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ARTICLE
Disease Ecology

Host and floral communities shape parasite prevalence and reproduction in intensively managed forests

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Abstract

Understanding how working landscapes can maintain viable wildlife populations is key to evaluating their conservation potential. We assessed the potential of intensively managed conifer forests for supporting healthy, productive bee populations in one of the major timber-growing regions of the world, the Pacific Northwest. We examined the direct effect of the number of years post-harvest and other forest characteristics on flowering plant and bee communities and their indirect effect on parasite prevalence (*Apicystis* spp., *Ascosphaera* spp., and *Crithidia* spp.) and reproduction of a native, forest-dwelling solitary bee (*Osmia lignaria*). Forest characteristics, including the time elapsed since harvest, influenced floral and bee community diversity and abundance and indirectly impacted parasite prevalence and offspring production. We found that increased bee diversity was associated with reduced parasite prevalence—consistent with a dilution effect—but the strength of the relationship varied across the different parasites. Additionally, bee abundance was more consistently associated with increased parasite prevalence, providing evidence of amplification. Floral abundance was only associated with lower *Apicystis* spp. prevalence. Across all parasite models, however, the R^2 values were <20%, indicating that additional factors shape bee communities beyond those we examined. Offspring production was positively related to floral diversity but not to parasite prevalence. Our results suggest that managing floral diversity is critical to enhancing the value of these landscapes for wild bee communities, both directly through promoting bee diversity and reproduction, and indirectly through facilitating parasite dilution.

KEYWORDS
clearcut, forest, Pacific Northwest, parasitism, timber, tree plantation, wild bees

INTRODUCTION

The goal of conservation in working landscapes is to support biodiversity (Kremen & Merenlender, 2018) and supply critical ecosystem services for the production of timber, food, fiber, and fuel (Cardinale et al., 2012). Whereas some working landscapes can provide valuable habitat and support healthy populations (Kremen & Merenlender, 2018), others can create ecological traps and/or population sinks (Ganser et al., 2019; Garibaldi et al., 2021; Santangeli et al., 2018). Human-modified landscapes can also facilitate the spread of infectious disease in wildlife (Brearley et al., 2013), which is among the top drivers of global extinction (Smith et al., 2006). Understanding the factors that maintain healthy, viable wildlife communities in working landscapes is necessary for evaluating their conservation potential (Gilroy & Edwards, 2017).

Intensively managed forests, approximately 7% of forests globally or ~0.28 billion ha (FAO and UNEP, 2020), are one such working landscape with conservation potential (Brockerhoff et al., 2008; Hanula et al., 2016; Hartley, 2002; Jose, 2009; Mola et al., 2021; Paquette & Messier, 2010; Rivers, Galbraith, et al., 2018; Stokely et al., 2021). Given the global decline of wild bees (Potts et al., 2016) and U.S. Endangered Species Act petitions and listings of several bee species (Graves et al., 2020; Jackson et al., 2022; U.S. Fish and Wildlife Service, 2021), the potential of intensively managed forests for providing wild bee habitat has gained interest among land managers (Rivers, Galbraith, et al., 2018). However, while closed-canopy forest does not support many wild bees (Ponisio et al., 2016; Simanonok & Burkle, 2019), timber harvest that removes a large portion of the canopy, such as clearcutting, creates potential pollinator habitat by increasing light availability to understory plants (Kilkenny & Galloway, 2008; Rivers & Betts, 2021; Taki et al., 2013). As the forest's canopy closes in the years post-harvest, the flowering plants and the bees it supports decline (Rivers & Betts, 2021; Zitomer et al., 2023). In Douglas-fir plantations in the Pacific Northwest (PNW), Rivers and Betts (2021) observed that flowering plant and bee abundance within harvested stands peaked approximately three years post-harvest and declined thereafter. In addition to the time since harvest, stand management, including herbicide use intensity and harvest residue removal, is known to affect plant–pollinator communities (Kormann et al., 2021; Rivers, Mathis, et al., 2018). Because recently harvested stands often occur within a matrix of closed-canopy forests in working forest landscapes, clearcut area may also impact bee community abundance and diversity. While there is growing evidence that managed early seral forests support diverse pollinator communities (Korpela et al., 2015; Rivers & Betts, 2021; Rivers, Mathis, et al., 2018; Rodríguez & Kouki, 2017; Taki et al., 2013), previous studies have focused on community-scale assessments without evaluation of population health or offspring production. In this study, we fill this critical gap by quantifying how the plant–bee community response to intensively managed forest characteristics influences infectious disease prevalence and offspring production.

Infectious parasites can strongly affect bee immunity, physiology, and reproduction (Liu et al., 2020; Paris et al., 2018). The sharing of floral resources is a common mode of disease transmission among pollinators, and an increase in host aggregation on floral resources can lead to an increase in disease prevalence ("amplification"; Cohen et al., 2021; Durrer & Schmid-Hempel, 1994; Halliday et al., 2020). Cohen et al. (2021) found that mass-blooming sunflower crops led to host aggregation and disease amplification. Similarly, Piot et al. (2019) found that wildflower resources adjacent to nonflowering crops are associated with an increased prevalence of parasites in bumble bees. Conversely, high host species diversity—even if accompanied by host aggregation—may dilute infection ("dilution"; Fearon & Tibbetts, 2021; Halliday et al., 2020). For example, bee richness diluted generalist RNA virus presence in bee communities (Fearon & Tibbetts, 2021). Flower abundance may further contribute to parasite dilution by helping to avoid aggregation in limited resources (Cohen et al., 2021; McNeil et al., 2020; Piot et al., 2021). As isolated areas containing floral resources within a matrix of closed-canopy forests, recently harvested stands have the potential to aggregate bee hosts into high densities, amplifying disease. Conversely, the dilution effects of host and flowering plant diversity may outweigh the amplification effect of host aggregation, leading to low parasite prevalence rates. Parasite prevalence, therefore, will depend on the relative strength of the amplification and dilution effects.

In addition to evaluating infectious disease presence, assessing the reproductive success of populations within working landscapes is necessary to understand whether these areas serve as ecological traps. Bee populations rely on the quality and accessibility of floral resources—most often pollen and nectar (Minckley & Roulston, 2006). Bee reproduction is influenced by floral resource availability (Woodard & Jha, 2017), interspecific competition (Thomson, 2004, 2016), and parasitism (Koch et al., 2017). In the social bee *Bombus*, nest density increases with flower availability within a 1-km radius (Knight et al., 2009) and lineage survival is higher in areas with higher quality local food resources (Carvell et al., 2017). In solitary bees, a study of experimentally placed *Osmia lignaria* nest boxes showed that reproductive output was

positively related to native plant abundance in urban landscapes (Palladini & Maron, 2014). Simanonok and Burkle (2019) showed that tree canopy closure after wildfire results in diminished floral resources and reduced nesting success of wood-cavity-nesting bee species. Conversely, fire severity, related to canopy openness and floral resources, was positively related to experimentally placed *O. lignaria* reproduction (Galbraith et al., 2021). By affecting flower resource abundance and diversity, the time since harvest in intensively managed stands may have a similar effect as succession post-wildfire on bee offspring production.

The number of bees in a community can reduce offspring production if bees compete for floral resources. For example, Thomson (2004) showed that proximity to honey bee colonies lowered bumble bee colony reproductive fitness and the abundance of foragers on flowers. Because the adult bees in a specific year result from resource availability in the prior year (Cohen et al., 2021), the number of bees emerging each year in regenerating stands may overshoot the diminished resources of the current year as the canopy closes, with competition further reducing reproductive output. Lastly, parasitism has been shown to affect the foraging efficiency, ultimately impairing bee reproduction (Koch et al., 2017). Though there is a growing literature on parasite prevalence in wild populations (Cohen et al., 2021; Fearon & Tibbetts, 2021; Figueroa et al., 2020; McNeil et al., 2020; Piot et al., 2019) parasite infection does not necessarily translate into fitness impacts, and few studies have examined the link between parasite prevalence and reproduction.

