ORIGINAL RESEARCH

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# Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest

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**Abstract**

The use of timber harvest residue as an energy source is thought to have environmental benefits relative to food-based crops, yet the ecological impact of this practice remains largely unknown. We assessed whether the abundance and diversity of wild bees (Apoidea) were influenced by the removal of harvest residue and associated soil compaction within managed conifer forest in western Oregon, USA. We sampled bees over two years (2014–2015) on study plots that were subjected to five treatments representing gradients in removal of harvest residue and soil compaction. We collected >7,500 bee specimens from 92 distinct species/morphospecies that represented five of the seven bee families. We trapped 3x more individuals in the second year of the study despite identical sampling effort in both years, with most trapped bees classified as ground-nesting species. Members of the sweat bee family (Halictidae) comprised more than half of all specimens, and the most abundant genus was composed of metallic green bees (*Agapostemon*, 33.6%), followed by long-horned bees (*Melissodes*, 16.5%), sweat bees (*Halictus*, 15.9%), and bumble bees (*Bombus*, 13.6%). In both years, abundance and observed species richness were greatest in the most intensive harvest residue treatment, with other treatments having similar values for both measures. Our study indicates that early successional managed conifer forest that has experienced removal of harvest residue can harbor a surprising diversity of wild bees, which are likely to have important contributions to the broader ecological community through the pollination services they provide.

**KEYWORDS**
bees, Douglas fir, forest biomass removal, intensive forest management, pollinator, timber harvest residue

## 1 | INTRODUCTION

Global population growth has led to an increased need for wood products, with production expected to more than double in the coming decades to satisfy societal demands (FAO, 2016). As technological innovations have advanced, there has been a concomitant expansion in how wood extracted from production forests can be used. For example, the development of transportation fuels from forest products has garnered increased attention given concerns about greenhouse gas production and an historic reliance on internationally sourced fossil fuels (Perlack et al., 2005). Production of biofuels created from renewable materials has expanded in recent years to include materials that have traditionally gone unused during harvest

operations (Riffell, Verschuyl, Miller, & Wigley, 2011; Root & Betts, 2016; Verschuyl, Riffell, Miller, & Wigley, 2011) including timber harvest residue (hereafter, harvest residue), such as logging slash and tree boles (Gan & Smith, 2006). The improved capacity to use harvest residue for biofuel feedstock has, in turn, allowed for the use of trees and tree residuals that have died from large-scale natural disturbance events (e.g., wildfire and insect kill) in addition to wood materials generated from other activities, including timber harvest and municipal solid waste (Barrette et al., 2015). This has resulted in an expanded biofuel market in North America and beyond, with expectations that this sector will increase in future decades (Perlack et al., 2005) and lead to a reduction in fossil fuel reliance and greenhouse gas emissions (Chu & Majumdar, 2012; Hill, Nelson, Tilman, Polasky, & Tiffany, 2006).

Despite their promise as a green energy source, the growing demand for harvest residue requires careful consideration of the potential trade-offs that may arise between the benefits of incorporating previously unused sources for biofuel production and the potential negative impacts of such practices on biodiversity and ecosystem function. To date, the vast majority of investigations to examine these trade-offs have focused on biofuel feedstock production within short-rotation systems, such as agricultural crops that are planted annually (Bennett, Meehan, Gratton, & Isaacs, 2014; Jager, Wang, Kreig, Sutton, & Busch, 2017; Stoms, Davis, Jenner, Nogeire, & Kaffka, 2012), with less attention paid to bioenergy production from perennial crops (Donner, Wigley, & Miller, 2017; Fritts et al., 2015; Riffell et al., 2011; Verschuyl et al., 2011). Nevertheless, empirical studies of the ecological impacts of nonfood feedstocks are needed given the expectation they have lower impacts on environmental health relative to high-input, food-based feedstock (e.g., corn and soybeans; Hill et al., 2006). Assessing the consequences of removing harvest residue at the time of harvest is of particular importance because this practice may have consequences for biodiversity in early successional forest (Root & Betts, 2016). These young forests are among the scarcest in North America (Askins, 2001; King & Schlossberg, 2014; Litvaitis, 1993; Thomas, Franklin, Gordon, & Johnson, 2006), yet they serve as critical habitat for an especially large pool of organisms, including a wide range of insect pollinators (Hanula, Ulyshen, & Horn, 2016) and groups like saproxylic beetles (Kaila, Martikainen, & Punttila, 1997), some of which are classified as sensitive or threatened (Andersson, Hjalten, & Dynesius, 2015; Djupstrom, Weslien, Hoopen, & Schroeder, 2012).

Insect pollinators, which include bees, flies, beetles, butterflies, and moths in temperate North America, comprise an ecologically and economically important group whose global pollinator services have been valued at >$100B annually (Gallai, Salles, & Settele, 2009). Insect pollinators are responsible for fertilizing nearly 90% of the world's ~350,000 flowering plants and therefore play a pivotal role in promoting biodiversity and maintaining food supplies at a global level (Calderone, 2012; Hoehn, Tscharntke, Tylianakis, & Steffan-Dewenter, 2008; Ollerton, Winfree, & Tarrant, 2011). Insect pollinators are often found within early successional forests (Hanula et al., 2016) and therefore have high potential to be impacted by removal of harvest residue during timber harvest operations. Empirical studies have recently demonstrated that the ecosystem services provided by pollinators can be strongly influenced by the loss of just a single pollinator species (Brosi & Briggs, 2013; Kaiser-Bunbury, Muff, Memmott, Muller, & Caflisch, 2010). This finding, coupled with long-term declines in managed honeybee (*Apis mellifera*) populations (NRC, 2007), has intensified concern regarding pollinators and their habitats (Allen-Wardell et al., 1998; Potts et al., 2010) and made it imperative to better understand the links between land management practices, pollinator populations, and the ecosystem services they provide (Garibaldi et al., 2011, 2013; Weiner, Werner, Linsenmair, & Bluthgen, 2014).

Among insect pollinators, bees (superfamily Apoidea) are considered to be the most important pollinator group in many systems because they are often numerically dominant and they are the only pollinator group that feeds solely on pollen and nectar throughout their entire life cycle (Brown & Paxton, 2009; Michener, 2007; Winfree, 2010). In temperate forest landscapes, bees are typically restricted to early successional forests where large postharvest influxes of sunlight, soil moisture, and nutrients can make them especially productive sites for flowering plants used by foraging bees (Hanula et al., 2016; Roberts, King, & Milam, 2017; Taki et al., 2013; Winfree, Griswold, & Kremen, 2007). Moreover, the disturbances that lead to early successional forest conditions (e.g., wildfire, timber harvest) can result in exposed soil and increase the amount of dead plant materials that are used by ground- and wood-nesting bees, respectively. Thus, forage and nesting sites, two critical habitat requirements for wild bees, are typically available in early successional forests at levels that can support bee populations (Hanula et al., 2016). Nevertheless, a basic understanding of bees within this forest type is lacking, especially with regard to how the removal of harvest residue influences bee communities. This latter component is of particular importance given the lack of information on this topic and the expected growth in the forest biofuel sector (Perlack et al., 2005).

