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Postharvest Bee Diversity is High but Declines Rapidly with Stand Age in Regenerating Douglas-Fir Forest

James W. Rivers¹ and Matthew G. Betts²

James W. Rivers (jim.rivers@oregonstate.edu), Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR 97331, USA; Current address: Department of Forest Engineering, Resources, & Management, Oregon State University, Corvallis, OR 97331, USA. Matthew G. Betts (matt.betts@oregonstate.edu), Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR 97331, USA; and Forest Biodiversity Research Network, Department of Forest Ecosystems & Society, Oregon State University, Corvallis, OR 97331, USA.

Abstract

Concerns about long-term pollinator declines have made assessing bee communities a priority in nonagricultural ecosystems, including managed forests. We assessed wild bee communities in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) stands one to 15 years after clearcut harvest in western Oregon, USA, testing the hypothesis that bee diversity would be high initially and then decline with time-dependent reductions in floral resources. We captured 2,009 individual bees that represented 67 distinct species/morphospecies in 20 genera and five families. Asymptotic estimators of bee diversity representing Shannon and Simpson diversity were greater in communities during the second half of the early seral period, indicating older early seral stands were less diverse and contained more common and dominant bee species. In addition, observed species richness and bee abundance peaked at approximately three years postharvest and declined thereafter by 20% and 30% per year, respectively. Because floral resources declined in concert with reductions in bee diversity as stands aged, food appears to be a key driver of forest bee communities. Our results indicate that postharvest Douglas-fir stands supported a diversity of bees, including important crop pollinators, but their value to bees was restricted to a relatively short window at the beginning of the early seral period.

Study Implications: Postharvest Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests supported a range of wild bee species during the early seral period and observed bee species richness and abundance was strongly associated with floral resources. However, stands within three years of harvest harbored the most bees and greatest bee diversity, indicating their values to bees is limited to a short window of time during the early seral period. Therefore, actions taken by managers that promote floral resources and maintain early seral conditions on the landscape are expected to have the greatest benefit to wild bees and other insect pollinators within managed forests.

Keywords: bee, Douglas-fir forest, early successional forest, intensive forest management, pollinator

Insect pollinators play indispensable roles because they pollinate >85% of the world's wild flowering plants (Ollerton et al. 2011) and 35% of agricultural crops (Klein et al. 2007), and they provide ecosystem services valued at \$175 billion annually (Gallai et al. 2009). Some insect pollinators have experienced extensive declines (Allen-Wardell et al. 1998, Biesmeijer et al. 2006, Potts et al. 2010, Cameron et al. 2011), which has led to intensifying concerns regarding a “pollinator crisis” that ultimately threatens global food security and the integrity of natural ecosystems. These concerns have led to heightened interest in evaluating how land-use activities influence pollinators and the ecosystem services they provide, including within managed ecosystems that are outside of traditional agricultural settings (e.g., forests managed for timber production). Of the insect pollinators that have experienced declines, bees are considered as the most important group within both natural and managed systems (Michener 2007, Brown and Paxton 2009, Winfree, 2010). The importance of bees as pollinators stems from their life-long dependence on floral rewards provided by flowering plants (i.e., nectar, pollen, and to a lesser extent, oils; Michener 2007, Brown and Paxton 2009), which serve to maintain flowering plant popu-

lations (Knight et al. 2005). Thus, efforts to conserve bees serve not only to enhance local biodiversity, but they can also help to maintain pollination services that support the trophic interactions that are essential for the healthy functioning of terrestrial ecosystems.

Bees are typically found in open habitats, and the great majority of research on this group has focused on quantifying bee diversity and pollination services within agroecosystems, grasslands, and rangelands. Nevertheless, bees occur in other ecosystems, including conifer forests that are intensively managed for timber production and vital to the world's economy (Hanula et al. 2016, Rivers et al. 2018a). Indeed, there is a growing body of literature that has demonstrated that bees are often found in temperate conifer forests after both natural (e.g., wildfire; Moretti et al. 2009, Ponisio et al. 2016, Galbraith et al. 2019a) and anthropogenic disturbances (e.g., timber harvest; Taki et al. 2013, Rodriguez and Kouki 2017, Rivers et al. 2018b, Galbraith et al. 2019b). Post-disturbance forests support bees by providing the resources that are critical for maintaining their populations, namely floral resources and nesting substrates (Roulston and Goodell 2011). Although several recent studies have begun to focus attention

on bees within managed conifer forests, we still have a poor understanding of wild bee communities within regenerating forests, and this is particularly true of conifer forests that are managed intensively for timber production (FAO 2016). For example, even basic knowledge of which bee species are found in postharvest conifer forests is limited; likewise, studies that document how bee communities are influenced by contemporary forest management practices are also scarce (Rivers et al. 2018a). Thus, additional research focused on these topics is needed to improve our understanding of how forest bee communities are structured, evaluate how wild bees are influenced by forest management activities, and determine whether pollinators in managed forests spill over into adjacent habitats and provide benefits to pollinator-dependent crops within mixed forest-agricultural production landscapes (Rivers et al. 2018a).

In this study, our goal was to quantify bee diversity in conifer forests managed intensively for timber production during the early seral period (i.e., initial conditions after a stand-replacing disturbance; Swanson et al. 2011). We focused our investigation on the early seral period for two reasons. First, it appears to provide the most favorable conditions for bees (Hanula et al. 2016), as canopy closure leads to marked decreases in solar radiation, air temperature, and floral resources (Herrera 1997, Kilkenny and Galloway 2008, Pollato et al. 2014) which together create unfavorable environments for bees and other insect pollinators. Second, intensive management is thought to result in a truncation in the length of the early seral period (Swanson et al. 2011, Donato et al. 2012, Betts et al. 2013), which further reduces the period during which bee populations are present within managed conifer forests.