We focus on one of the world's major timber-growing regions, the PNW of North America (Oregon Forest Resources Institute, 2023), to evaluate the potential of intensively managed forests for supporting healthy, productive bee populations. Past work in this system has documented diverse bee communities, with bee diversity and abundance decreasing with time since harvest (Rivers & Betts, 2021; Zitomer et al., 2023). Here, we examine the direct effect of time since harvest and other forest characteristics on flowering plant and bee communities and their indirect effect on parasite prevalence and reproduction in a native, forest-dwelling solitary bee (*O. lignaria*). Specifically, we test whether, by affecting plant–pollinator community characteristics, forest characteristics (1) lead to parasite amplification or dilution and, in turn, (2) impact bee reproduction. We also test for a link between parasite prevalence and bee reproduction. As one of the first studies to evaluate bee health and reproduction in intensively managed forests, our work advances our understanding of how such areas support wild bee communities within managed forest landscapes.

METHODS

Study system

Our study was conducted in the Coast Range Mountains of western Oregon in the PNW, a globally important timber production region (Figure 1). Oregon leads all U.S. states in producing softwood lumber, with >70% of timber harvest occurring on private industry and state land holdings (Oregon Forest Resources Institute, 2023) such as those evaluated in this study. Our study region is a coastal temperate rainforest within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin & Dyrness, 1973) that receives 250–300 cm of precipitation annually, primarily as winter rain. Douglas-fir (*Pseudotsuga menziesii*) is the most important commercial tree species in this area, with stands often containing a diversity of grasses, ferns, flowering plants (e.g., American vetch, *Vicia americana*; Pacific starflower, *Lysimachia latifolia*; fireweed, *Chamerion angustifolium*), and broadleaf shrubs (e.g., vine maple, *Acer circinatum*; blackberries and other berries *Rubus* spp.; Oregon grape, *Berberis nervosa*; salal, *Gaultheria shallon*). We selected 60 stands on private (three companies) and state lands (Oregon Department of Forestry, ODF) that had been harvested 0–35 years before 2018 (Figure 1), with the majority of stands <15 years old because of the rapid canopy closure that occurs within intensively managed conifer forests (Rivers & Betts, 2021). We calculated the age of 55 stands using a shapefile of forest disturbance 1986–2019 (Clary, 2020) detected using the LandTrendr temporal segmentation algorithm (Kennedy et al., 2010). We used landowner-reported stand ages for five stands where no disturbance was detected. Road access to one of the selected stands was blocked during fieldwork, so only 59 stands were surveyed.

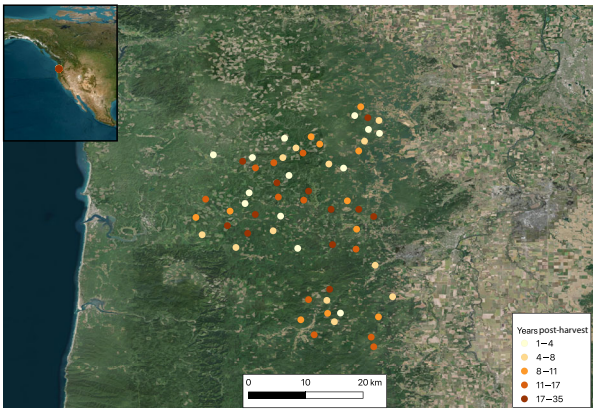

FIGURE 1 Locations of the survey stands in the Coast Range of Oregon, USA. Surveyed stands vary in the number of years post-harvest from 1 to 35.

O. lignaria reproduction and parasite prevalence

We used *O. lignaria* as a focal bee because it is native to our study region and often found in forest habitats (Galbraith et al., 2021). Because it is a cavity nester, it is also an ideal species for estimating reproductive output. Following the methods of Galbraith et al. (2021), we placed new BinderBoardTM laminate nest blocks (Pollinator Paradise, Parma, ID) at each of the 59 surveyed stands in early spring of 2019. The blocks at two stands were badly damaged by marauding American black bears (*Ursus americanus*), leaving 57 stands with successful nest blocks. Each nest block was mounted at the top of a 1.5-m metal t-post and contained 32 nesting chambers, each lined with a new paper straw. Below each nest block, we affixed one PVC cocoon holding chamber (2.5 cm diameter × 10 cm long) containing 20 females and 25 males *O. lignaria* cocoons. Each chamber was capped, but one end cap contained a small hole oriented in the same direction as the openings of the nest block to maximize the likelihood that emerging females would detect the nest block upon emergence. The holes were 7–8 mm in diameter, which is known to be favored by *O. lignaria*. We deployed cocoons at the nest boxes for approximately two weeks starting in mid-April 2019 to coincide with the spring emergence period in wild *Osmia* populations.

We used two nest blocks at each stand to characterize *O. lignaria* reproduction independent of the blocks from which we collected females for parasite assays (see below). Each of these blocks was set 20 m from the stand center. The first block was set at a randomly selected azimuth, and the second was set 180° from that azimuth so that the blocks were located 40 m apart in each stand. The nest box holes were lined with sterile paper straws. We allowed all females within these blocks to undergo normal nesting behaviors so we could quantify nesting activity. Females in this group of nests were allowed to complete breeding, at which time nests were removed from the field, taken to a storage facility, and held at ambient temperature until the fall to allow larvae to develop. In the fall of 2019, nests were brought to the USDA-ARS Bee Biology Laboratory in Logan, UT, where each nest straw was x-rayed to quantify the number of offspring produced by nesting females. We use this value—hereafter referred to as offspring production—to evaluate how the floral and bee communities influence *O. lignaria* reproduction. The offspring were verified as all *O. lignaria* after emergence. No *Osmia cornifrons*, a non-native *Osmia* known to use similar nest boxes as *O. lignaria*, were detected at any of our stands.

In addition to the reproduction data, we selected 27 sites for collecting data on parasite presence. These 27 sites were a random sample of the 59 stands where the bee community was surveyed, stratified to represent the full age gradient and all ownership types. Within this subset of sites, we placed two additional nest blocks to quantify parasite prevalence. These blocks were set 20 m from the stand center at 90° and 270° from the originally selected random azimuth. We regularly monitored nesting activity after bees were placed on stands. When nesting females occupied approximately 10 nest chambers, we attempted to capture females to assess parasite loads using sterile nitrile gloves and a sterile 15-mL centrifuge tube. To collect females, we waited for a female to return from a foraging trip and enter her nest chamber, and then placed the clear centrifuge tube over the entrance. To expedite the capture of the females, which often were reticent to leave the nest chamber, we removed nest straws with a sterilized pair of forceps and used the forceps to transfer each female into a separate centrifuge tube. We then immediately placed the tube on dry ice in a cooler and resterilized our equipment before continuing with captures. We collected as many females as possible, up to 10 individuals at each of the two nest blocks from which we characterized parasite load. Samples were kept on dry ice in the field and stored in a −80°C freezer until analysis. From the same *O. lignaria* cocoons that were deployed in the field, we collected two types of controls: (1) adults that emerged in the lab in sterile petri dishes and then were frozen immediately ($N = 10$) and (2) adults dissected from cocoons before emergence ($N = 14$). From these controls, we assessed preforaging parasite prevalence (i.e., parasites contracted from contact with infected nest materials).

Parasite screening

We screened 365 individuals across the forest stands and 24 controls. We screened each bee for parasites that vary by taxonomy, symptoms, and transmission, including *Apicystis* spp. (neogregarine), *Ascosphaera* spp. (fungus), and *Crithidia* spp. (trypanosomatid) using parasite-specific primers for genus-level identification (Cohen et al., 2021). *Ascosphaera* spp. has been detected across multiple wild bee taxa, including *Osmia* (Evison & Jensen, 2018; Figueroa et al., 2021; Strobl et al., 2019). *Ascosphaera* spp. causes "chalkbrood," which is actively managed in commercial production of *Osmia* and other megachilids to avoid brood losses (Pitts-Singer & Cane, 2011; Sedivy & Dorn, 2014). Active replication of *Crithidia* spp. in *Osmia* has been confirmed in laboratory studies (Figueroa et al., 2021; Lim et al., 2023; Ngor et al., 2020; Strobl et al., 2019) and is associated with reduced survival (Figueroa et al., 2021; Strobl et al., 2019). *Apicystis* spp. is found in *Osmia* and other wild bees at

high rates (Cohen et al., 2020; Graystock et al., 2020; Tian et al., 2018). *Apicystis* spp. are associated with reduced survival in *Osmia* (Tian et al., 2018). In this study, we use parasite presence as a metric for bee health. One limitation of this approach is that we are unable to assess the disease status of a host (i.e., whether the parasite was pathogenic, and thus the bee exhibited disease symptoms). Given the many studies showing that negative impacts are possible (e.g., Figueroa et al., 2021; Strobl et al., 2019; Tian et al., 2018), we assume that the presence of these parasites in the gut of bees has the potential to have a negative impact on bee health.