In this study, we quantified the influence of removing harvest residue on wild bee communities as part of a broader experiment undertaken by the Northwest Advanced Renewables Alliance (NARA, https://nararenewables.org/)

whose primary goal was to test the efficacy of harvest residue as feedstock for alternative jet fuel and coproducts. Jet fuel consumption is expected to increase by 40% over the next 25 years (USEIA, 2017), and as noted above, the use of harvest residue is thought to provide environmental benefits relative to traditional food-based crops that have been produced for biofuel feedstock, such as corn or soybeans (Hill et al., 2006). We assessed wild bee communities across a gradient of management intensity in which the extent of harvest residue removal and soil compaction was experimentally manipulated; both of these factors are expected to influence habitat quality for bees. As most bees are solitary-nesting and place their nests underground (Cane, 1991; Michener, 2007), the removal of harvest residue and resultant exposure of soil has the potential to favor ground-nesting species. In contrast, other species require pithy stems or use existing cavities in wood for nesting (hereafter, cavity-nesting bees; Cane, Griswold, & Parker, 2007), so removal of harvest residue could decrease abundance and diversity of this group through a reduction in the availability of potential nest sites. Thus, we tested the hypothesis that removing greater levels of harvest residue was associated with greater abundance and diversity of ground-nesting bees and lower abundance and diversity of cavity-nesting bees. The way in which soil compaction may impact wild bees is less clear, as ground-nesting bees can dig nests in a wide range of soil types and levels of compactions (Cane, 1991; Michener, 2007) and wood-nesting bees are not directly impacted by soil compaction. Therefore, we did not have any a priori predictions regarding how soil compaction levels would influence bee abundance and diversity. Given the dearth of research regarding how removal of harvest residue influences pollinating insects, our study is the first to investigate the potential impacts of this management action on wild bees and therefore provides information that can be used to evaluate the influence of this practice on a critical component of biodiversity found within intensively managed forests.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

We quantified bee abundance and richness on the western edge of the Cascade Mountains (44.02°N, 122.45°W, 650 masl) as part of the broader NARA study noted above. As the first step in site selection, only forest management units within the vicinity of Springfield, Oregon, that had the following characteristics were considered: (a) scheduled for harvest in spring 2013, (b) composed of uniform soil with low rock content, (c) large enough to contain a minimum of 28 study plots, and (d) could be accessed by heavy equipment needed for implementing experimental

treatments. A pool of 40 sampling units met these criteria, and a single harvest unit south of the Mackenzie River was selected randomly to undergo logistically intensive field experiments. Study plots ($n = 28$), each 0.41 ha, were established on the site prior to harvest, and each plot was randomly assigned to a distinct combination of biomass removal and soil compaction treatments. Specifically, each plot was randomly assigned to one of three biomass removal treatments of increasing intensity: (a) bole removal (i.e., tree boles removed while leaving crowns, felled understory, and forest floor), (b) tree removal (i.e., all aboveground living vegetation removed), or (c) tree and forest floor removal (i.e., all surface organic matter removed and bare soil exposed), as well as one of two levels of soil compaction: (a) no compaction (i.e., trees felled off plot and all cutting occurs off plot) and (b) moderate compaction (i.e., excavator driven systematically across entire plot; see Table 1). We note that the most intensive biomass removal treatment (tree and forest floor removal) could not be undertaken without causing changes to soil bulk density, therefore resulting in five unique treatment combinations. In addition, a subset of plots containing two of the five treatment combinations described above (i.e., tree removal and moderate soil compaction, and tree and forest floor removal and moderate soil compaction) are scheduled to receive supplemental fertilization (i.e., 225 kg N/ha) at approximately 20 years postharvest (i.e., in the year 2033), ultimately resulting in seven unique treatment combinations from three factors (i.e., biomass removal, soil compaction, and fertilization) throughout the full-study schedule. Given the time lag of fertilization treatments, this led us to effectively sample bees on five treatment combinations in the course of the current study, with $n = 4$ replicate plots for three of the treatments that will not be subjected to future fertilization and $n = 8$ replicate plots for two of the treatments, of which half of those plots are scheduled for future fertilization treatments.

### 2.2 | Sampling of bees and floral resources

We surveyed wild bee communities on study plots at three times each during the 2014 (i.e., 1–3 July, 29–31 July, and 19–21 August) and 2015 seasons (i.e., 1–3 July, 29–31 July, and 21–23 August). We adopted this sampling approach because our goal was to sample bee species across the summer flight season while also avoiding collection of foundress bumble bee (*Bombus* spp.) queens to minimize the impact of our sampling on local populations of this group, which is especially well represented in the Pacific Northwest (Williams, Thorp, Richardson, & Colla, 2014). To sample bees, we used unscented blue vane traps, which are highly reflective in the UV-A and UV-B spectra and are proven effective for sampling foraging bees in

**TABLE 1** Description of the five treatment combinations comprising of two factors (biomass removal and soil compaction) whose influence was assessed on wild bee abundance and species richness. Treatment combination codes correspond to organic matter and soil compaction treatments described in Powers et al. (2005), and treatments are listed in the order of increasing intensity (A–E)

| Treatment designation | Treatment description | Biomass removal treatment | Soil compaction treatment |
|---|---|---|---|
| A | Bole removal + no soil compaction | Tree boles removed; crowns, felled understory, and forest floor remain. | Trees were felled off plot, and no heavy equipment run within plot boundary |
| B | Bole removal + moderate soil compaction | Tree boles removed; crowns, felled understory, and forest floor remain. | Entire plot compacted to an intermediate bulk density |
| C | Tree removal + no soil compaction | All aboveground living vegetation removed; forest floor retained. | Trees were felled off plot, and no heavy equipment run within plot boundary |
| D | Tree removal + moderate soil compaction | All aboveground living vegetation removed; forest floor retained. | Entire plot compacted to an intermediate bulk density |
| E | Tree and forest floor removal + moderate soil compaction | All surface organic matter removed; bare soil exposed. | Entire plot compacted to an intermediate bulk density |

open habitats (Stephen & Rao, 2005, 2007 ). On each plot, we affixed each of three dry traps (i.e., containing no fluid preservative) to the top of a 1.5 m high metal t-post that was located 5 m equidistant from the center of each study plot. We placed the first blue vane trap along a randomly selected azimuth originating from the plot center, with each additional trap situated 120° from the previous azimuth to provide full coverage of the plot. We left blue vane traps in place during each sampling round for approximately 48 hr, after which we move them into a cooler containing dry ice to kill, by freezing, all bees captured within each trap. Collected bees were then sorted into separate containers for pinning and identification at Oregon State University. We note that although our lethal sampling approach had the potential to reduce local bee populations, this was unlikely for two reasons. First, a recent study that assessed the impacts of lethal removal did not detect an effect of regular and repeated lethal trapping on bee communities (Gezon, Wyman, Ascher, Inouye, & Irwin, 2015). Of note, that study collected bees over a longer time period (5 years) and more frequently (5–9 times per season) than the sampling we undertook in our study (Gezon et al., 2015). Second, if our sampling methodology substantially reduced local populations, we would have been unlikely to document a 3-fold increase in bee abundance in the second year of sampling (see Results).