We quantified bee diversity measures by calculating Hill numbers (Hill 1973), which have several advantages relative to other diversity measures (Chao et al. 2014) and have garnered increased interest as a comprehensive approach for estimating species diversity within biological communities (Ellison 2010). We evaluated Hill numbers for bee communities in stands one to seven years postharvest (hereafter, “young” early seral stands) and contrasted them with those in stands eight to 15 years postharvest (hereafter, “old” early seral stands). Second, we tested the hypothesis that observed bee species richness and abundance would be influenced by the time since harvest. We predicted that both of these measures would be greatest in stands in the first several years after harvest when flowering plants dominate (Stokely et al. 2020), after which they would decrease until the time of canopy closure. Finally, we quantified how floral resources changed with time since harvest to determine whether potential changes in bee communities were correlated with the food resources that are critical for sustaining bee populations.

Materials and Methods

We conducted our work in the Coast Range mountains of western Oregon, USA, a globally important timber production area and a leading supplier of softwood lumber in the United States (OFRI 2019). Regenerating conifer stands in this region exhibit marked changes in vegetative composition and structure throughout the early seral period, with canopy closure occurring as early as 12–15 years postharvest (Adams et al. 2005, Hayes et al. 2005; Rivers et al. unpub-

lished data). We conducted this study during July–August 2014 at the McDonald-Dunn Forest (44.6°N, 123.3°W) north of Corvallis, Oregon, USA, an experimental forest of approximately 4,550 ha that is owned by the College of Forestry at Oregon State University and whose goal is to support university instruction and research. This forest is located on the eastern edge of the Oregon Coast Range and harbors two different plant association types: Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco)/hazelnut (*Corylus cornuta* Marshall)/brome-grass (*Bromus vulgaris* [Hook.] Shear) and Douglas-fir/vine maple (*Acer circinatum* Pursh)/salal (*Gaultheria shallon* Pursh) (Franklin and Dyrness 1988). Annual precipitation averages 100 cm and occurs primarily from November to May. Summers tend to be hot and dry with mean June to August temperatures of 27.1°C and an average of 4.7 cm of precipitation (Maguire and Chambers 2005).

To quantify changes in bee diversity, we selected $n = 14$ stands managed for timber production that averaged 15.4 ha (range: 5.7–29.9 ha) and were harvested one to 15 years prior to sampling in 2014. All stands were second-growth forest that were replanted with Douglas-fir seedlings after harvest, except for a single stand that was planted to a mixture of Douglas-fir and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). Each stand was treated with a site-specific mix of herbicides to control competing vegetation within one year of planting in a manner that is typical for intensively managed stands in this region (S. Fitzgerald 2014, pers. commun.). On average, stand centers—where trapping occurred—was 2.9 km distant from each other (range: 339–7,967 m), which is beyond the typical foraging distances expected for the majority of wild bee species in our study area (Gathmann and Tschardt 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010).

During 2014 we sampled bees in three sampling rounds that were separated by three to four weeks (i.e., 2–4 July, 30 July–1 August, and 20–22 August); this resulted in a total of 42 samples obtained (14 stands \times three sampling rounds/stand). We purposefully did not collect bees during the early part of summer (May–June) because of the potential for trapping foundress bumble bee queens (*Bombus* spp.) that could have negatively affected colony establishment and persistence, especially for uncommon and rare bumble bee species. We used blue vane traps to sample bees, which reflect in the UV-A and UV-B spectra (Stephen and Rao 2005) and have been used successfully to quantify wild forest bee communities in regenerating conifer forests (Rivers et al. 2018b, Galbraith et al. 2019a). We placed three traps in the center of each stand, with each trap attached with a black plastic electric fence insulator on a separate 1.8 m high metal T-post mounted vertically. We placed each post 5 m from the geographic center of the stand with the first post placed at a randomly chosen azimuth; the second and third posts were then placed 120° and 240° from the first azimuth, respectively, to provide equal spacing (i.e., 8.7 m) between adjacent traps. We did not add any preservatives or attractants to traps following previous work (Rivers et al. 2018b); the rate at which bees may escape from such “dry” traps is unknown. After traps were in place for 48 h, we retrieved them and killed all insects they contained via freezing using a cooler containing dry ice. During each sampling round we also quantified the floral resources available to foraging bees along a 2 \times 10 m

belt transect that was centered on the location of each trap, and we tallied the number of individual flowers/inflorescences that were in bloom as an index of available floral resources (Table S1).

We used keys from Michener (2007) and Stephen et al. (1969) to identify specimens to the generic level, and used both regional synoptic collections and local keys to obtain species-level identifications for the genera *Agapostemon* (Stephen et al. 1969), *Anthophora* and *Ceratina* (www.discoverlife.org), *Bombus* (Williams et al. 2014), and *Halictus* (Roberts 1973). Species-level keys for several groups in the Pacific Northwest, USA, are currently unavailable in our region including *Lasioglossum* (*Dialictus*) and *Lasioglossum* (*Evylaeus*), so we were restricted to identifying individuals to morphospecies for those groups. Bees from our study were identified by L. Best (Oregon State University) and A. Moldenke (Oregon State University) with assistance from K. Wright (Texas A&M University) for specimens in the genus *Melissodes*.

We used the R statistical environment (v4.0.2; R Core Team 2020) for all analyses. We initially pooled all bee samples that were captured in all three traps on each stand for each of the three sampling rounds, and we quantified floral resources in a similar manner. This resulted in three measures (i.e., observed bee species richness, bee abundance, and floral resources) for each stand, which allowed us to evaluate how these response variables were influenced by the timing of sampling within the season. In addition, we calculated Hill numbers (see below) to compare bee diversity measures in young early seral stands (i.e., one to seven years postharvest) to those in old early seral stands (i.e., eight to 15 years postharvest). We selected these two periods because they represented a natural breakpoint in the distribution of time since harvest in our data set and because ongoing work on bee communities in early seral Douglas-fir stands indicates bee diversity measures change markedly between these two time periods (Rivers et al., unpublished data).

