphylos patula		1	1	2
Purshia tridentata		2		
Ceanothus prostratus		3	4	
Ericameria bloomeri	2	4	1	1
Symphoricarpos mollis	1		2	4
Apocynum androsaemillefolium	3			3
Ribes cereum	4		3	2

Data availability

Data will be made available on request.

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