During each sampling round, we also quantified floral resources within a 2 × 10 m belt transect that was centered on each blue vane trap. For analysis, we summed the total number of individual flowers/inflorescences that were in bloom during and available to bees for each blue vane trap for use as a covariate in analysis (hereafter floral density). Study plots were routinely sprayed with herbicide during the growing season in both years because of broader

project objectives, resulting in very low densities of flowering plants throughout our study.

In addition to using blue vane traps to sample bees, which is thought to target foraging individuals (Stephen & Rao, 2007), we also used emergence traps to capture ground-nesting bees as they emerged from nest chambers in the soil. To do this, we selected $n = 10$ stands at both extremes of the treatment intensity continuum; traps were assigned to $n = 4$ stands in treatment A (boles removed and no soil compaction) and $n = 6$ stands in treatment E (tree and forest floor removal, and moderate soil compaction). Prior to deploying emergence traps, we gridded each stand into 1 × 1 m squares; we then randomly selected two squares for trap placement, with a single black and white emergence trap (60 × 60 × 60 cm; www.bugdorm.com) put in place on July 1, 2014, within each selected grid square. Each trap contained a collecting vial at the top of the trap that held alcohol, and flaps at the bottom edge of traps were covered with heavy chains and buried with soil and/or woody debris to prevent escape by insects that emerged in the trap. We removed specimens from collecting vials regularly throughout the field season, adding additional alcohol as needed. Traps remained in place until October 3, 2014, when they were removed, resulting in a total of 1,900 trap-days (95 days/trap × two traps/stands × 10 stands). Given the modest yield from emergence traps (see 6), we chose not to use sample bees in this manner during the second year of the study.

We identified each bee to genus using keys from Michener (2007) and Stephen, Bohart, and Torchio (1969) before identifying species/morphospecies using regional synoptic collections and the following genera-specific local keys: *Agapostemon*, *Anthophora*, and *Ceratina*: Discoverlife.org; *Bombus*: Williams et al., 2014; *Halictus*: Roberts,

1973; *Colletes*: Stephens, 1954; *Osmia*: Sandhouse, 1939). No species keys were available for some genera (i.e., *Nomada* and *Lasioglossum* [*Dialictus*]) for our region, so we were restricted to identifying individuals to morphospecies in these groups. Voucher specimens from the study are housed in the Oregon State University Arthropod Collection in Corvallis, OR (https://osac.oregonstate.edu/).

## 2.3 | Statistical analysis

We initially tested for treatment effects on abundance and observed species richness using the PROC GLIMMIX modeling function in SAS v.9.4. We attempted to model our data using Poisson regression, but they were overdispersed; therefore, we used a negative binomial distribution with a log link which better fit our data. We constructed similar models for two separate response variables (abundance and species richness) that contained treatment (five levels), year (two levels), sampling round (three levels), floral density, and a treatment × year interaction as fixed effects, with individual stand as a random effect. To calculate stand-level abundance, we summed all individuals captured in all traps on a stand in each year, and we used the same approach to calculate observed species richness at the stand level. Finally, we used library "ncf" in the R statistical environment to test for spatial autocorrelation for measures of abundance and richness between study plots over the course of the study.

Observed levels of species richness may not reflect true community composition, so we also evaluated observed measures compared to robust estimators of species richness. We used the program EstimateS (Colwell, 2013) to calculate abundance-based species richness estimates using a nonparametric estimator, Chao1 (Chao, 1984), with asymmetric 95% confidence intervals (CIs). We used the classic estimator because it performs better when CV for abundance distribution >0.5, which was the case with some of our data (J. W. Rivers, C. L. Mathis, A. R. Moldenke & M. G. Betts, unpublished data). We also used EstimateS (Colwell, 2013) to construct rarefaction curves to standardize a comparison of data among treatments, and we extrapolated richness estimates using the procedures of Colwell et al. (2012) to evaluate how species richness was expected to change with additional sampling effort. We also used program EstimateS to calculate Morisita–Horn index to assess the proportion of shared species within each treatment between successive years of sampling. To do this, we first calculated a Morisita–Horn index value for each pairwise sample combination within each treatment within each year ($n = 70$ index values for treatments 1–3 and $n = 280$ index values for treatments 4–5 in each year); we then calculated a mean from all index values for each treatment × year combination. Unless otherwise noted, we report marginal least-squares means and their associated 95% confidence intervals (CIs), with effect sizes as marginal model-derived parameter estimates ($\hat{\beta}$) and their associated 95% CIs; both of these estimates were taken as the mean value for each covariate within each model. We did not use corrections for our pairwise comparisons in our models, as such approaches can lead to unacceptably high type II errors (Nakagawa, 2004).

## 3 | RESULTS

### 3.1 | Descriptive bee community measures

Over the course of our study, blue vane traps were in place for 1,008 trap-days (i.e., 28 stands × 3 traps/stand × 2 days/trap/sampling round × 3 sampling rounds/year × 2 years); during this period, we trapped 7,536 individual bees comprising 92 distinct species/morphospecies in five families (Table 2). The majority of captured bees were classified into Halictidae (60.1%) and Apidae (38.8%), with the remaining representing Megachilidae (75 individuals), Andrenidae (two individuals), and Colletidae (one individual). The non-native European honeybee (*Apis mellifera*) comprised 7.8% of our sampled bees; however, its inclusion did not affect our treatment-based results (J. W. Rivers, C. L. Mathis, A. R. Moldenke & M. G. Betts, unpublished data), so we retained this species in all of our analyses.

Bee abundance peaked during the second sampling period in the first year and the first sampling period in the second year; observed species richness was greatest during the second sampling period in both years (Table 3). Bee abundance was 3x greater in the second year of the study (2014: $n = 1,891$, 2015: $n = 5,645$) despite having identical effort and sampling at the same time of the season in both years. Observed species richness increased by approximately 20% in the second year of the study (2014: $n = 69$ species, 2015: $n = 83$ species), with 60 species captured at least once in both years. Species composition varied between years; 9.8% of the taxa we captured in 2014 were not observed in 2015, and 25.0% of the taxa we captured in 2015 were not observed in the initial year of sampling. With respect to nesting substrate, the vast majority of species that we captured that tended their own nests (i.e., were not cleptoparasites) were ground-nesting species (87.1%), with 4.4% representing *Bombus* spp. that nest both above and belowground and <1% of classified as cavity-nesting species. Less than 1% of bees captured in blue vane traps were classified as cleptoparasites, including species in the genera *Coelioxys* (two species, two individuals), *Nomada* (two species, 28 individuals), *Bombus* (*Psithyrus*) (one species, one individual), *Sphecodes* (five species, eight individuals), and *Triepeolus* (one species, 15 individuals).