We extracted DNA from each bee with the Qiagen DNeasy blood and tissue kit. To lyse samples, we added 180 μL Buffer ATL to each sample, two sterile 5-mm stainless steel beads, and approximately 100 μL of 0.1-mm zirconia beads in a Qiagen Tissue Lyser II. We included one negative and positive control per sample plate. We also confirmed that each sample contained bee DNA by amplifying a EF-1α gene sequence associated with bees (Hines et al., 2006). We resolved amplicons with electrophoresis on a 1% agarose gel.

Characterization of wild bee and flowering plant communities

We surveyed wild bee and flowering plant communities in each stand in early May and early June 2019 to coincide with *O. lignaria* nesting activity. These surveys were conducted in the context of a larger sampling effort (see Zitomer et al., 2023), but here, we describe only a subset of sampling relevant to the timing of *O. lignaria* nesting activity in 2019. To survey bee communities, we used two different approaches. First, we utilized passive trapping methods, combining blue vane traps and bowl traps deployed thrice during the season. We placed traps along a 40-m transect at the center of the stand, perpendicular to the transect on which *O. lignaria* nest blocks were located. We installed two blue vane traps (SpringStar, Inc. [now BanfieldBio Inc.], Woodinville, WA) mounted on 1.5-m metal t-posts at the end of each transect, with two rows of bowl traps painted white, fluorescent yellow, and fluorescent blue (New Horizons Supported Services, Inc., Marlboro, MD) with three bowl traps per color in between the vane traps. We spaced bowl traps 5 m apart with alternating colors in two parallel lines along the main transect; all bowl traps were mounted ca. 20 cm off the ground, and any vegetation overhanging the trap was trimmed. We deployed the traps for 48 h with soapy water, then collected the specimens.

In addition to passive trapping, we also netted wild bees that we observed visiting flowers along three transects in the center of each stand. We alternated netting and passive sampling at stands while the *O. lignaria* were active, with netting taking place during favorable conditions (i.e., air temperature >16°C, wind speed of <3 on Beaufort wind scale). To sample bees, we established a 20-m-long transect that radiated outward from the middle of the stand from a randomly selected azimuth; we also sampled from two additional transects of the same length and offset by 120 and 240, respectively. We walked along each transect at a steady pace for 15 min using a stopwatch to keep time, netting any bees observed visiting flowers within 1.5 m on either side of the transect. When we netted a floral visitor, we paused the stopwatch while we processed the specimen, restarting when netting resumed. Bees were identified as species or morphospecies (for species in the subgenus *Lasioglossum* Dialictus; the genera *Triepeolus*, *Sphecodes*, *Nomada*, and *Hylaeus*; and some species of *Osmia* and *Andrena*) by L. Best at Oregon State University.

We quantified floral resources by counting the number of stems of every species observed flowering in the transects and multiplying it by the average number of blooms/stem observed on 10 stems per species. We counted inflorescences rather than individual flowers for species with many tiny flowers per inflorescence: *Daucus carota*, *Trifolium repens*, *Toxicodendron diversilobum*, and head inflorescences of all species in the Asteraceae family.

Our response variables of interest (offspring production and parasite prevalence) are the accumulation of the bees' floral and bee community experiences through the *O. lignaria* flight season, so we selected metrics that would summarize that experience—the mean bee/floral abundance and diversity across the flight season. We chose the mean because we wanted a metric that would capture extremes of floral availability and the bee community context, both the highs and the lows, which would impact the resources to which a bee had access and the other hosts it encountered. In addition, each bee survey method (net, pan, vane) represents a sample of the bee community on that day, each with its own bias (Prendergast et al., 2020). We therefore took the mean across the different methods to represent the bee species at a stand. In these calculations, we included the non-native European honey bee (*Apis mellifera*), which was rarely encountered and only in low abundance.

STATISTICAL MODELS

We used structural equation models implemented within a Bayesian framework to investigate the effects of forest characteristics on (1) bee parasitism and (2) offspring

production via their effects on flowering plant and bee communities (Figure 2).

Model 1.1: Years post-harvest and stand characteristics

In the first model, we modeled the direct effects of years since a stand was harvested on floral species diversity and abundance (Figure 2, arrow a). Because floral diversity and abundance peaked after the first year post-harvest, we also included a squared term for a curvilinear fit. Flower and bee abundance were calculated as means over a season, so we assumed Gaussian error. Different landowners have standard practices concerning herbicide application frequency, quantity, application method, and the degree of residue removal post-harvest, which are known to affect flowering plant communities (Kormann et al., 2021; Rivers, Mathis, et al., 2018). Because the specific combinations of management techniques are not reported publicly for private companies, we included landowner identity (the three private companies and ODF) in the models as a proxy for general differences in stand management (Figure 2, arrow b). To account for elevational differences between stands, which are known to affect plant abundance and diversity, we