To quantify diversity measures, we used the iNEXT package (v2.0.20, Hsieh et al. 2020) to create sample-sized-based and coverage-based rarefaction and extrapolation sampling curves for three Hill numbers ($q = 0$, $q = 1$, $q = 2$; Chao et al. 2014, Hsieh et al. 2016). Hill numbers represent the effective number of species for several diversity metrics, including species richness ($q = 0$), the exponential of Shannon index ($q = 1$, hereafter Shannon diversity), and the inverse of the Simpson concentration ($q = 2$, hereafter Simpson diversity). Hill numbers are gaining favor for evaluating diversity measures within ecological communities (e.g., Cerullo et al. 2019, Galbraith et al. 2019b, Loy et al. 2020) because they are intuitive to understand, are based on a robust statistical framework, can be used to make “fair” comparisons between different communities based on sample coverage, and offer several additional advantages when compared with traditional diversity metrics (Chao and Jost 2012, Chao et al. 2014, Hsieh et al. 2016). For bee communities in both young and old early seral stands we constructed separate sample-size-based rarefaction and extrapolation curves, coverage-based rarefaction curves, and sample-completeness curves, each with 95% confidence intervals (CIs), which, when not overlapping, provide evidence of strong differences in ecological communities (Chao et al. 2014, Hsieh et al. 2016). We also used the iNEXT package to calculate estimates of ob-

served and estimated bee diversity for the first three Hill numbers for both young and old early seral stands. In addition, we used nonmetric multidimensional scaling (NMDS) in the vegan package (v2.5–6; Oksanen et al. 2019) to evaluate the degree to which young and old early seral bee communities shared member species. Specifically, we used the metaNMDS function for ordination, and the adonis2 function to evaluate differences between bee communities in young and old early seral stands, setting the permutation level to 1,000 (Oksanen et al. 2019).

Finally, we used linear mixed modeling to quantify how observed bee species richness and abundance varied as a function of stand-level characteristics. First, we used the glmmTMB function of the glmmTMB package (Brooks et al. 2017) to construct a model with a Poisson distribution and a log link that contained observed species richness as the response variable, time since harvest (continuous) and sampling round (three levels) as fixed effects, and stand identity as a random effect. We used the same model structure and approach to model bee abundance with the exception that we used a negative binomial distribution with a log link because of high heterogeneity in the number of individuals trapped across stands. For both observed species richness and abundance models we did not include floral density as a covariate because floral density had a strong, negative correlation with time since harvest ($r = -0.60$). Instead, we constructed a separate model to quantify the relationship between floral density and stand age using the glmmTMB function to construct a linear mixed model with a negative binomial distribution and a log link because of the high heterogeneity in floral density at the stand level. This model contained floral density as the response variable, time since harvest and sampling round as fixed effects, and stand identity as a random effect. For all three models, we opted to incorporate a linear term for time since harvest because it allowed us to capture general time-dependent changes while minimizing the chance of model overfitting a modest data set. No offsets were needed in any model because effort was constant on all sites and during all sampling rounds for both bees and floral resources. We confirmed the fit of models using the DHARMA package (Hartig 2020), we computed fixed effects tests using the car package (Fox and Weisberg 2019), and we used the emmeans package (Lenth 2020) to calculate marginal means and 95% CIs. Finally, we used the moran.test function in the spdep package (Bivand and Wong 2018) to evaluate spatial autocorrelation for residuals of observed bee richness and bee abundance across stands separately for each round.

Results

During the course of our study, we captured a total of 2,009 bees representing 67 species/morphospecies in 20 genera and five families (Table 1). The most commonly encountered taxa in our samples were species in three genera: *Bombus* (38.5% of captures, representing nine species), *Apis* (23.5%, one species), and *Halictus* (18.4%, four species). We also captured bees in the cleptoparasitic genera *Bombus* (*Psithyrus*) ($n = 2$ individuals), *Nomada* ($n = 2$ individuals), and *Sphex* ($n = 1$ individual; Table 1). The majority of nonparasitic bees were assigned to the ground-nesting guild (58.4%), followed by the hive-nesting (i.e., *Apis*; 23.6%), ground/aboveground (10.1%), and stem-nesting guilds

Table 1. Taxonomic diversity, nest site location, and abundance of wild bees captured at the McDonald-Dunn Forest in western Oregon across three sampling rounds during summer 2014. Abundance of each species is presented as the number of individuals captured in young (one to seven years post harvest) or in old (eight to 15 years postharvest) early seral stands.