**TABLE 2** Abundance of bee species captured with blue vane traps in each of the five treatments and across the entire study and their nest site location, with the number of study plots listed parenthetically for each treatment. See Table 1 for treatment description of treatment designations

| Family | Species | Nest location | Treatment | | | | | Total |
| | | | A (n = 4) | B (n = 4) | C (n = 4) | D (n = 8) | E (n = 8) | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Andrenidae | *Andrena prunorum* | Ground[1] | 0 | 0 | 0 | 1 | 0 | 1 |
| Andrenidae | *Andrena trevoris* | Ground[1] | 0 | 0 | 1 | 0 | 0 | 1 |
| Apidae | *Anthophora urbana* | Ground[1] | 0 | 3 | 7 | 7 | 4 | 21 |
| Apidae | *Apis mellifera* | Cavity/hive[1] | 76 | 64 | 49 | 160 | 239 | 588 |
| Apidae | *Bombus appositus* | Ground/aboveground[2] | 2 | 2 | 2 | 6 | 5 | 17 |
| Apidae | *Bombus caliginosus* | Aboveground/ground[2] | 36 | 45 | 36 | 71 | 86 | 274 |
| Apidae | *Bombus fervidus* | Ground[2] | 2 | 3 | 2 | 3 | 7 | 17 |
| Apidae | *Bombus flavifrons* | Ground[2] | 0 | 0 | 0 | 1 | 1 | 2 |
| Apidae | *Bombus griseocollis* | Aboveground/ground[2] | 1 | 1 | 1 | 1 | 0 | 4 |
| Apidae | *Bombus mixtus* | Ground/aboveground[2] | 4 | 3 | 3 | 10 | 14 | 34 |
| Apidae | *Bombus nevadensis* | Ground/aboveground[2] | 0 | 0 | 1 | 0 | 0 | 1 |
| Apidae | *Bombus sitkensis* | Ground[2] | 1 | 1 | 1 | 2 | 1 | 6 |
| Apidae | *Bombus vosnesenskii* | Ground[2] | 100 | 100 | 113 | 176 | 181 | 670 |
| Apidae | *Bombus (Psithyrus) suckleyi* | Cleptoparasite[2] | 0 | 0 | 0 | 0 | 1 | 1 |
| Apidae | *Ceratina acantha* | Stem[1] | 1 | 1 | 1 | 2 | 1 | 6 |
| Apidae | *Ceratina pacifica* | Stem[1] | 0 | 1 | 0 | 0 | 1 | 2 |
| Apidae | *Melissodes agilis* | Ground[1] | 0 | 0 | 0 | 1 | 0 | 1 |
| Apidae | *Melissodes communis* | Ground[1] | 79 | 67 | 70 | 140 | 167 | 523 |
| Apidae | *Melissodes lupina* | Ground[1] | 6 | 3 | 3 | 12 | 51 | 75 |
| Apidae | *Melissodes metenua* | Ground[1] | 46 | 10 | 20 | 56 | 137 | 269 |
| Apidae | *Melissodes microsticta* | Ground[1] | 22 | 15 | 12 | 34 | 46 | 129 |
| Apidae | *Melissodes rivalis* | Ground[1] | 22 | 36 | 15 | 77 | 91 | 241 |
| Apidae | *Melissodes robustior* | Ground[1] | 0 | 1 | 0 | 0 | 1 | 2 |
| Apidae | *Nomada mutans* | Cleptoparasite[1] | 1 | 3 | 3 | 9 | 11 | 27 |
| Apidae | *Nomada* sp. 1 | Cleptoparasite[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Apidae | *Triepeolus* sp. 1 | Cleptoparasite[1] | 1 | 2 | 3 | 4 | 5 | 15 |
| Colletidae | *Colletes kincaidii* | Ground[1] | 1 | 0 | 0 | 0 | 0 | 1 |
| Halictidae | *Agapostemon texanus* | Ground[1] | 0 | 0 | 0 | 0 | 3 | 3 |
| Halictidae | *Agapostemon virescens* | Ground[1] | 318 | 273 | 399 | 505 | 1,034 | 2,529 |
| Halictidae | *Dufourea campanulae* | Ground[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Halictidae | *Halictus confusus* | Ground[1] | 0 | 0 | 0 | 1 | 1 | 2 |
| Halictidae | *Halictus farinosus* | Ground[1] | 21 | 33 | 26 | 61 | 112 | 253 |
| Halictidae | *Halictus ligatus* | Ground[1] | 96 | 66 | 42 | 72 | 87 | 363 |
| Halictidae | *Halictus rubicundus* | Ground[1] | 3 | 3 | 2 | 8 | 14 | 30 |
| Halictidae | *Halictis tripartitus* | Ground[1] | 146 | 81 | 67 | 113 | 145 | 552 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 1 | Ground[1] | 2 | 0 | 2 | 6 | 4 | 14 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 2 | Ground[1] | 2 | 1 | 7 | 5 | 7 | 22 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 3 | Ground[1] | 4 | 1 | 1 | 2 | 5 | 13 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 4 | Ground[1] | 0 | 1 | 0 | 0 | 2 | 3 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 5 | Ground[1] | 3 | 9 | 4 | 14 | 12 | 42 |

(Continues)

**TABLE 2** (Continued)

| Family | Species | Nest location | A (n = 4) | B (n = 4) | C (n = 4) | D (n = 8) | E (n = 8) | Total |
|--------|---------|---------------|-----------|-----------|-----------|-----------|-----------|-------|
| | | | **Treatment** | | | | | |
| Halictidae | *Lasioglossum (Dialictus)* sp. 6 | Ground[1] | 8 | 7 | 16 | 26 | 31 | 88 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 7 | Ground[1] | 0 | 2 | 2 | 2 | 6 | 12 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 8 | Ground[1] | 2 | 2 | 1 | 4 | 7 | 16 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 9 | Ground[1] | 1 | 0 | 0 | 1 | 4 | 6 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 10 | Ground[1] | 0 | 1 | 1 | 0 | 4 | 6 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 11 | Ground[1] | 5 | 3 | 3 | 8 | 11 | 30 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 12 | Ground[1] | 9 | 11 | 12 | 19 | 39 | 90 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 13 | Ground[1] | 3 | 3 | 2 | 9 | 2 | 19 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 14 | Ground[1] | 7 | 5 | 4 | 27 | 28 | 71 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 15 | Ground[1] | 9 | 7 | 12 | 22 | 35 | 85 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 16 | Ground[1] | 0 | 1 | 0 | 0 | 1 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 17 | Ground[1] | 0 | 0 | 2 | 0 | 0 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 18 | Ground[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 19 | Ground[1] | 0 | 0 | 0 | 1 | 1 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 20 | Ground[1] | 0 | 0 | 2 | 0 | 0 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 21 | Ground[1] | 0 | 0 | 1 | 0 | 1 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 22 | Ground[1] | 0 | 1 | 0 | 5 | 4 | 10 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 23 | Ground[1] | 1 | 1 | 0 | 1 | 0 | 3 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 1 | Ground[1] | 0 | 0 | 10 | 4 | 2 | 16 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 2 | Ground[1] | 0 | 0 | 0 | 0 | 5 | 5 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 3 | Ground[1] | 7 | 7 | 15 | 7 | 11 | 47 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 4 | Ground[1] | 0 | 0 | 0 | 2 | 0 | 2 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 5 | Ground[1] | 5 | 2 | 4 | 3 | 1 | 15 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 6 | Ground[1] | 3 | 1 | 2 | 0 | 3 | 9 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 7 | Ground[1] | 0 | 0 | 1 | 0 | 0 | 1 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 8 | Ground[1] | 0 | 0 | 1 | 0 | 2 | 3 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 9 | Ground[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Halictidae | *Lasioglossum anhypops* | Ground[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Halictidae | *Lasioglossum egregium* | Ground[1] | 1 | 0 | 0 | 1 | 2 | 4 |
| Halictidae | *Lasioglossum mellipes* | Ground[1] | 0 | 0 | 0 | 1 | 1 | 2 |
| Halictidae | *Lasioglossum olympiae* | Ground[1] | 6 | 7 | 8 | 21 | 20 | 62 |
| Halictidae | *Lasioglossum pacificum* | Ground[1] | 1 | 2 | 0 | 8 | 7 | 18 |
| Halictidae | *Lasioglossum pavonotum* | Ground[1] | 1 | 4 | 9 | 14 | 9 | 37 |
| Halictidae | *Lasioglossum sisymbrii* | Ground[1] | 6 | 2 | 3 | 3 | 8 | 22 |
| Halictidae | *Lasioglossum titusi* | Ground[1] | 1 | 0 | 0 | 2 | 0 | 3 |
| Halictidae | *Lasioglossum trizonatum* | Ground[1] | 0 | 0 | 0 | 1 | 1 | 2 |
| Halictidae | *Sphecodes* sp. 1 | Cleptoparasite[1] | 0 | 0 | 1 | 0 | 0 | 1 |
| Halictidae | *Sphecodes* sp. 2 | Cleptoparasite[1] | 0 | 1 | 1 | 0 | 0 | 2 |
| Halictidae | *Sphecodes* sp. 3 | Cleptoparasite[1] | 0 | 0 | 0 | 1 | 1 | 2 |
| Halictidae | *Sphecodes* sp. 4 | Cleptoparasite[1] | 1 | 0 | 0 | 1 | 0 | 2 |
| Halictidae | *Sphecodes* sp. 5 | Cleptoparasite[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Megachilidae | *Anthidium emarginatum* | Ground[3] | 1 | 1 | 1 | 1 | 0 | 4 |