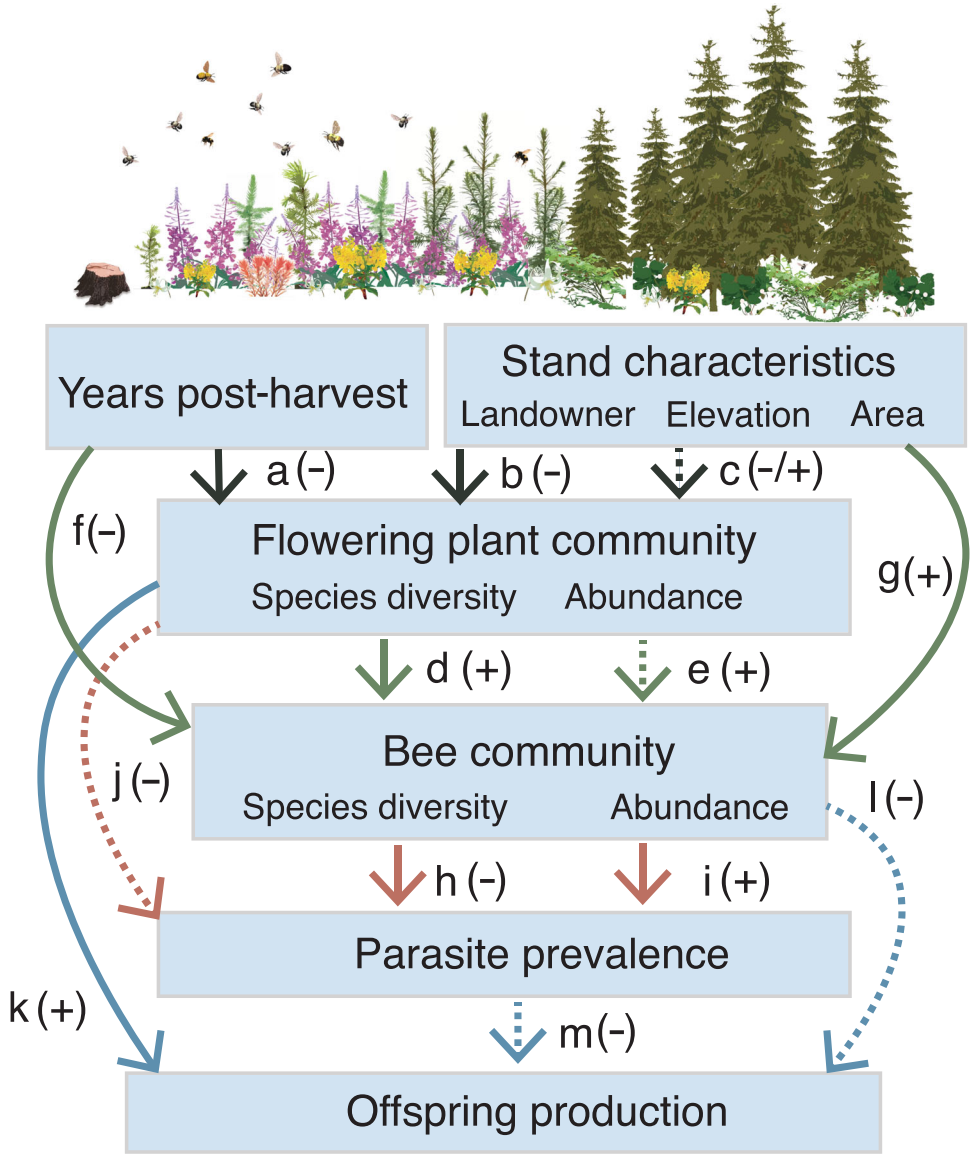

FIGURE 2 Conceptual framework: the hypothesized relationships between forest characteristics, plant–bee communities, bee health, and reproduction. Arrows represent hypothesized links (each assigned a letter to distinguish between them in the text). The expected direction of the hypothesized relationships is denoted by a + or − beside each arrow (Model 1.1 = black arrows, Model 1.2 = green arrows, Model 1.3 = red arrows, Model 2 = blue arrows). Arrows are dashed if we did not find evidence of the hypothesized relationship.

also included elevation as an explanatory variable (Figure 2, arrow c).

Model 1.2: Plant–pollinator community interactions

In the second level of the model, floral abundance and diversity were included as explanatory variables of bee community abundance and diversity (Figure 2, arrows d and e). We also included a direct effect of the number of years post-harvest on the bee community (Figure 2, arrow f), with the hypothesis that nonfloral resources used by bees (i.e., for nesting) might be affected by the number of years post-harvest. Like the floral model, we included a squared term of years post-harvest. In addition, because the area of open habitat available to bees may affect their abundance and diversity, we included stand area as an explanatory variable (Figure 2, arrow g). As with the plants, we assumed a Gaussian error because bee abundance and diversity were seasonal means. We did not have an a priori hypothesis about the direct effects of stand management or elevation on bees, so these links were not included in this level of the model.

Model 1.3: Parasite prevalence

In the third layer of the model, we included the effect of bee diversity and abundance (Figure 2, arrows h and i) and floral abundance (Figure 2, arrow j) on parasite presence (0,1), assuming binomial error. We included each parasite individually as response variables and, in a separate model, as combined (1 if any parasite was present, 0 if the bee had no parasites; hereafter, "any parasite"). Across the different models, we included intercepts for stand identity drawn from common distributions (i.e., referred to as random effects in a frequentist framework). In the parasite model, we also included intercepts for the nest block from which the adult bee was collected, drawn from common distributions.

Model 2: Offspring production

We built a model analyzing the effect of parasite prevalence and the flowering plant–bee community on *O. lignaria* offspring production. Because data were collected at different scales (the offspring production was at the level of a nest box and the parasite data were at the level of an individual bee), we could not build on Model 1 and instead created a second model. As we collected offspring production data from more stands than we surveyed parasites (31 of the 57 stands with successful nest boxes), missing values were imputed using multiple imputation by chained equations with the R package mice (van Buuren & Groothuis-Oudshoorn, 2011). Multiple imputation uses observed data and associations to predict missing values and captures the uncertainty involved in the predictions by imputing multiple datasets. In a Bayesian framework, the posterior distributions of the missing values are sampled, and then those samples are substituted for the missing data to form an imputed dataset. We generated 100 imputed datasets.

We examined the impacts of floral abundance and diversity (resource availability; Figure 2, arrow k), bee abundance (interspecific competition; Figure 2, arrow l), and parasitism rate (parasite prevalence/total individuals tested at a stand; Figure 2, arrow m) on offspring production, assuming a negative binomial error. We modeled the same relationships as Model 1.3 on parasitism rate to account for possible indirect effects of the bee and floral community on offspring production through their effect on parasite prevalence. Because each stand had multiple nest boxes, we included random intercepts drawn from common distributions for stand identity.

For the parasite models (Model 1), three Markov chain Monte Carlo (MCMC) chains were run for 10^4 iterations after an initial burn-in of 10^2 iterations using STAN via the R package brms (Bürkner, 2017). For the offspring models (Model 2), we fit the model using the 100 imputed datasets to average across them (using the function brm_multiple from the brms package; Bürkner, 2022), which required more iterations to converge, so we ran these models for 5×10^4 iterations with a burn-in of 2.5×10^2. We used brms's recommended default, uninformative priors: flat over all real numbers for the means of the distributions of the top-level parameters and Student's t-distribution $(3,0,2.5)$ for the variances. Analyses were conducted in R 4.3.1 (R Core Team, 2015). We used standard practices for assessing convergence, including examining the chains, bulk and tail effective sample size, and R-hat values. Bürkner (2022) notes that R-hats >1 on imputed datasets can be false positives concerning convergence, so we relied on chain examination to determine convergence. To judge support for our hypotheses, we evaluated what percent of the posterior of a parameter was above or below 0. If 95% or more of the posterior was above or below zero, we considered this to be strong support for a relationship between the response and the explanatory variable under consideration. If 90% or more of the posterior was above or below zero, we considered this to be some support for a relationship between the response and explanatory variable under consideration (Ponisio et al., 2019). We calculated

Bayesian R^2 values for each model (using the function bayes R_2; Bürkner, 2017; Gelman et al., 2019).

RESULTS

We collected and identified 2461 wild bees comprising 96 unique species and morphospecies from 20 genera (including males and females) during the period that *O. lignaria* were foraging in stands. The five most abundant genera were (1) *Halictus* ($N = 673$), (2) *Lasioglossum* ($N = 624$), (3) *Agapostemon* ($N = 327$), (4) *Melissodes* ($N = 271$), and (5) *Bombus* ($N = 251$). The five most speciose genera were (1) *Lasioglossum* ($N = 24$), (2) *Andrena* ($N = 13$), (3) *Bombus* ($N = 9$), (4) *Osmia* ($N = 9$), and (5) *Hylaeus* ($N = 6$). We observed 117 species of flowering plants in regenerating stands. We screened 420 *O. lignaria* individuals for parasites. Seventy-eight percent of the individuals had at least one parasite. Forty-six percent of the bees screened were positive for *Crithidia* spp., 44% were positive for *Ascophaera* spp., and 33% were positive for *Apicystis* spp. Only 1 (4.2%) of the 24 control individuals tested positive for *Apicystis* spp. and 3 of 24 (12.5%) tested positive for *Ascophaera* spp. Most of the controls (20/24, 83.3%) tested positive for *Crithidia* spp., indicating there was a high rate of infection prior to foraging. The proportion of infected individuals did not vary between controls that emerged in the lab or dissected from cocoons. The average number of *O. lignaria* offspring in a nest box was 160 ± SD 72, totaling 17,753 offspring across all nests.

Model 1.1: Years post-harvest and forest characteristics

As we hypothesized, we found strong support for a negative relationship between years post-harvest and floral and bee diversity and abundance (Table 1, Figure 3). We also found some evidence that floral diversity varied between landowners, with one company's stands having lower diversity than ODF-managed stands (Table 1). We did not find strong evidence that floral abundance varied between landowners. We did not find strong evidence for

TABLE 1 Parameter estimates for the models with bee and plant community characteristics as response variables.