Family	Species/Morphospecies	Nest Site Location	Abundance	
			Young Early Seral	Old Early Seral
Andrenidae	<i>Andrena prunorum</i> *	Ground ¹	0	2
Apidae	<i>Anthophora bomboides</i>	Ground ¹	3	0
Apidae	<i>Anthophora terminalis</i>	Rotting wood/stem ¹	4	0
Apidae	<i>Anthophora urbana</i>	Ground ¹	4	2
Apidae	<i>Apis mellifera</i> *	Cavity/hive ¹	379	94
Apidae	<i>Bombus appositus</i> *	Ground/aboveground ²	25	10
Apidae	<i>Bombus californicus</i> *	Ground/aboveground ²	43	32
Apidae	<i>Bombus caliginosus</i>	Aboveground/ground ²	32	12
Apidae	<i>Bombus flavifrons</i> *	Ground ²	5	2
Apidae	<i>Bombus griseocollis</i> *	Aboveground/ground ²	34	11
Apidae	<i>Bombus mixtus</i> *	Ground/aboveground ²	20	7
Apidae	<i>Bombus nevadensis</i> *	Ground/aboveground ²	33	18
Apidae	<i>Bombus sitkensis</i> *	Ground ²	4	1
Apidae	<i>Bombus vosnesenskii</i> *	Ground ²	383	101
Apidae	<i>Bombus (Psithyrus) flavidus</i>	Social parasite ²	1	0
Apidae	<i>Bombus (Psithyrus) insularis</i> *	Social parasite ²	1	0
Apidae	<i>Ceratina acantha</i> *	Stem ¹	24	102
Apidae	<i>Ceratina micheneri</i> *	Stem ¹	0	1
Apidae	<i>Ceratina pacifica</i>	Stem ¹	0	1
Apidae	<i>Eucera edwardsii</i> *	Ground ¹	1	1
Apidae	<i>Melissodes lupina</i>	Ground ¹	8	4
Apidae	<i>Melissodes metenua</i>	Ground ¹	4	0
Apidae	<i>Melissodes microsticta</i>	Ground ¹	10	2
Apidae	<i>Melissodes rivalis</i> *	Ground ¹	63	8
Apidae	<i>Melissodes robustior</i>	Ground ¹	2	1
Apidae	<i>Nomada mutans</i>	Cleptoparasite ¹	2	0
Colletidae	<i>Hylaeus bisinuitis</i>	Stem ¹	3	2
Colletidae	<i>Hylaeus citrinifrons</i>	Stem ¹	0	1
Colletidae	<i>Hylaeus episcopalis</i>	Stem ¹	0	1
Halictidae	<i>Agapostemon texanus</i>	Ground ¹	2	1
Halictidae	<i>Agapostemon virescens</i> *	Ground ¹	16	11
Halictidae	<i>Halictus farinosus</i> *	Ground ¹	134	64
Halictidae	<i>Halictus ligatus</i> *	Ground ¹	42	17
Halictidae	<i>Halictus rubicundus</i> *	Ground ¹	17	15
Halictidae	<i>Halictus tripartitus</i> *	Ground ¹	59	21
Halictidae	<i>Lasioglossum (Dialictus) sp. 1</i>	Ground ¹	1	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 2</i>	Ground ¹	1	1
Halictidae	<i>Lasioglossum (Dialictus) sp. 3</i>	Ground ¹	0	1
Halictidae	<i>Lasioglossum (Dialictus) sp. 4</i>	Ground ¹	3	1
Halictidae	<i>Lasioglossum (Dialictus) sp. 5</i>	Ground ¹	2	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 6</i>	Ground ¹	1	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 7</i>	Ground ¹	1	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 8</i>	Ground ¹	2	1
Halictidae	<i>Lasioglossum (Dialictus) sp. 9</i>	Ground ¹	1	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 10</i>	Ground ¹	2	1
Halictidae	<i>Lasioglossum (Dialictus) sp. 11</i>	Ground ¹	2	0
Halictidae	<i>Lasioglossum (Dialictus) sp. 12</i>	Ground ¹	0	1
Halictidae	<i>Lasioglossum (Evylaeus) sp.</i>	Ground ¹	1	0
Halictidae	<i>Lasioglossum egregium</i>	Ground ¹	5	9

Table 1. Continued

Family	Species/Morphospecies	Nest Site Location	Abundance	
			Young Early Seral	Old Early Seral
Halictidae	<i>Lasioglossum olympiae</i> *	Ground ¹	0	1
Halictidae	<i>Lasioglossum pacificum</i> *	Ground ¹	11	4
Halictidae	<i>Lasioglossum sisymbrii</i>	Ground ¹	2	0
Halictidae	<i>Lasioglossum titusi</i> *	Ground ¹	4	1
Halictidae	<i>Lasioglossum</i> sp.	Ground ¹	15	8
Halictidae	<i>Sphecodes</i> sp.	Cleptoparasite ¹	1	0
Megachilidae	<i>Anthidium manicatum</i>	Cavity ³	1	0
Megachilidae	<i>Ashmeadiella cactorum</i>	Unknown ⁴	1	0
Megachilidae	<i>Heriades carinata</i>	Cavity ⁹	1	0
Megachilidae	<i>Hoplitis producta</i>	Stem ¹	0	3
Megachilidae	<i>Megachile montivaga</i>	Cavity ⁶	2	2
Megachilidae	<i>Megachile pascoensis</i>	Unknown ¹⁰	1	1
Megachilidae	<i>Megachile peribata</i> *	Ground ⁷	3	0
Megachilidae	<i>Megachile relativa</i>	Ground/wood ⁷	0	1
Megachilidae	<i>Megachile rotundata</i>	Cavity ¹	1	0
Megachilidae	<i>Osmia atriventris</i>	Wood ⁸	0	1
Megachilidae	<i>Osmia densa</i>	Wood ⁸	1	2
Megachilidae	<i>Osmia juxta</i>	Unknown ¹⁰	1	0
Total			1425	584

* Species that were also detected in Burikam (1987).

References: ¹Michener 2007, ²Williams et al. 2014, ³Gonzalez and Griswold 2013, ⁴Hurd and Michener 1955, ⁵Sedivy et al. 2013, ⁶Baker et al. 1985, ⁷Hobbs and Lilly 1954, ⁸Cane et al. 2007, ⁹Matthews 1965, ¹⁰J.H. Cane 2020 personal communication.

(6.9%), with <4% assigned to cavity- and wood-nesting guilds. Most nonparasitic individuals were classified as polylectic (94.8%), with 5.2% classified as oligolectic and a single specimen classified as a pollen specialist (i.e., *Osmia atriventris*). Of the nonparasitic species captured, 62.2% of individuals were classified as eusocial species, with 22.6% classified as primitively eusocial species and 15.3% classified as solitary species.