(Continues)

**TABLE 2**  (Continued)

| Family | Species | Nest location | A (n = 4) | B (n = 4) | C (n = 4) | D (n = 8) | E (n = 8) | Total |
|--------|---------|---------------|-----------|-----------|-----------|-----------|-----------|-------|
| | | | | | Treatment | | | |
| Megachilidae | *Anthidium manicatum* | Cavity[3] | 2 | 2 | 0 | 1 | 4 | 9 |
| Megachilidae | *Ashmeadiella californica* | Pithy stem[4] | 0 | 0 | 0 | 0 | 1 | 1 |
| Megachilidae | *Coelioxys rufitarsis* | Cleptoparasite[1] | 0 | 0 | 0 | 1 | 0 | 1 |
| Megachilidae | *Coelioxys* sp. 1 | Cleptoparasite[1] | 0 | 0 | 0 | 1 | 0 | 1 |
| Megachilidae | *Dianthidium ulkei* | Ground/cavity[1] | 0 | 0 | 0 | 0 | 1 | 1 |
| Megachilidae | *Hoplitis albifrons* | Pithy stem[5] | 0 | 0 | 0 | 0 | 1 | 1 |
| Megachilidae | *Megachile montivaga* | Cavity[6] | 1 | 9 | 5 | 8 | 3 | 26 |
| Megachilidae | *Megachile nevadensis* | Unknown | 0 | 0 | 1 | 0 | 0 | 1 |
| Megachilidae | *Megachile perihirta* | Ground[7] | 3 | 4 | 7 | 4 | 11 | 29 |
| Megachilidae | *Osmia densa* | Wood[8] | 0 | 0 | 0 | 1 | 0 | 1 |
| | Total | | 1,080 | 915 | 1,020 | 1,771 | 2,750 | 7,536 |

*Note.* References: [1]Michener (2007); [2]Williams et al. (2014); [3]Gonzalez and Griswold (2013); [4]Hurd and Michener (1955); [5]Sedivy, Dorn, and Muller (2013); [6]Baker, Kuhn, and Bambara (1985); [7]Hobbs and Lilly (1954); [8]Cane et al. (2007).

**TABLE 3**  Bee abundance and observed species richness for each of the sampling rounds across the 2014–2015 seasons

| Year | Sampling round | Bee abundance | Bee richness |
|------|----------------|---------------|--------------|
| 2014 | 1 | 497 | 49 |
| | 2 | 949 | 50 |
| | 3 | 445 | 39 |
| 2015 | 1 | 2,219 | 58 |
| | 2 | 1,833 | 67 |
| | 3 | 1,593 | 43 |

**TABLE 4**  Species composition and abundance for ground-nesting bees captured with $n = 20$ soil emergence traps placed on stands from July 1 to October 3, 2014. Note that all individuals were captured from a single treatment (i.e., treatment E in Table 1)

| Family | Species | Abundance |
|--------|---------|-----------|
| Andrenidae | *Andrena trevoris* | 1 |
| Halictidae | *Halictus tripartitus* | 6 |
| Halictidae | *Lasioglossum sisymbrii* | 1 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 3 | 2 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 12 | 3 |
| Halictidae | *Lasioglossum (Dialictus)* sp. 15 | 1 |
| Halictidae | *Lasioglossum (Evylaeus)* sp. 5 | 1 |

During 2014, our 20 emergence traps yielded a total of 15 individuals comprising seven distinct species; these included a single *Andrena trevoris* with the remaining bees belonging to the family Halictidae (Table 4). All individuals captured in emergence traps originated from the most intensive treatment (E; see Table 1). Assuming the density

of bees we measured was representative of nesting activity in the most intensive treatment (15 bees/4.32 m² = 3.47 bees/m²), this resulted in an apparent density estimate of >14,000 bees/stand for this treatment.

## 3.2 | Treatment effects on abundance and observed species richness

When considering abundance, we detected treatment effects ($F_{4,131} = 2.56$, $p = 0.042$), as well as effects of year ($F_{1,131} = 193.38$, $p < 0.001$) and sampling round ($F_{2,131} = 14.77$, $p < 0.001$), with no treatment × year interaction ($F_{4,131} = 1.40$, $p = 0.238$; Figure 1a). Multiple contrasts revealed that treatment-level differences were driven by greater abundances in the most intensive treatment (treatment E vs. treatment A: $\hat{\beta} = 0.47$ [95% CI: 0.03, 0.92], $t_{1,131} = 2.12$, $p = 0.036$; treatment E vs. treatment B: $\hat{\beta} = 0.60$ [95% CI: 0.16, 1.04], $t_{1,131} = 2.68$, $p = 0.008$; treatment E vs. treatment C: $\hat{\beta} = 0.40$ [95% CI: −0.03, 0.84], $t_{1,131} = 1.83$, $p = 0.070$; treatment E vs. treatment D: $\hat{\beta} = 0.44$ [95% CI: 0.08, 0.79], $t_{1,131} = 2.43$, $p = 0.016$). We found that stand-level abundance was 3x greater in 2015 relative to 2014 ($\hat{\beta} = 1.27$ [95% CI: 1.09, 1.45], $t_{1,131} = 13.91$, $p < 0.001$), with a greater number of individuals captured in every treatment in the second year of the study ($p < 0.001$ in all cases).