Response variable	Explanatory variable	Estimate	SE	LB-95%	UB-95%	*R*-hat	Bulk ESS	Tail ESS	$p > 0$	$p < 0$
Floral diversity	**Years post-harvest (log)**	−0.63	0.12	−0.86	−0.4	1	5420.89	3551.18	0**	1**
	Years post-harvest^2 (log)	−0.13	0.09	−0.3	0.06	1	6396.47	3779.43	0.08*	0.92*
	Elevation	−0.08	0.13	−0.34	0.17	1	5768.28	3761.45	0.26	0.74
	ODF vs. OwnerA	−0.57	0.44	−1.44	0.28	1	3776.53	3563.28	0.09*	0.91*
	ODF vs. OwnerB	−0.04	0.4	−0.83	0.74	1	3859.07	3271.99	0.46	0.54
	ODF vs. OwnerC	0.29	0.41	−0.49	1.13	1	3586.99	3430.26	0.76	0.24
Floral abundance	**Years post-harvest (log)**	−0.59	0.14	−0.87	−0.32	1	6259.03	3767.94	0**	1**
	Years post-harvest (log)^2	0.03	0.11	−0.16	0.25	1	6303.93	4019.98	0.61	0.39
	Elevation	−0.19	0.15	−0.5	0.1	1	5344.96	3537.64	0.11	0.89
	ODF vs. OwnerA	0.16	0.49	−0.79	1.16	1	3784.51	3837.26	0.62	0.38
	ODF vs. OwnerB	−0.03	0.45	−0.92	0.85	1	3785.78	3389.27	0.47	0.53
	ODF vs. OwnerC	0.12	0.47	−0.82	1.01	1	3535.71	3871.7	0.6	0.4
Bee diversity	**Years post-harvest (log)**	−0.53	0.09	−0.7	−0.35	1	4668.03	3457.66	0**	1**
	Years post-harvest (log)^2	0.12	0.06	0.01	0.22	1	5807.35	3643.29	0.98**	0.02**
	Floral diversity	0.33	0.08	0.17	0.49	1	4835.52	3482.15	1**	0**
	Clearcut area (hectares)	0.04	0.07	−0.11	0.18	1	4707.1	3251.49	0.7	0.3
Bee abundance	**Years post-harvest (log)**	−0.64	0.21	−1.06	−0.25	1	5187.56	3599.53	0**	1**
	Years post-harvest (log)^2	0.1	0.14	−0.17	0.37	1	5712.29	3516.54	0.78	0.22
	Floral abundance	0.09	0.18	−0.25	0.45	1	5115.41	3751.81	0.69	0.31
	Clearcut area (hectares)	0.27	0.19	−0.1	0.64	1	5057.21	3560.83	0.93*	0.07*

Note: ** and * indicate 95% (strong support) or 90% (support) (the variable name is also bolded). All *R*-hats were equal to 1, indicating chain convergence.
Abbreviations: ESS, effective sample size; ODF, Oregon Department of Forestry; UB and LB, upper and lower highest density 95% credible intervals; $p > 0$ and $p < 0$, proportion of the posterior samples greater than and less than 0.

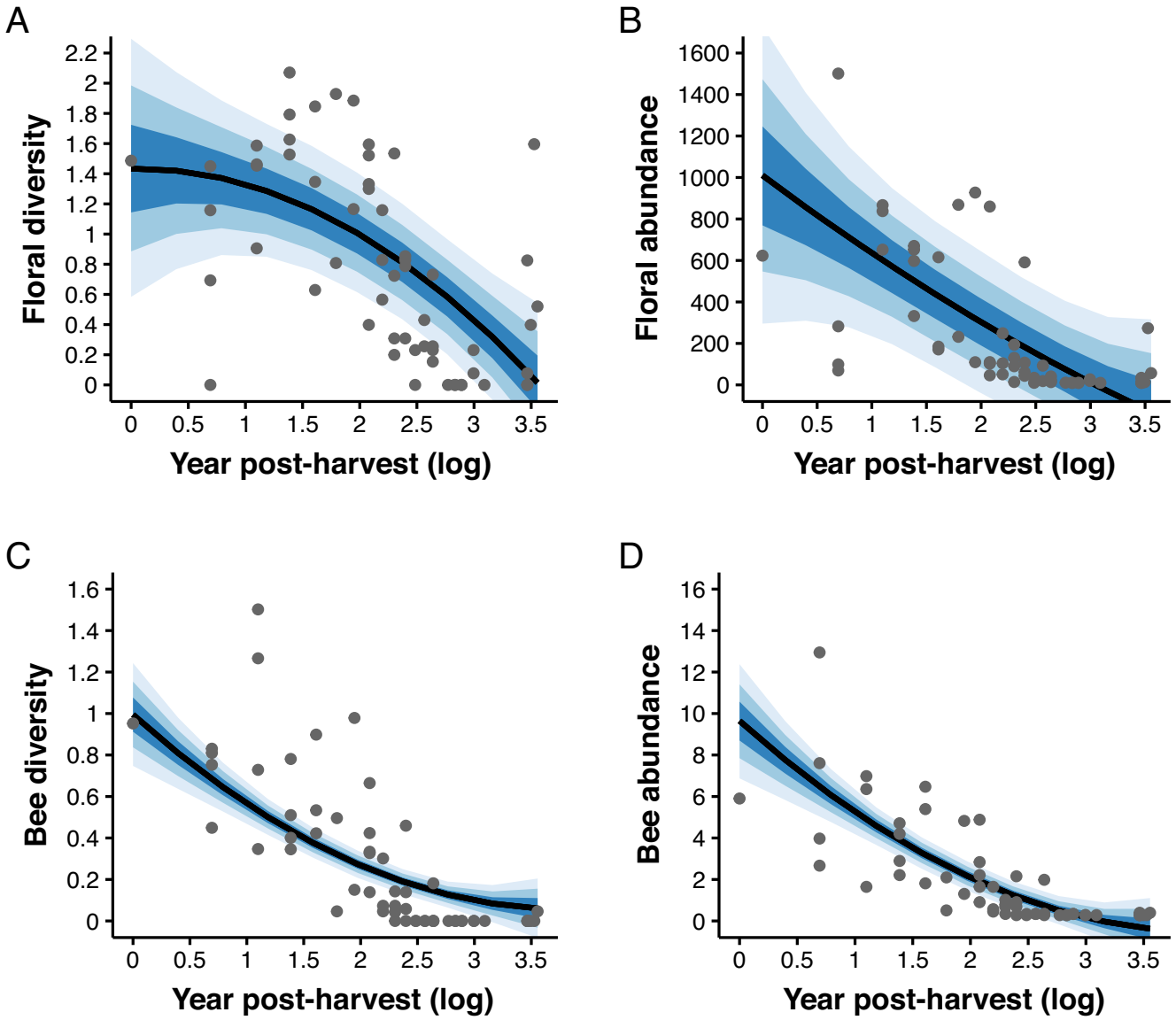

FIGURE 3 We found the years post-harvest had a strong negative effect on the flowering plant (A, B) and bee community (C, D) abundance (the number of flowers per transect or the number of bees averaged across survey methods [net, pan, vane]) and diversity (Shannon diversity metric). The solid black line indicates the slope estimate (mean of the posterior), and the colored fill from dark to light blue are the 50%, 80%, and 95% credible intervals around the estimate. The points are averages over the *O. lignaria* flight season for each stand. The *x*-axes are log-transformed.

a negative relationship between a stand's elevation and floral abundance or diversity (Table 1).

Model 1.2: Plant–pollinator community interactions

We found some evidence that stand area positively impacted bee abundance but not diversity (Figure 4A, Table 1). As expected, we found strong evidence that bee diversity was positively related to floral diversity (Figure 4B). However, we did not find a strong relationship between bee and floral abundance (Table 1). The R^2 values for the models varied and were all greater than 0.2: (1) floral abundance 0.43 (95% quantiles: 0.22–0.59); (2) floral diversity 0.44 (95% quantiles: 0.25–0.60); (3) bee abundance 0.53 (95% quantiles: 0.25–0.69); and (4) bee diversity 0.74 (95% quantiles: 0.63–0.81).