Bee Communities in Young versus Old Early Seral Stands

When comparing bee diversity measures between young and old early seral stands, we found that both periods were similar for both observed and estimated bee species richness, with widely overlapping 95% CIs for the latter (Table 2, Figure 1). We found that Shannon and Simpson diversity were greater for old early seral stands when compared with young early seral stands, yet we detected no difference between the young and old stands when considering estimated bee species richness (Table 2). For both young and old early seral stands, the curves for estimated species richness increased slowly beyond the reference sample (i.e., the sample obtained from trapping; Figure 1a), whereas the curves for Shannon and Simpson diversity leveled off beyond the reference sample (Figure 1b, c). The coverage of young early seral stands was estimated as 98.8% for the reference sample size of 1,425 individuals, and 96.8% for old early seral stands for the reference sample size of 584 individuals, indicating the sample coverage deficit was low (i.e., 1.2–3.2%; Figure 1d–f). Applying a traditional rarefaction to standardize sample coverage to the smaller of the two sample sizes (n = 584 individuals) resulted in a sample coverage of 97.4% for young early seral stands in compari-

Table 2. Observed and asymptotic diversity estimates (95% confidence intervals [CI]) for bee communities in young (one to seven years postharvest) and old (eight to 15 years postharvest) early seral stands on the McDonald-Dunn Forest in western Oregon across three sampling rounds during summer 2014.

Early Seral Stand Type	Diversity Measure	Hill Number	Observed Diversity	Estimated Diversity	Estimated Diversity (95% CI)
Young	Species richness	$q = 0$	56	72.0	61.1, 106.5
Old	Species richness	$q = 0$	46	71.7	54.3, 125.5
Young	Shannon diversity ¹	$q = 1$	11.8	12.1	11.8, 13.1
Old	Shannon diversity ¹	$q = 1$	14.9	15.9	14.9, 17.7
Young	Simpson diversity ²	$q = 2$	6.2	6.3	6.2, 6.7
Old	Simpson diversity ²	$q = 2$	9.3	9.4	9.3, 10.5

¹ Equivalent to exponential of Shannon index and estimates the effective number of common species (Chao et al. 2014).

² Equivalent to inverse Simpson concentration and estimates the effective number of dominant species (Chao et al. 2014).

son with 96.8% for old early seral stands. Thus, sample completeness allowed for robust comparison, and the two early seral periods were very similar as evidenced by overlapping CIs for sampling completeness curves (Figure S1). We also found strong evidence of compositional differences of wild bee species between young and old early seral stands using

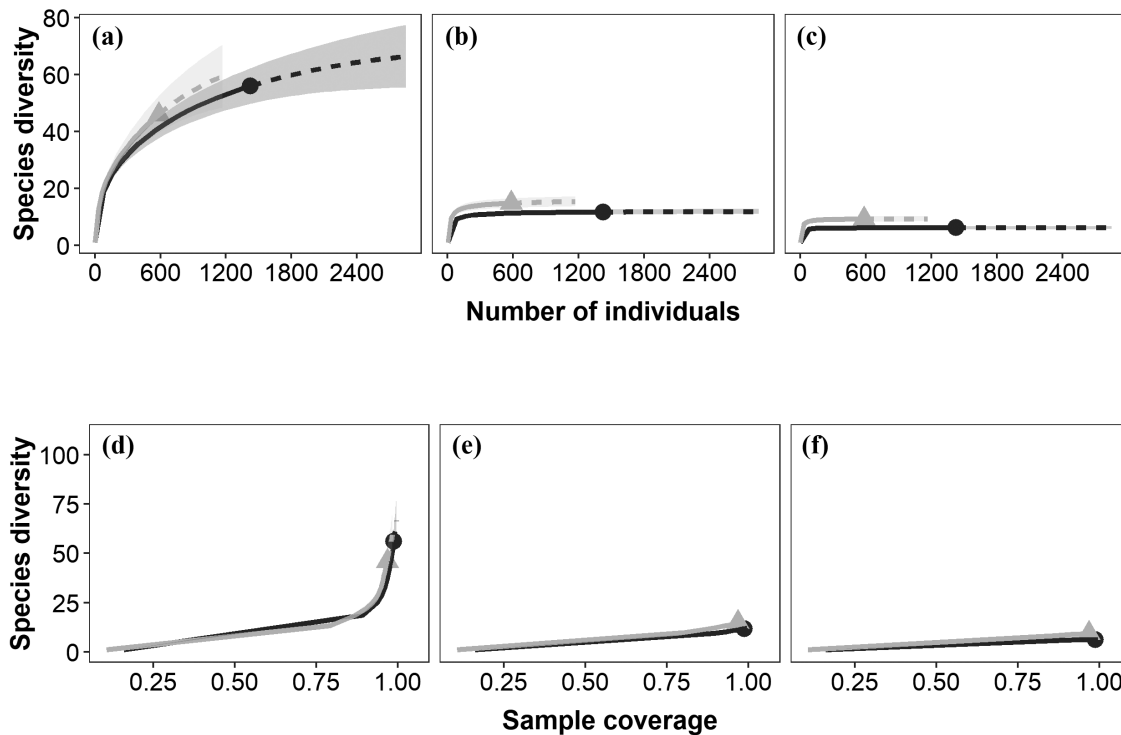


Figure 1. Sample-size-based rarefaction and extrapolation curves for wild bees in young early seral forest (one to seven years postharvest; black circle) and old early seral forest (eight to 15 years postharvest; gray triangle) for three diversity orders (a) species richness ($q = 0$), (b) Shannon diversity ($q = 1$), and (c) Simpson diversity ($q = 2$). Coverage-based rarefaction and extrapolation curves for wild bees in young early seral forest (one to seven years postharvest; black circle) and old early seral forest (eight to 15 years postharvest; gray triangle) for three diversity orders (d) species richness ($q = 0$), (e) Shannon diversity ($q = 1$), and (f) Simpson diversity ($q = 2$). Reference samples (i.e., the sample obtained from trapping) are shown by filled symbols, solid lines represent rarefaction curves, dashed lines represent extrapolation curves, and shaded regions represent 95% confidence intervals. Curves in (a–c) for both groups were set to two times the sample size following Chao et al. (2014); in contrast, coverages in curves in (d–f) were extrapolated to 99.6% for young early seral forest stands and coverage was extrapolated to 98.4% in old early seral forest stands; in both cases, this reflects a doubling of each reference sample.

