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ORIGINAL PAPER

Plant-Pollinator Networks Simplify And Dominant Floral Visitors Shift with Time Since Harvest in Regenerating Douglas-fir Plantations

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Abstract

Pollination services are critical for supporting healthy forests, so understanding the structure of plant-pollinator interactions can improve conservation outcomes for land managers. We evaluated changes in plant-pollinator interaction networks across a 35-year stand age gradient in intensively managed Douglas-fir (*Pseudotsuga menziesii*) forests of western Oregon, USA, representing successional conditions across a typical harvest rotation. We hand-netted insects visiting flowers in bloom on 60 stands, resulting in 928 recorded interactions. Bees were the most observed floral visitors regardless of stand age, representing 75.8% of recorded interactions, followed by flies (14.4%), wasps (5.2%), beetles (1.9%), and butterflies (0.4%). The most visited flowers were *Hypochaeris radicata*, *Crepis capillaris*, *Rubus ursinus*, *Digitalis purpurea*, and *Lucanthemum vulgare*. Of these, only *Rubus ursinus* is native to the region; 71% of recorded visits were to non-native plants. In stands < 15 years post-harvest – where most interactions occurred – the number of bee species in networks and network interaction diversity decreased with time since harvest. Several characteristics of plant-bee networks found to be important in non-forest settings, such as network modularity, connectance, and robustness, varied little relative to time since harvest. Our study demonstrates that most pollinator-plant interactions in Douglas fir stands occurred shortly after harvest. Furthermore, the role of

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Study Implications Plant-pollinator interaction networks can provide detailed information about the influence of management actions on ecosystems. We found evidence that actions to promote pollinator habitat in managed forests should continue to focus on the first years following harvest, when the majority of plant-pollinator interactions are occurring. However, we also found ongoing plant-pollinator activity where flowering plants remained in close-canopy forests. Furthermore, bees were the main floral visitors across the age gradient, but flies played a larger role in the networks as stands aged, so managers should consider the potential for older forests to provide habitat for non-bee pollinators. Non-native plants and pollinators were present across stand ages, but especially prominent within the plant-pollinator networks of younger stands, where non-native plants were the most visited floral hosts. Because non-native species dominated the interactions observed in our study, managers seeking to enhance pollinator habitat by removing non-native plants should also consider actions that promote native flowering plants.

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different plant and insect taxa – including non-native species – changed as stands aged; non-native species of both plants and bees played a large role in networks but were most prominent in recently harvested stands.

Keywords Native bees · Pollination networks · Managed forests · Non-native species

Introduction

Current approaches to conserve biodiversity often focus disproportionately on species richness (Valiente-Banuet et al. 2015), with less emphasis on the ecological roles of organisms. Ecological networks, which characterize patterns of interactions between organisms, can supplement traditional sampling approaches by identifying species that have the strongest impacts on community stability, measuring network-level responses to environmental change, and predicting the impacts of species loss on ecosystem function (Harvey et al. 2017; Keyes et al. 2021). Given the importance of pollination for maintaining biodiversity in terrestrial systems (Kearns & Inouye 1997; Ollerton et al. 2011; Wei et al. 2021), the high extinction risk of many pollinator species (Cornelisse et al. 2025), and the high priority given to pollinator conservation globally (IPBES 2016), plant-pollinator networks have the potential to enhance land management decisions beyond reliance on biodiversity surveys alone. Plant-pollinator networks can be studied to identify which species and interactions are most important for network stability and function (Rafferty & Cosma 2024), identify the conditions associated with extinction cascades (Vanbergen et al. 2017b), and indicate how robust an assemblage of plants and pollinators is to species loss (Astegiano et al. 2015). However, network-based approaches have been under-utilized in research aimed at informing management despite their potential for advancing conservation efforts in managed landscapes (Kaiser-Bunbury & Blüthgen 2015; Borchardt et al. 2021).

Managed forests are emerging as a new area of potential for pollinator conservation, and there has been heightened interest in understanding how forest management activities impact habitat availability for this group (Hanula et al. 2016; Rivers et al. 2018; Ulyshen et al. 2024). Nevertheless, few studies have examined plant-pollinator networks within temperate forests, and the varied findings to date are insufficient to develop a robust understanding of how forest management activities impact network structure. For example, one study found that managed old-growth (≥ 135 years old) pine (*Pinus sylvestris*) stands typically had greater interaction evenness and interaction diversity (variables are associated with good community health; Tylianakis et al. 2010; Kaiser-Bunbury and Bluthgen 2015) when compared to recently cleared areas (Devoto et al. 2012). In another study, nestedness (i.e., the degree that generalist species are highly connected, but specialists are only connected via generalists) was greater in thinned stands compared to untreated stands, indicating management activities in these ponderosa pine (*P. ponderosa*) forests led to more robust networks (Davies et al. 2023). Given the mounting evidence that forest management influences plant-pollinator networks, additional research is needed to more comprehensively inform management, with a particular focus on the effects of harvest.