Model 1.3: Parasite prevalence

The R^2 for the parasite models were all less than 0.2 for bees infected with: (1) any parasite 0.06 (95% quantiles: 0.02–0.11); (2) *Ascophaera* spp. 0.11 (95% quantiles: 0.05–0.17); (3) *Apicystis* spp. 0.15 (95% quantiles:

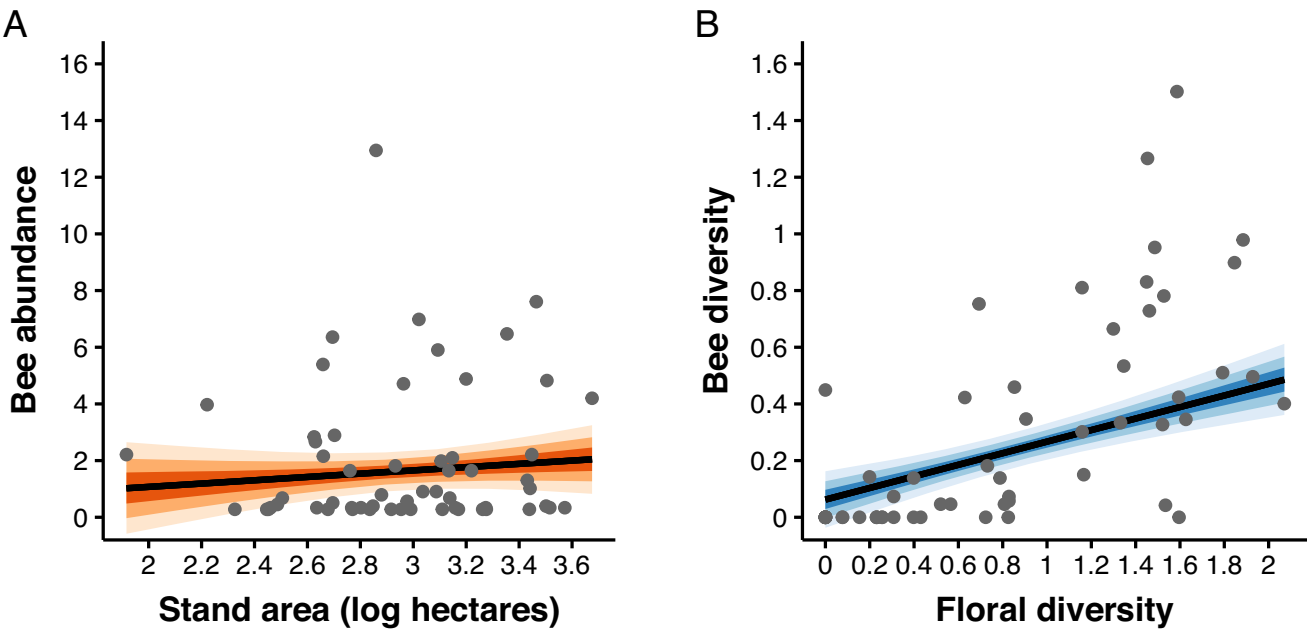

FIGURE 4 We found a positive relationship between bee abundance (the number of bees averaged across survey methods [net, pan, vane]) and stand area (log hectares) (A), and between floral diversity and bee diversity (Shannon diversity metric) (B). The solid black line indicates the slope estimate (mean of the posterior), and the colored fill from dark to light are the 50%, 80%, and 95% credible intervals around the estimate. If [95%–100%] of the posterior was above or below zero, the curves are shades of blue. If [90%–95%) of the posterior was above or below zero, the curves are shades of orange. If [0%–90%) of the posterior was above or below zero, the curves are gray. The points represent averages over the *O. lignaria* flight season for each stand. The *x*-axis for stand area is log-transformed.

0.09–0.22); and (4) *Crithidia* spp. 0.08 (95% quantiles: 0.03–0.14). Though a large proportion of the variance in the data was not accounted for by the variables we tested, the inclusion of several of the variables was still supported by the data. When all parasites were combined, we also saw strong support for a positive relationship between bee abundance and parasite prevalence (Table 2, Figure 5A). In the stand with the lowest bee abundance, an average of 73% of *O. lignaria* had a parasite, while in the stand with the highest bee abundance, nearly all individuals tested positive (Figure 5A). For each of the parasites individually, we also found evidence that parasite prevalence was positively related to bee abundance, suggesting that bee abundance amplifies parasitism (Table 2, Figure 5D,G,J). Support for this relationship was strongest for *Apicystis* spp. and *Ascophaera* spp. prevalence, with less of an effect for *Crithidia* spp. We note that one stand had many more bees than the mean bee abundance. When that stand was removed from the analysis, the support for a positive relationship between bee abundance and parasite prevalence was weakened (e.g., only 90% of the posterior was greater than zero for bees infected with *Apicystis* spp.; 89% of the posterior was greater than zero for bees infected with *Ascophaera* spp.; and <50% of the posterior was greater than zero for bees infected with *Crithidia* spp.). We examined the data and found no reason to suspect that this stand should be dropped from the analysis, as it likely represents the upper range of bee abundance in our system.

When all the parasites were combined, we found strong evidence that host diversity dilution determines whether a bee had any parasite (Table 2, Figure 5B). Ninety-five percent of bees tested positive for a parasite at the lowest bee diversity stand, while only half had a parasite at the highest (Figure 5B). For bees infected with *Ascophaera* spp., we found strong evidence that bee diversity was negatively related to parasite prevalence, suggesting host diversity dilution for this parasite (Table 2, Figure 5E). We found some evidence for host dilution of *Crithidia* spp. infections (Figure 5K), and less support for *Apicystis* spp. infections (Figure 5H, only 89% of the posterior was less than zero). When the parasites were combined, we did not find strong evidence for a relationship between parasite prevalence and flowering plant abundance (Table 2, Figure 5C), or in *Ascophaera* spp. and *Crithidia* spp. infections (Table 2, Figure 5F,L). However, we did find some support for this relationship in *Apicystis* spp. infections (Table 2, Figure 5I).

Model 2: Offspring production

Lastly, we found strong evidence that offspring production is positively related to floral diversity (Table 2,

TABLE 2 Parameter estimates for the models with parasite prevalence and offspring production as response variables.

Response variable	Explanatory variable	Estimate	SE	LB-95%	UB-95%	*R*-hat	Bulk ESS	Tail ESS	$p > 0$	$p < 0$
Ascophaera prevalence	**Bee abundance**	0.97	0.54	−0.12	2.01	1	11,702.9	9080.69	0.96*	0.04*
	Bee diversity	−0.78	0.3	−1.35	−0.19	1	15,479.44	10,928.97	0.01**	0.99**
	Floral abundance	−0.07	0.44	−0.97	0.77	1	12,291.53	10,968.52	0.43	0.57
Apicystis prevalence	**Bee abundance**	1.25	0.8	−0.38	2.78	1	10,099.76	9618.85	0.95**	0.05**
	Bee diversity	−0.48	0.41	−1.3	0.32	1	12,556	11,146.53	0.11	0.89
	Floral abundance	−0.94	0.66	−2.26	0.36	1	10,688.74	10,186.75	0.07*	0.93*
Crithidia prevalence	**Bee abundance**	0.66	0.46	−0.23	1.56	1	12,709.13	11,216.12	0.93**	0.07**
	Bee diversity	−0.38	0.25	−0.85	0.12	1	16,715.93	12,168.38	0.06*	0.94*
	Floral abundance	0.04	0.37	−0.7	0.75	1	14,599.42	11,320.34	0.55	0.45
Any parasite prevalence	**Bee abundance**	1.06	0.58	−0.06	2.24	1	7804.31	8459.45	0.97**	0.03**
	Bee diversity	−0.65	0.32	−1.29	−0.02	1	9702.06	8798.24	0.02**	0.98**
	Floral abundance	−0.22	0.42	−1.06	0.59	1	9346.14	8841.86	0.29	0.71
Offspring	Site-level parasitism rate	0.04	0.07	−0.1	0.18	1.24	573.11	1926.99	0.71	0.29
	Floral abundance	0.08	0.07	−0.06	0.22	1.01	16,007.74	81,622.87	0.88	0.12
	Floral diversity	0.15	0.07	0.01	0.3	1.01	10,278.79	44,016.11	0.98**	0.02**
	Bee abundance	−0.05	0.07	−0.18	0.09	1.01	19,433.39	96,135.07	0.23	0.77

Note: ** and * indicate 95% (strong support) or 90% (support) (the variable name is also bolded). All *R*-hats were equal to 1, indicating chain convergence, except in the offspring models, which is expected because the parameters were fit across multiple imputed datasets. Thus, we relied on visual examination to assess convergence (Bürkner, 2022).