NMDS ($r^2 = 0.30$, $F_{1,11} = 4.21$, $p = .007$; Figure 2). Of the 67 species we captured, 35 species (52.2%) were shared between young and old early seral stands, 21 species (31.3%) were only detected on young early seral stands, and 11 species (16.4%) were unique to old early seral stands (Table 1). Finally, we found no evidence of spatial autocorrelation for either observed bee species richness or bee abundance (range of Moran's I statistic: -0.13 to -0.10 , all $p > .58$).

Influence of Time Since Harvest on Bee Communities and Floral Resources

When modeling observed bee richness as a function of time since harvest we found strong evidence that richness was influenced by time since harvest ($\chi^2 = 13.01$, $df = 1$, $p < .001$) and sampling round ($\chi^2 = 7.43$, $df = 2$, $p = .024$); this model indicated that observed bee richness was expected to decline by an average of 20% for each year since harvest ($\beta = 0.80$ [95% CI: 0.71, 0.90]; Figure 3a). Observed bee species richness was 0.7 \times lower in the first round relative to the second round (95% CI: 0.6, 0.9; $t = -2.70$, $p = .011$) and 1.2 \times higher in the second round than the third round (95% CI: 0.9, 1.5; $t = 1.55$, $p = .131$), but only 0.9 \times lower relative to the third round (95% CI: 0.7, 1.1; $t = -1.17$, $p = .251$). Similarly, we found that bee abundance was strongly influenced by both time since harvest ($\chi^2 = 9.71$, $df = 1$, $p = .002$) and sampling round ($\chi^2 = 25.15$, $df = 2$, $p < .001$), with bee abundance expected to decline by an average of 30% for each year since harvest ($\beta = 0.70$ [95% CI: 0.56, 0.88]; Figure 3b). Bee abun-

dance estimates in the first round were 0.4 \times lower than the second round (95% CI: 0.3, 0.6; $t = -4.35$, $p < .001$) and 0.4 \times lower than the third round (95% CI: 0.2, 0.6; $t = -4.52$, $p < .001$); in contrast, abundance in the second round was very similar to that observed in the third round (ratio = 1.0 [95% CI: 0.6, 1.4], $t = -0.26$, $p = .794$). Finally, floral resource density was strongly influenced by time since harvest ($\chi^2 = 7.36$, $df = 1$, $p = .007$) and sampling round ($\chi^2 = 61.71$, $df = 2$, $p < .001$), with floral resource density expected to decline by an average of 28% for each year since harvest ($\beta = 0.72$ [95% CI: 0.57, 0.91]; Figure 3c). There was strong evidence that floral resources declined across the season: floral density in the first round was 2.9 \times greater than the second round (95% CI: 1.8, 5.0; $t = 4.23$, $p < .001$) and 8.9 \times greater than the third round (95% CI: 5.1, 15.7; $t = 7.85$, $p < .001$), with the floral resource density in the second round being 3.0 \times that of the third round (95% CI: 1.8, 5.2; $t = -4.35$, $p < .001$).

Discussion

Our study found that observed bee richness and abundance peaked several years after harvest and then declining rapidly as stands approached canopy closure. Additionally, old early seral stands had higher values for Shannon and Simpson diversity, indicating they supported bee communities that were less diverse and contained a greater proportion of common species and dominant species (Chao et al. 2014), respectively. Of the five diversity measures we examined, only estimated

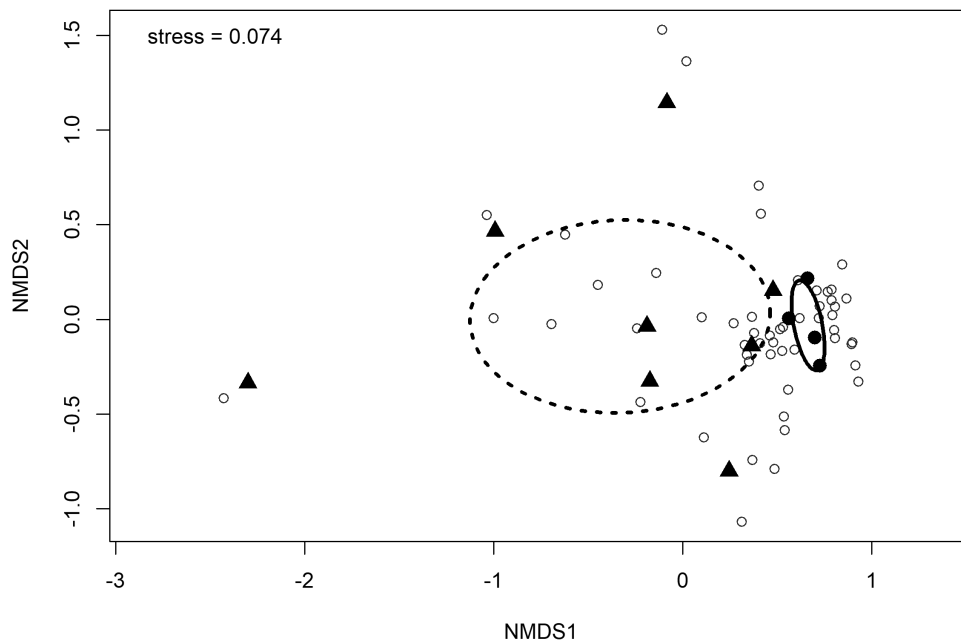


Figure 2. Nonmetric multidimensional scaling output indicating strong separation in compositional diversity of wild bee communities within young (filled circles, solid line) and old early seral forest (filled triangles, dashed line); individual bee species are shown by open circles. Ellipses show 95% confidence regions for the location of group centroids. R^2 values exceeded 0.98 in stress plots for both linear and nonmetric fits.