When examining observed species richness, we detected an effect of treatment ($F_{4,131} = 6.54$, $p < 0.001$), year ($F_{1,131} = 98.81$, $p < 0.001$), and sampling round ($F_{2,131} = 88.58$, $p < 0.001$), with no treatment × year interaction ($F_{4,131} = 1.93$, $p = 0.110$; Figure 1b). Similar to abundance, treatment E had a greater number of species than the other treatments (treatment E vs. treatment A:
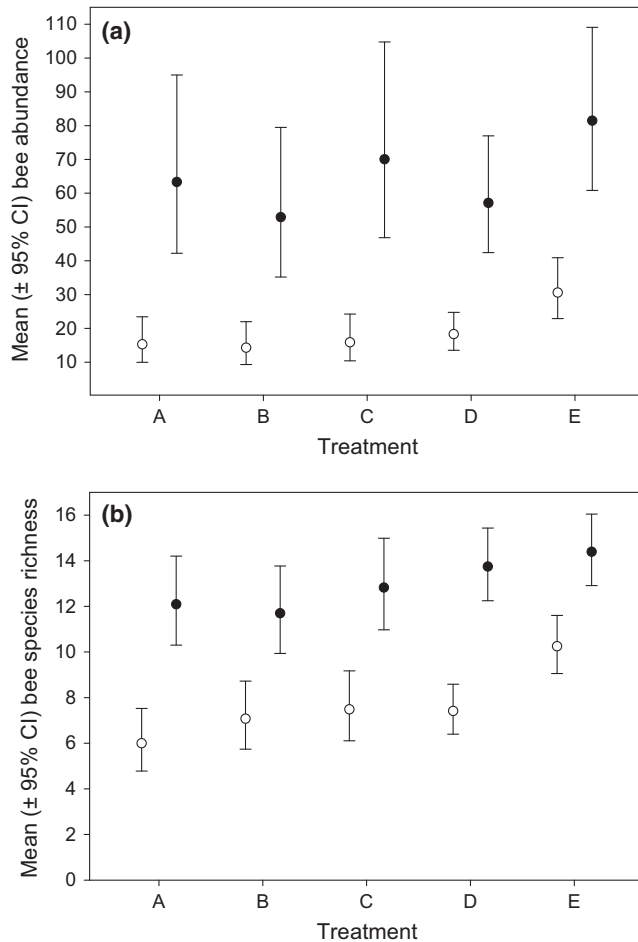
**FIGURE 1** Mean (±95% CI) estimates for bee (a) abundance and (b) observed species richness for sampling with blue vane traps that took place in 2014 (open circles) and 2015 (closed circles). All comparisons made between years within a treatment were greater in 2015 ($p \leq 0.002$) for both measures

$\hat{\beta} = 0.35$ [95% CI: 0.19, 0.52], $t_{1,131} = 4.28$, $p < 0.001$; treatment E vs. treatment B: $\hat{\beta} = 0.29$ [95% CI: 0.13, 0.45], $t_{1,131} = 3.64$, $p = 0.004$; treatment E vs. treatment C: $\hat{\beta} = 0.21$ [95% CI: 0.06, 0.37], $t_{1,131} = 2.78$, $p = 0.006$; treatment E vs. treatment D: $\hat{\beta} = 0.19$ [95% CI: 0.06, 0.31], $t_{1,131} = 3.03$, $p = 0.003$). As noted above, stand-level observed richness estimates were higher in the second year of the study ($\hat{\beta} = 0.54$ [95% CI: 0.43, 0.65], $t_{1,131} = 9.94$, $p < 0.001$), and similar to abundance, we found greater species richness in every treatment in the second year of the study ($p \leq 0.002$ in all cases).

## 3.3 | Nonparametric estimators of species richness and community attributes

For all treatment × year combinations, observed species richness values were significantly lower than Chao1 estimators (i.e., the lower bounds of the 95% CI of the Chao1 estimators were greater than observed estimates; Table 5).

Nonparametric richness estimators were variable, with no clear pattern for either treatment or year. The slope of species accumulation curves varied across treatment, with the extrapolation of species richness reaching an asymptote for treatments A, B, and C; the slopes in the more intensive treatments (D and E) did not reach an asymptote, suggesting additional species would be detected through additional sampling (Figure 2). In general, Morisita–Horn measurements of similarity increased with increasing treatment intensity, and measurements were variable between the two years of the study (Figure 3), with no strong differences between years as indicated by overlapping 95% CI interval.

We did not detect substantial positive spatial autocorrelation for our global abundance model (maximum Moran's $I < 0.2$, $p > 0.12$); our global richness model exhibited spatial autocorrelation, but only at the maximum distance class (Moran's $I = 0.62$, $p = 0.008$) which is likely to be an artifact of low sample size of spatial pairs at this scale, resulting in spurious correlations. In both models, autocorrelation at fine spatial scales (i.e., among adjacent plots) was very small (Moran's $I < 0.01$; Supporting Information Figure S1) and indicates spatial autocorrelation was unlikely to have biased parameter estimates or significance tests.

## 4 | DISCUSSION

Our investigation is the first of its kind to assess how the experimental removal of harvest residue influences wild bee abundance and diversity, and it detected an unexpected number of bee species within regenerating managed conifer forest subjected to intensive biomass removal and soil compaction. The pool of species we detected was dominated by ground-nesting species in the family Halictidae (namely *Agapostemon*, *Halictus*, and *Lasioglossum*) that appeared to use exposed soil on study plots and perhaps adjacent areas (e.g., roadsides) for nesting; in contrast, few cavity-nesting species were detected during the course of our study. This likely reflects the type of dead vegetation present on study sites, particularly logging slash from mature Douglas fir trees that lacked the hollow and/or pithy stems required by common cavity-nesting bees in our region (e.g., *Ceratina* and *Hylaeus*). Similarly, our study plots lacked standing dead wood (i.e., snags) and other downed woody debris that could have served as nest sites for some cavity-nesting bees that nest in logs and snaps (e.g., *Osmia* that use preexisting tunnels created by wood-boring beetle larvae; Cane et al., 2007); this dearth of dead wood and debris was due to both the harvest methods used and the second growth nature of stands prior to harvest. Some of the genera that were commonly encountered in our study (e.g., *Agapostemon* and *Lasioglossum*) have a wide distribution and are found in a range of disturbed habitats (e.g., cornfields;

**TABLE 5** Abundance, observed species richness, and estimates of mean richness and 95% CIs based on the Chao1 estimator as calculated using program EstimateS (Colwell, 2013). Treatment designations follow those in Table 1

| Treatment | Year | *n* | Abundance | Observed richness | Chao1 richness (mean) | Chao1 richness (95% CI) |
|---|---|---|---|---|---|---|
| A | 2014 | 4 | 232 | 31 | 59 | 38, 146 |
|   | 2015 | 4 | 848 | 44 | 84 | 56, 184 |
| B | 2014 | 4 | 197 | 36 | 61 | 43, 124 |
|   | 2015 | 4 | 718 | 45 | 56 | 48, 82 |
| C | 2014 | 4 | 211 | 36 | 44 | 38, 63 |
|   | 2015 | 4 | 809 | 49 | 85 | 60, 167 |
| D | 2014 | 8 | 469 | 42 | 56 | 46, 93 |
|   | 2015 | 8 | 1,302 | 58 | 125 | 76, 301 |
| E | 2014 | 8 | 782 | 54 | 72 | 60, 111 |
|   | 2015 | 8 | 1,968 | 60 | 73 | 64, 101 |

Wheelock & O'Neal, 2016). Although such species may not be good indicators of habitat quality because of their high tolerance to disturbance, they are gaining recognition as providing critical pollination services due in part due to their abundance and wide distributions (Kleijn et al., 2015; Winfree, Fox, Williams, Reilly, & Cariveau, 2015). This indicates that early successional forests, even those that have undergone removal of harvest residue, can harbor pollinators that are likely contributing to the maintenance of biodiversity in forests (Hanula et al., 2016), and such species may even play an indirect role in supporting food production by maintaining source populations of wild bees that may colonize agricultural areas within mixed-production landscapes (Monasterolo, Musicante, Valladares, & Salva, 2015).