Abbreviations: ESS, effective sample size; ODF, Oregon Department of Forestry; UB and LB, upper and lower highest density 95% credible intervals; $p > 0$ and $p < 0$, proportion of the posterior samples greater than and less than 0.

Figure 6). On average, the lowest floral diversity stand had 85 fewer offspring (~130) per block than the highest diversity stand (~220). We did not find strong evidence that floral abundance, bee abundance, or parasitism affected offspring production (Table 2). The R^2 (pooled across the 100 imputed datasets and model fits) for the offspring model was 0.27 (95% quantiles: 0.02–0.61).

DISCUSSION

Previous studies have documented the existence of bee populations within recently harvested, intensively managed forests (Rivers & Betts, 2021; Rivers, Galbraith, et al., 2018; Rivers, Mathis, et al., 2018; Zitomer et al., 2023), and our results suggest these communities can be both healthy and productive—depending on forest characteristics. Specifically, by influencing the floral and host community, we found that forest characteristics can shape the prevalence of parasites and offspring production. For most parasites, increasing bee diversity was associated with parasite dilution and bee abundance was associated with amplified parasite prevalence. The forest characteristics that influenced bee diversity—and indirectly parasite dilution—were floral diversity and the number of years post-harvest (Rivers & Betts, 2021; Zitomer et al., 2023). Host abundance—and indirectly, disease amplification—was influenced by the number of years post-harvest and stand area. Floral diversity also had a direct, positive relationship with offspring production, potentially because different flowers provide complementary nutritional resources (Centrella et al., 2020).

However, community characteristics did not explain a large percentage of the variation in the parasite prevalence, as evidenced by the low R^2 values across the models. The model with the lowest R^2 was that of *Crithidia* spp. prevalence. A large proportion of the *O. lignaria* screened as controls that were never allowed to forage tested positive for *Crithidia* spp., suggesting that many individuals emerge already infected. Though the community context might impact the ability to fight off these infections (Dolezal & Toth, 2018; Logan et al., 2005) and thus could still detect a community influence, the high rate of infection preforaging may explain why so little of the variability in the data was explained by the variables tested. There are many variables that are difficult to measure in the field that may affect the risk of infection, such as the nutritional status of a bee at the time of emergence, host and parasite genotypes (Barribeau et al., 2014), and the bee microbiome

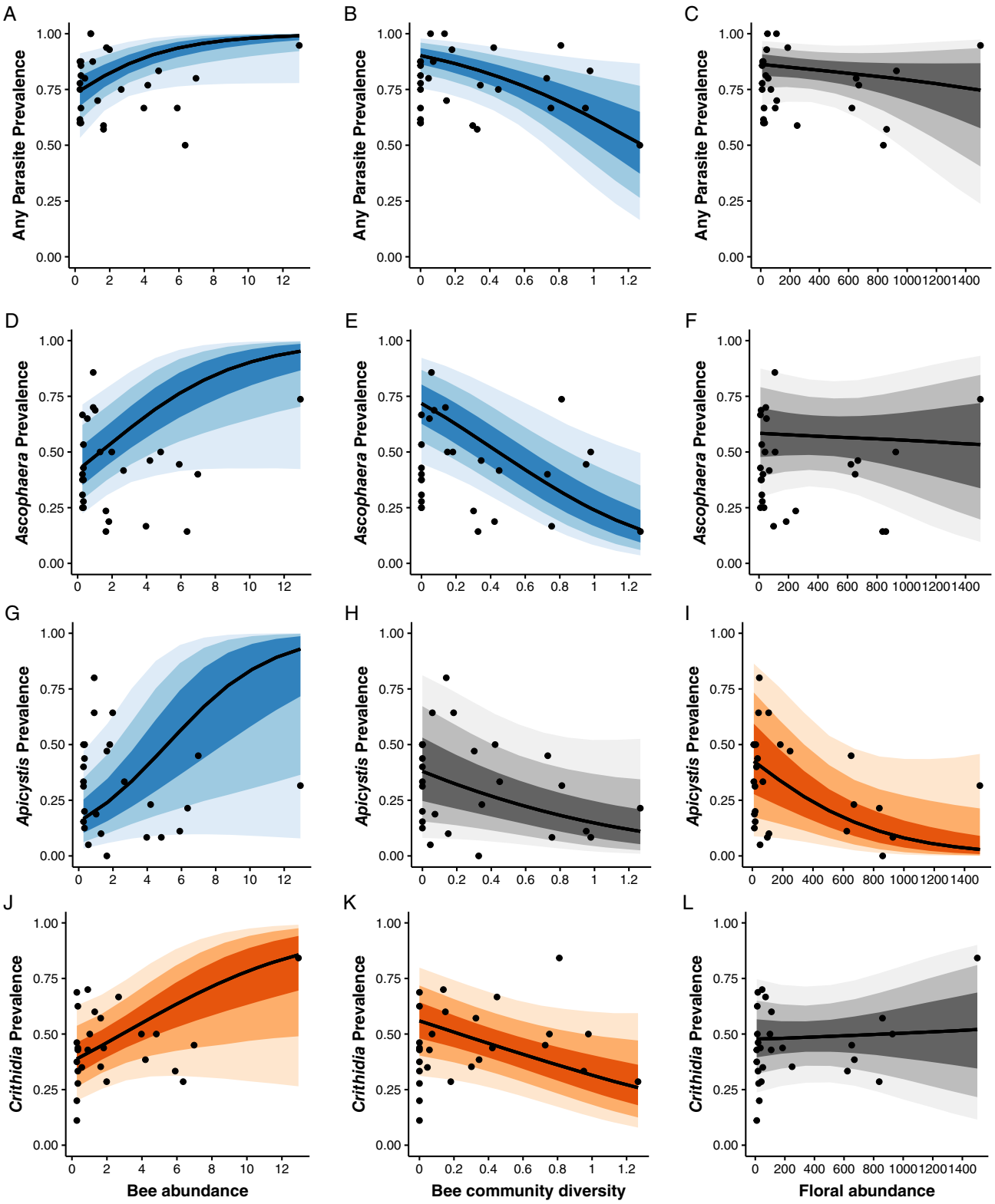

FIGURE 5 Evidence for the effect of bee abundance (number of bees averaged across survey methods [net, pan, and vane]), bee diversity (Shannon diversity metric), and floral abundance (the number of flowers per transect) on the proportion of individuals that tested positive for one or more parasites (A–C), and each parasite, individually (D–L). The solid black line indicates the slope estimate (mean of the posterior), and the colored fill from dark to light are the 50%, 80%, and 95% credible intervals around the estimate. If [95%–100%] of the posterior was above or below zero, the curves are shades of blue. If [90%–95%) of the posterior was above or below zero, the curves are shades of orange. If [0%–90%) of the posterior was above or below zero, the curves are gray. The points represent averages over the *O. lignaria* flight season for each stand.

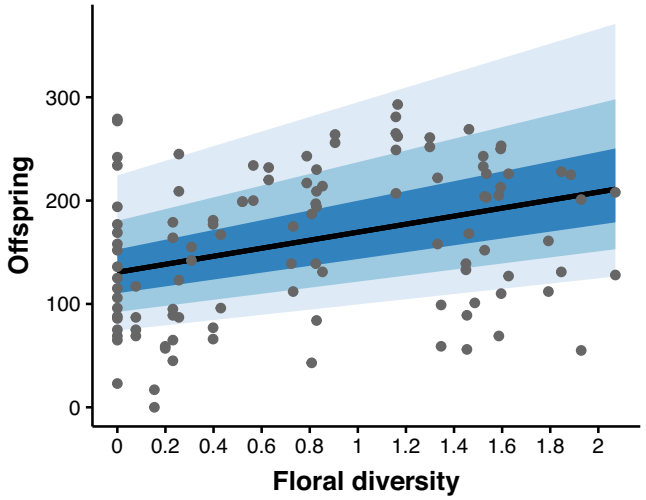

FIGURE 6 We found flower diversity (Shannon diversity metric) was positively related to offspring production (the number of bee offspring per nest block). The solid black line indicates the slope estimate (mean of the posterior), and the colored fill from dark to light blue are the 50%, 80%, and 95% credible intervals around the estimate. The points represent the number of bee offspring at each of two replicate nest boxes at a stand.