species richness was similar between young and old early seral stands. Taken together, this indicates a strong, negative relationship between bee diversity measures and time since harvest within regenerating conifer stands. Floral resource density generally tracked the same pattern of change in bee diversity, suggesting that food resources was a key driver for supporting bee populations and that floral resource declines resulted in less diverse bee communities. Among their key habitat needs, wild bees in temperate regions require open habitats with flowering plants and thermally favorable microhabitats (Hanula et al. 2016), and such conditions are uncommon or missing altogether from intensively managed conifer stands that have undergone canopy closure. This occurs because older forests have limited openings that allow light to reach the forest floor; this leads to cooler, darker environments with a dearth of flowering plants in bloom that contrasts strongly to early seral conditions that provide floral resources required by wild bees. Changes in floral resource availability may also occur through the use of herbicides that restructure plant communities, although this important topic remains unexamined within early seral communities and should be the focus of future work.

The peak in bee diversity that we found in young early seral stands appears to be a result of floral resources that increased after harvest and coincided with the period when nesting substrates were still available ground-nesting bees. Thus, our study suggests that recently harvested conifer stands may provide the best habitat for supporting populations of bees and other insect pollinators within forest landscapes under intensive timber production. In contrast, insect pollinators occurring in forest landscapes with multiple ownerships managing for diverse objectives may have less reliance on recently harvested stands for support their populations. For instance, postcanopy closure stands that are thinned (Neill and Puettmann 2013) or older stands with treefall gaps might provide small canopy openings that have adequate re-

sources for supporting insect pollinators in conifer forests of western North America, as has been found in eastern mixed hardwood forests (Proctor et al. 2012, Jackson et al. 2014, Mullally et al. 2019) and southern pine ecosystems (Hanula et al. 2015, Ulyshen et al. 2020). It remains unknown, however, how silvicultural systems that make use of uneven-aged regeneration methods influence the diversity of insect pollinators, so studies focusing on this topic will be particularly valuable (Rivers et al. 2018a). It is also worth noting that our study was restricted to a single year, and insect populations can have marked interannual fluctuations depending on local environmental conditions. Nevertheless, ongoing work in western Oregon has found that relationship between stand age and bee diversity measures holds even when bee populations undergo marked changes between years (Rivers et al., unpublished data), suggesting that the strong relationship we found in this study is robust against interannual population fluctuations.

An alternative but non-mutually-exclusive explanation for the pattern we observed posits that our stands were visited by bees that foraged on stands yet nested outside of harvest units. This may have occurred for two reasons. First, commuting distance between nest sites and foraging areas scales with body size in bees (Gathmann and Tschardt 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010), so larger bees can move over a larger area during foraging bouts. Based on published relationships (Greenleaf et al. 2007) the body size of many bees captured in our study (median intertegular distance = 2.19 mm; Rivers, unpublished data) were of sufficient size that would allow them to commute to the middle of stands—where trapping occurred—from locations outside the stand boundaries, such as roadsides areas. Second, the areas adjacent to the secondary roads that bordered some of our stands may have supported bee populations because roadside areas are generally open with extensive exposed soil and abundant flowering plants (Hanula et al. 2016), al-

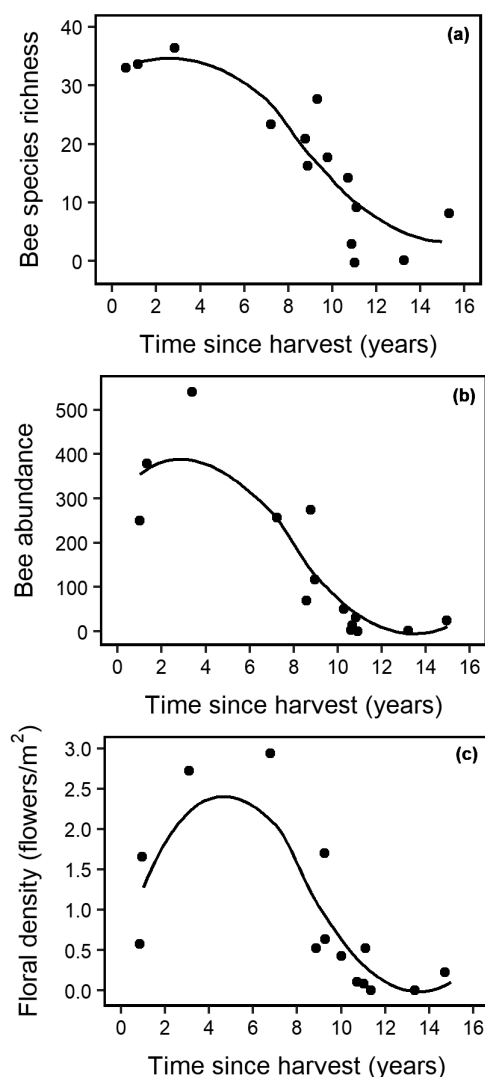


Figure 3. Relationships between time since harvest and (a) observed bee species richness, (b) bee abundance, and (c) floral density within early seral conifer stands in the Oregon Coast Range during summer 2014. The peak of bee diversity coincided with a peak in floral density in regenerating stands and occurred in the first half of early seral period. Note that fitted lines using a nonparametric local regression smoother (LOESS) are presented for plotting purposes, and that linear mixed models were used to evaluate the relationships between response variables and time since harvest (see “Methods”).

though it should be noted that roadside areas can have negative impacts on flowering plants (Waser et al. 2017). Thus, if bees did not nest within the boundaries of our study sites, it is plausible that some species nested in adjacent roadside areas and traveled to the interior of sites where they were captured, at least for the larger-bodied species that can move large foraging distances. If true, this suggests that roadside areas might be important areas for supporting bee populations within intensively managed landscapes. Regardless of the origins of the bees we captured, it is clear that they used early seral stands, and additional work should focus on determining where wild bees typically nest in managed forest landscapes and how contemporary management activities affect their populations. For example, roadsides might provide nesting habitat that facilitates dispersal within managed

forest landscapes but chemical treatment of roadsides (e.g., herbicide spraying of noxious weeds), which is a widespread practice and is mandated on some landownerships, may negate the benefits of roadside areas to pollinators.