Our study site was typical to other conifer forests subjected to clear-cut harvest in the type of dead vegetation it contained, as the composition of postharvest vegetation within managed conifer stands can have a limited understory component due to herbicide application. Thus, regenerating stands often lack habitat features that may be critical for a subset of bee species, such as cane-producing plants (e.g., *Rubus*) that provide nesting substrates for stem-nesting bees. Although these habitat features may not be present immediately after harvest, forest succession often results in the eventual addition of such plants which may provide habitat for species with cavity-nesting requirements. For example, whitebark raspberry (*Rubus leucodermis*) and the non-native Himalayan blackberry (*Rubus armeniacus*) often occur within early successional forest in our region, and their hollow stems are used by some stem-nesting bees (e.g., *Ceratina*; Rivers & Moldenke, personal observations). Thus, it seems likely that stem-nesting species may be found in regenerating conifer stands only after an adequate amount of time has passed for cane-producing plants to colonize stands, a hypothesis that should be tested

in future studies examining bee diversity within early successional forests across an age gradient.

Observed species richness increased during our study, with turnover restricted to species that were detected rarely with our sampling approach. This was not a surprising result given that ecological communities in general have low evenness and are typically dominated by a small pool of species (McGill et al., 2007), which also holds true for bees (Moldenke, 1975). However, it is noteworthy that the number of individuals captured increased 3-fold from the first (2014) to the second year of sampling (2015). What explains this large change over the timescale of a single year? The plots on which we worked were approximately 70 years old at the time they were harvested in spring 2013. Bees are typically restricted to open habitats (Michener, 2007) and are much less abundant within mature forest (Hanula et al., 2016; Roberts et al., 2017; Taki et al., 2013; Winfree et al., 2007), so it was likely that few, if any, bees were present on our study sites prior to harvest. Thus, the first opportunity for bees to establish on our study sites would have occurred during summer 2013 after timber harvest took place. This means that the bees we captured in 2014 were the offspring of the first generation of bees to colonize the study sites, assuming the bees we captured originated from study plots (see below). This result suggests that the increase we observed across years was due to local population growth, new colonizations, or both. It also emphasizes the importance of multiyear studies because bee populations can be highly variable across years due to a range of environmental factors (Roulston & Goodell, 2011). Thus, additional investigations that evaluate how bees and other pollinator communities change with time since disturbance within forests will be especially helpful to pinpoint the time period(s) during which managed forests provide the most suitable habitat for this group.
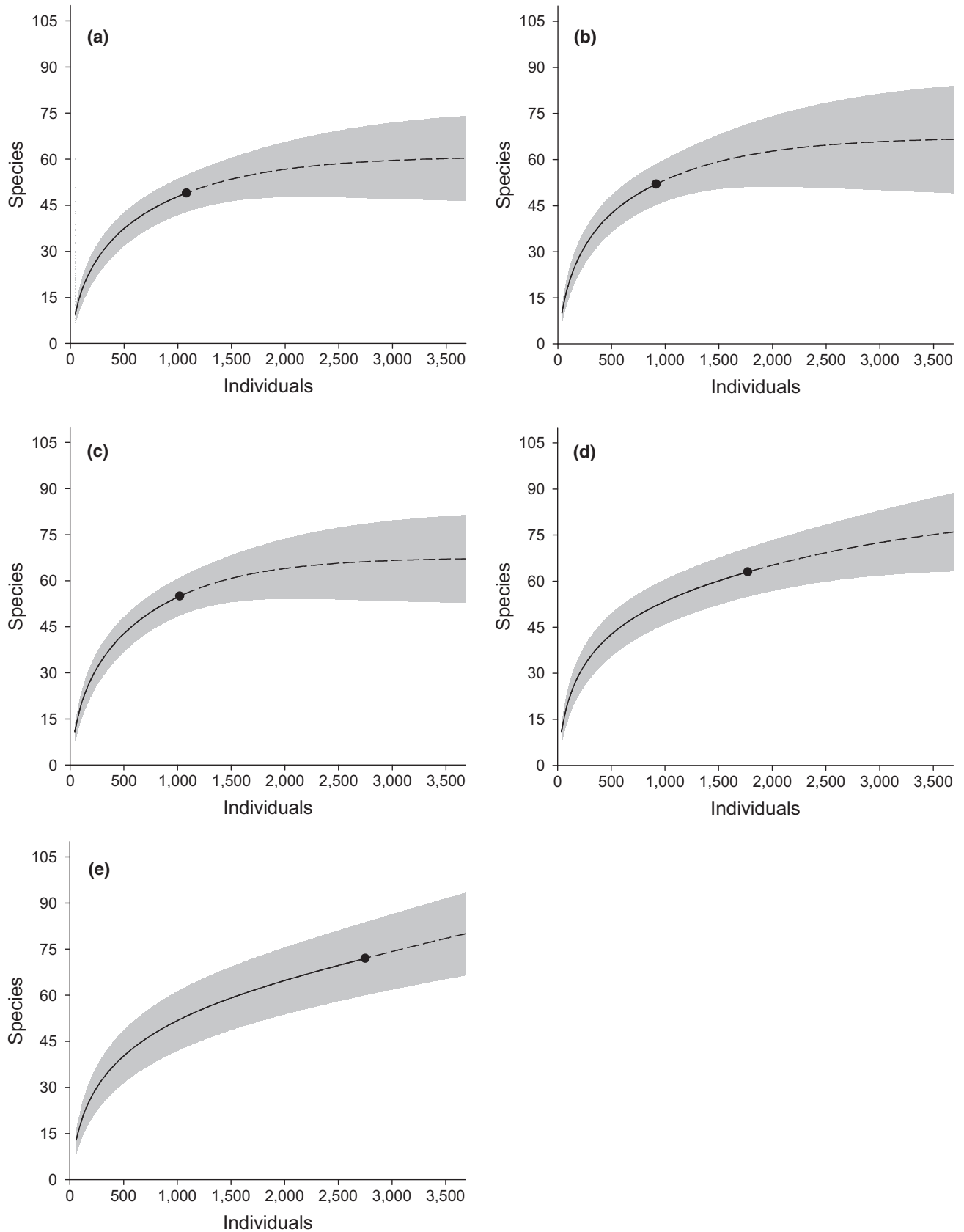
**FIGURE 2** Individual-based rarefaction (solid lines) and extrapolation curves (dashed lines) for bees collected over the course of the study for treatments a–e, with 95% unconditional confidence intervals (shaded area). See Table 1 for description of treatment designations
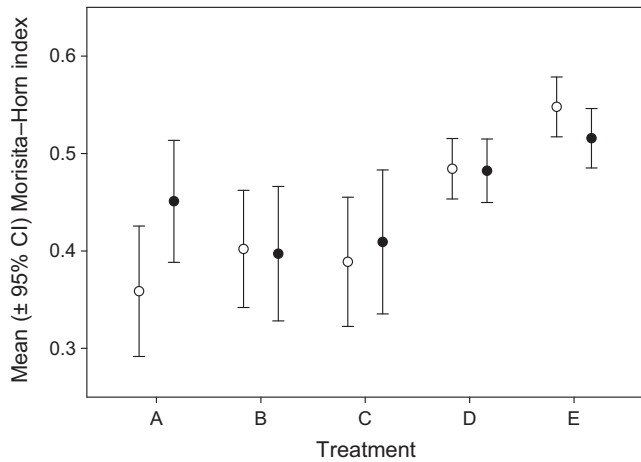
**FIGURE 3** Mean (±95% CI) Morisita–Horn index values for sampling that took place during 2014 (open circles) and 2015 (closed circles). Point estimates were obtained using program EstimateS (Colwell, 2013) to calculate a Morisita–Horn index value for each pairwise sample combination for each treatment within each year and then by calculating means and associated 95% CIs across all index values for each treatment × year combination