(Engel et al., 2016). Future studies are needed to determine the consistency of both the community effects on parasite prevalence and the proportion of variation in the data the community context explains. If community context continues to explain only a small proportion of the variation in infection in other systems, this would provide a rationale for exploring other variables. Another noteworthy aspect of our results is that the relationships between the host community and parasite prevalence were clearly influenced by the few stands with the highest bee abundance. Because we studied a representative sample of forest stands, we conducted parasite screenings in fewer stands with high bee abundance compared to stands with few bees because stands with high abundance are more rare (Rivers & Betts, 2021). Still, we note that further study of the drivers of high bee abundance in regenerating stands will help clarify the relationship between host abundance to parasite prevalence.

Taken together, our results suggest that maintaining and/or restoring a diverse flowering plant community is an important consideration when managing forests for healthy bee populations. Landowner identity affects a stand's floral diversity, suggesting that differences in stand management can impact floral communities. Therefore, approaches that increase bee diversity via plant community restoration could promote offspring production directly and parasite dilution indirectly. Restoring or maintaining diverse floral resources may be especially important in large, recently harvested stands when bee abundance and the potential for parasite amplification are highest. Though not often practiced, floral enhancements in harvested forests, which could be established in burned slash pile scars or in log landings (Lee et al., 2021), may provide a way to bolster floral diversity (Sexton et al., 2020) and subsequently bee diversity. Interestingly, we did not detect an effect of floral abundance on wild bee abundance or *O. lignaria* offspring production. The lack of a strong relationship between the bee communities and floral abundance may be because the stands with the highest floral abundance were dominated by non-native species such as Himalayan blackberry (*Rubus bifrons*), St. Johnswort (*Hypericum perforatum*) and foxglove (*Digitalis purpurea*) that native bees may prefer less than native species (e.g., Morandin & Kremen, 2013; Seitz et al., 2020; Williams et al., 2011). As suggested in other systems, floral enhancements should focus on native plant species (Menz et al., 2010). However, additional research is needed to understand how floral enhancements can support bee communities while promoting enough host diversity to minimize parasite amplification.

Another management strategy to increase floral diversity in stands is reducing herbicide use intensity (Kormann et al., 2021). In the moist, high-productivity forests of the PNW, herbicide is often used in tree plantations to reduce competing vegetation and increase tree growth and survival (Kormann et al., 2021). Kormann et al. (2021) observed that increasing levels of aerial herbicide application resulted in fewer flowering plant species and individuals than the no-herbicide control (Kormann et al., 2021; Stokely et al., 2021). Kormann et al. (2021) also found that wild bee richness declined at similar rates as plant communities with changes in herbicide intensity, though abundance was not strongly impacted (Kormann et al., 2021; Stokely et al., 2021). Our results suggest that floral diversity supports bee reproduction and host diversity dilutes parasitism, so reducing herbicide intensity may be particularly useful for promoting healthy bee communities. Importantly, Kormann et al. (2021) caution that reducing herbicide intensity results in a trade-off, where floral biodiversity increases but tree growth decreases because of competition. These tradeoffs may dissipate if economic discount rates are applied, given the high cost of herbicide application (Kormann et al., 2021). Additional incentives such as certifications or cost-share programs like those in other working landscapes may help make less intensive herbicide use economically viable.

We found similar levels of parasite prevalence in our system as in other community-wide surveys of wild bees in human-modified systems (Cohen et al., 2021, 2022). For example, in both our intensively managed forest

system and intensively managed agriculture in the California Central Valley, only ~20%–25% of the bees screened had no microbial parasites. The most common parasites in our system were *Crithidia* spp., and *Ascophaera* spp. *Crithidia*, although historically associated with bumble bees, is observed at high rates in *Osmia* and other megachilids (Cohen et al., 2020; Figueroa et al., 2021; Ngor et al., 2020). *Ascophaera* is also common in *Osmia* (Klinger, 2015) and introduced *Osmia* species bringing their associated *Ascophaera* lineages have been hypothesized to contribute to the decline of native *Osmia* species (Hedtke et al., 2015; LeCroy et al., 2020). The high proportion of bees with one or more parasites in our system and others (Cohen et al., 2021, 2022) suggests that supporting immune system function to fight off these parasites is likely a regular metabolic cost incurred by wild bee populations (Goulson et al., 2015; Tyler et al., 2006).

We did not find evidence for several of the relationships we hypothesized. First, we only found evidence for a negative relationship between floral abundance and parasite prevalence in *Apicystis* spp., though this has been demonstrated in other studies of bee parasites (Cohen et al., 2021). Cohen et al. (2021) did not examine the prevalence of each species group of parasites; however, *Apicystis* spp. was the most common infection in their study system (54.8% of bees were infected). It may be that the floral abundance-dilution effect in this system was related to *Apicystis* spp. being the most common parasite. *Apicystis* spp. transmission may be more affected by the plant community than the other parasites. The mechanism for why this would be the case has not been explored by any study and therefore warrants future examination. We also did not find evidence of a relationship between parasite prevalence and *O. lignaria* offspring production, though laboratory studies have linked parasitism to reduced foraging efficiency and reproduction (Koch et al., 2017). One explanation is the methodological difficulty of linking parasitism to reproduction in the field. The parasite prevalence data we assessed were at the level of an individual, and we were unable to tie individual bees to their production of offspring in this study because females were destructively sampled and could only be reliably captured at the nest before they had completed nesting. Although we recorded in which nest box straw a female bee was captured, *O. lignaria* females often fill multiple nest straws or take over half-finished nest straws, so we could not directly link a female bee to her offspring in the field. Alternatively, parasite prevalence may not strongly impact reproduction compared with community characteristics such as floral diversity. Without the ability to ascribe the offspring of each cell in a nest to a specific female bee, which is not possible in the field unless pedigrees are determined genetically, we cannot differentiate between these two explanations of our results.

Although bee abundance and floral abundance are often correlated, we did not find strong evidence of this relationship in our data. However, the resolution of our data is at the flight-season level in order to capture the full scale of community interactions by *O. lignaria*. At a finer resolution (i.e., on a specific day), bee and floral abundance may be more closely related. Lastly, we did not find evidence that bee abundance negatively impacted *O. lignaria* offspring production, suggesting that solitary bees in this system are not experiencing density-dependent growth. Due to the patchy nature of clearcuts within older stands, it may be difficult for bees to find and colonize new patches, and thus total abundance may be lower than the carrying capacity of the stand.

While management practices that restore pollinator communities in some working landscapes (especially agriculture) are well-established (e.g., Kremen et al., 2019), our understanding of how to manage intensively managed forests for pollinators lags behind (Rivers, Galbraith, et al., 2018). This is likely because, until recently, forests were not seen as providing suitable habitat for bees (Rivers & Betts, 2021; Ulyshen et al., 2023). Our study and others have shown that intensively managed forests can support diverse and abundant bee and flowering plant communities (Rivers & Betts, 2021; Zitomer et al., 2023), and that management to enhance floral diversity may be able to bolster the utility of these forests for bee conservation. With appropriate management, harvested forests should be considered important to the global efforts to curb bee decline.

AUTHOR CONTRIBUTIONS

All authors contributed to the study's design. Lauren C. Ponisio conducted the analyses, made the figures, and led the manuscript preparation. Hamutahl Cohen and Jocelyn Zorn led molecular lab work and contributed to the manuscript. Sara M. Galbraith and James W. Rivers led the study design, conducted fieldwork, and contributed to the manuscript preparation. Rachel A. Zitomer led the data cleaning and contributed to manuscript preparation. James W. Rivers and Lauren C. Ponisio provided funding for the project.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ponisio & Cohen, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.10042166.

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