We found that regenerating, intensively managed conifer forest supported a diversity of bee species that comprised 10–15% of the species thought to occur in Oregon, despite our decision to avoid sampling in spring to avoid increasing mortality rates of foundress queen bumble bees during colony establishment. Thus, it is perhaps not surprising that asymptotic species richness estimates suggested our observed bee richness measures were conservative and that additional sampling would have resulted in the detection of new species. We note that our findings are generally concordant with work undertaken at our study site approximately 30 years prior to our work (Burikam 1987) which recorded 80 bee species in stands three to 14 years postharvest; however, that study did not present data on abundance so only presence data can be compared. The higher species richness total from that study was due to a much larger number of *Andrena* (22 species detected in Burikam [1987] versus one species in our study) and appears to reflect sampling undertaken in the spring that occurred earlier than in our study, as spring is when species in this genus are most active in our region (A. Moldenke 2020, pers. commun.). Of note, nearly all the bumble bee species and their social parasites that we detected in our study were also recorded previously by Burikam (1987). An important exception was *B. occidentalis*, a species that we did not detect in our study but is currently of conservation concern because of large-scale declines throughout the western United States (Cameron et al. 2011, Graves et al. 2020).

During the course of our work, we captured a number of species that are considered important pollinators of agricultural crops, including the European honeybee (*Apis mellifera*), sweat bees (*Halictus* spp.), long-horned bees (*Melissodes* spp.), and bumble bees (*Bombus* spp.). Of these, bumble bees were the most well-represented group in our study with nine species captured plus two additional social parasitic species that rely exclusively on *Bombus* as hosts; together these species represented nearly 40% of our captures. Although we did not detect it in this study, an additional bumble bee—*B. melanopygus*—is also found in regenerating stands in our area and has an early spring flight season that ends prior to the period when our sampling occurred. Thus, approximately 40% of the bumble bee species found in the Pacific Northwest were captured during the course of our study (Williams et al. 2014). Bumble bees are particularly important for the pollination services they provide to plants in natural systems and to pollinator-dependent agricultural crops (Memmott et al. 2004, Fontaine et al. 2006, Hegland and Totland 2008), including the most abundant bumble bee recorded in our study, *B. vosnesenskii* (Rao and Stephen 2009, Stephen et al. 2009, Broussard et al. 2011). Bumble bees pollinate a wide range of agricultural crops within our study region throughout the year (Rao and Stephen 2010), from early season blueberries (Stephen et al. 2009) to red clover seed in late summer (Rao and Stephen 2009). Given concerns about long-term bumble bee population declines and the pathogens that contributed to these declines (Cameron et al. 2011, Meeus et al. 2011, McArt et al. 2017, Cameron and Sadd 2020), additional work is needed to understand interactions between bumble bees in production forests and agricultural crops,

including an assessment of the extent to which forest bumble bee populations contribute to agricultural crops in mixed production landscapes. Such benefits may accrue directly through pollination “spillover” effects (Blitzer et al. 2012) or indirectly through forests providing source populations that are available to colonize agricultural areas. Although bumble bees were most plentiful group, more focused study on other bee species known to benefit crops will also be fruitful given the adjacency between regenerating forests and pollinator-dependent crops in many regions, including our study area (Rao and Stephen 2010).

Conclusions

Our findings that intensively managed conifer forests supported a diverse bee community compliments a growing number of studies that has found that wild bee populations are supported by conifer forests in western North America (Heil and Burkle 2018, Rhoades et al. 2018, Rivers et al. 2018b, Galbraith et al. 2019a, Foote et al. 2020), pine and deciduous forests in the southeastern United States (Ulyshen et al. 2010, 2020, Miljanic et al. 2019), and deciduous forests in eastern North America (Proctor et al. 2012, Roberts et al. 2017, Milam et al. 2018, Smith et al. 2019, Odanaka and Rehan 2020). Thus, it is clear that forest ecosystems, including conifer forests managed intensively for timber production, support a wide range of insect pollinators. This is particularly important in North America given that forests comprise approximately one-third of the land base (World Bank 2016) and trees cover >50% of most US states (Nowak and Greenfield 2012); thus, the continued study of the role bees and other insect pollinators play in these ecosystems will be an important avenue for future research. In particular, we view two next steps as critical for additional study. First, there is a particularly strong need for evaluating how management activities that occur within forested landscapes influence pollinators (Rivers et al. 2018a), which encompasses such distinct topics as evaluating the influence of timber harvest approaches on pollinators and their habitat, assessing how secondary road creation and maintenance affects pollinators, and understanding how multiple-use objectives—such as allowing the placement of European honey bee hives in forest ecosystems—ultimately influence forest pollinator health. Second, it is clear that initiatives to conserve pollinators on broader spatial (e.g., regional) scales must include forest ecosystems if they are to be truly comprehensive, particularly in areas where agricultural croplands share the landscape with managed forests. Given their importance, research on both of these topics should be undertaken in concert to maximize conservation efforts and ensure that insect pollinator populations and the services that they provide to natural and managed ecosystems are maintained into the future.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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