The vegetation immediately surrounding our study sites did not change appreciably during the course of our study, so the increase in abundance we observed in the second year of our study appears likely to be attributed to local population growth. Fine-scale temporal (i.e., annual) data are lacking on how bee populations increase over time in regenerating conifer forests, but studies indicate that bee populations can increase quickly after other major disturbance events, such as wildfire (Love & Cane, 2016; Potts et al., 2003). Indeed, temperate bees are generally considered to be a disturbance-dependent group (Michener, 2007; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009), so it is not surprising that many species were able to colonize newly available habitat shortly after timber harvest occurred. Nevertheless, how bee communities change with time since disturbance in forested landscapes and how management actions alter the availability of critical habitat features (i.e., floral resources and nesting substrates) through time remain poorly understood in managed conifer landscapes. Therefore, studies addressing both of these topics are urgently needed within these areas given long-standing concerns about pollinator population declines (Allen-Wardell et al., 1998; Potts et al., 2010). We also note that there has been concern as to whether repeated lethal sampling might reduce local bee populations (Gezon et al., 2015), especially as part of multiyear studies. Given the 3-fold increase in the number of individuals between in our second year of sampling, this did not appear to be the case in our study with the methods we employed.

Our study found that abundance and richness of bees were greatest in the most intensive treatment, which experienced soil compaction and had whole trees and the forest floor removed. When considering the level of disturbance, this result was unexpected and ran counter to our initial prediction based on previous studies reporting intensive disturbance is not typically associated with increases in bee abundance or species richness (Williams et al., 2010; Winfree et al., 2009; Winfree, Bartomeus, & Cariveau, 2011). Thus, it is especially important to consider the type of disturbance when evaluating how agents of disturbance influence bee communities. In the most intensive treatment in our study, the disturbance that took place resulted in the removal of organic material and the exposure of mineral soil, thereby allowing ground-nesting bee to access nesting substrates that were previously unavailable (Cane, 1991; Cane & Neff, 2011; Potts et al., 2005). Blue vane traps were hung well above the sparse vegetation on study plots, so their detectability appeared to be similar among our treatments (Rivers, personal observation), suggesting treatment differences were responsible for drawing in large numbers of ground-nesting bees to the most disturbed study plots. We find it particularly noteworthy that we detected a treatment effect given the close proximity of study plots to one other and the relatively large foraging ranges of many bee species in our study, based on their body size (Gathmann & Tscharntke, 2002; Greenleaf, Williams, Winfree, & Kremen, 2007; Zurbuchen et al., 2010), both of which would have facilitated movements between study plots and treatments. This provides additional support for the idea that the removal of organic material was a key component that attracted bees to highly disturbed sites in our study, and it suggests that exposing mineral soil through removal of harvest residue and other organic materials may create new nesting areas for ground-nesting species within managed forest landscapes.

Although bees require both nesting sites and floral resources to maintain populations, the patterns we observed were unlikely to have been driven by floral resources, for two reasons. First, herbicides were used to control competing vegetation such that nearly half of the plots for which floral resources were measured (44%) contained no flowers during our sampling periods (J. W. Rivers, C. L. Mathis, A. R. Moldenke & M. G. Betts, unpublished data). Second, the mean flowering stem density for the most intensive treatment (0.61 flowers/20 m$^2$) was nearly identical to that of a similar treatment (D) that lacked forest floor removal (0.58 flowers/20 m$^2$); thus, floral densities in both treatments were so low that floral resources were likely to exert little, if any, influence on the number and composition of bees visiting traps. Where nesting bees ultimately found food resources is unclear, but we suspect the margins of our study site may have provided suitable floral resources, along with roadside areas in the general vicinity of our study. Other early successional forest within the vicinity of

our study site may have also provided food resources for bees; agricultural areas were unlikely to provide forage for most bees given they were ≥4 km away from our study site (Rivers, personal observation).

In our study, we used blue vane traps to sample bees, in part, because the dearth of floral resources on our study sites did not allow for netting. Like any sampling method, blue vane traps have biases and therefore cannot be assumed to sample the entire bee community. Given our investigation was focused on testing for relative differences among experimental treatments and not aimed at quantifying the entire bee community, using blue vane traps provided a sampling approach that was consistent across all treatments over the course of our study. Moreover, the open habitat in which we sampled bees made it such that blue vane traps could be seen from beyond individual plots, at least by human observers (Rivers, personal observation). Thus, if blue vane traps served as an especially strong stimulus to attract bees and drew them from beyond our study plots, that stimulus would have been consistent across all study plots and not resulted in any treatment-specific biases. Indeed, that we detected treatment differences despite this possibility makes it even more apparent that the treatment differences we detected have biological significance. In addition to restrictions about the type of sampling used, we were also constrained in the timing of our study. Specifically, we were unable to sample bees early in the season due to concerns about trapping foundress bumble bee (*Bombus*) queens. Thus, although our sampling does not encompass the entire wild bee flight season, it does allow us to test for treatment-level differences and provide a conservative estimate of the bee biodiversity using our study sites.

Biofuel production is expected to expand as part of a global approach to provide sustainable energy (Chu & Majumdar, 2012), so it seems likely that harvest residue will continue to be used as biofuel feedstock in the foreseeable future. As the first of its kind to evaluate pollinator response to removal of harvest residue, our study has found that bee abundance and diversity can be high within stands subject to intensive management related to biomass harvest and that extensive removal of harvest residue may be compatible with providing habitat for some bee populations, especially ground-nesting species. An important consideration, however, is the spatial extent to which the removal of harvest residue and accompanying management actions (e.g., herbicide application) could negatively influence bee populations. If removal of harvest residue is extensive and exposes bare soil used by ground-nesting bees, intentional seeding of adjacent areas to create foraging opportunities for provisioning females could be a relatively simple action that might enhance local bee populations under such condition (Cane & Love, 2016). More broadly, wild bees have received very little study relative to other aspects of forest management (Hanula et al., 2016); therefore, additional investigations are needed to understand more fully how bees and other pollinators are impacted by large-scale management actions.

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## SUPPORTING INFORMATION

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

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