In this study, we quantified how plant-pollinator networks changed with time since harvest in commercial timberlands using a space-for-time substitution, and we evaluated the relative contributions of different insect visitors to network structure. Our previous research within intensively managed conifer plantations has shown that harvest reduces canopy cover, increases flowering plant abundance, and enhances pollinator abundance and diversity. However, intensive forest management also results in rapid canopy closure after harvest, and bee habitat declines in tandem (Rivers & Betts 2021; Zitomer et al. 2023). Therefore, evaluating changes in network structure across time will help determine whether increasing canopy cover reduces resources similarly among plants and pollinators, or if new connections form as stands regenerate after harvest. Collectively, this better understanding of how insect visitors use floral resources within these systems will allow for more informed management decisions in post-harvest settings.

To quantify changes to plant-pollinator networks relative to stand age, we first examined how interactions between different flower-visiting insect groups (i.e., bees, flies, wasps, and butterflies) and flowering plants shifted with time since harvest. We hypothesized that we would observe fewer interactions with increasing time since harvest, and that the identity of flowering plants and insect visitors in the networks would shift with stand age. In addition we focused on bees – the dominant pollinator group found on our sites – and hypothesized that stand age would influence bee-flower network characteristics that have a demonstrated practical application to conservation management (Kaiser-Bunbury & Blüthgen 2015). We hypothesized that interaction diversity, which is influenced by both the number of links observed and the evenness of interaction distribution across partners in the network (Kaiser-Bunbury & Blüthgen 2015; Guimarães 2020), would decrease with time since harvest and replanting, as the closed canopy and sparse floral resources are known to have fewer bees and floral resources (Rivers & Betts 2021; Zitomer et al. 2023). We also hypothesized that interaction evenness (the evenness of interaction distribution across partners in the network) and connectance (which is the realized proportion of possible links within the network) would decrease and modularity, or the extent to which species are compartmentalized into nodes of semi-independent groups (Kaiser-Bunbury & Blüthgen 2015; Guimarães 2020), would increase as only a few, less connected specialist species would remain in the closed canopy forests. Finally, we hypothesized that the robustness of networks would decrease as stands aged, with bees and flowers becoming increasingly sensitive to species loss of the component group.

Methods

Study System

We conducted our study during the summer flight season for pollinating insects (mid-May through August) during 2018–2019 in the Oregon Coast Range, USA. The Oregon Coast Range encompasses 2.1 million hectares of forest in western Oregon (Creutzberg et al. 2017) and lies within a moderate, moist climate that supports some of the most productive forest ecosystems in the world (Spies et al. 2002). Precipitation typically ranges from 150 to 300 cm per year and occurs primarily between October and March as rain, with mostly dry weather during the summer months (Spies et al. 2002). In the central region of the Coast Range – where this study took place – dominant tree species include Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) as well as hardwoods (e.g., red alder [*Alnus rubra*], big-leaf maple [*Acer macrophyllum*]) and shrubs (e.g., false azalea [*Menziesia ferruginea*], salmonberry [*Rubus spectabilis*]). Forests are a substantial component of land cover in this region, with approximately 39% of the Coast Range composed of private industrial forests and additional forest tracts managed by the USDA Forest Service, Oregon Department of Forestry, and Tribes (Creutzberg et al. 2017). Forest management varies by landowner, but much of the private industrial forest land consists of stands managed using intensive forest management practices, such as shortened harvest rotations (~40–50 years; Spies et al. 2002), herbicide treatments, and planting genetically improved nursery stock (Talbert and Marshall 2005).

Experimental Design

We collected network data in coordination with a broader effort to characterize the bee community in managed conifer forests of the Coast Range (see Zitomer et al. 2023). We selected 60 commercial harvest units (hereafter, stands), 1–35 years post-harvest, that represent successional conditions that ranged from harvest to the end of a typical timber rotation for commercial Douglas-fir stands in the region. We selected stands occupying different points along the time-since-harvest continuum that were managed by the Oregon Department of Forestry and three private landowners (Starker Forests, Weyerhaeuser, and Manulife Investment Management) and therefore represented a range of intensive forest management practices in the study region. Stands averaged 20.8 ha (range: 7.7–39.5 ha) and 305 m above sea level (range: 97–630 m). We ensured that stand centroids were separated by ≥ 2 km to reduce spatial autocorrelation among sampling sites and minimize non-independence of pollinator communities based on typical insect pollinator foraging ranges (Zurbuchen et al. 2010).

Sampling of Insect-Flower Interactions

In our study we defined plant-pollinator networks as observed interactions between potential insect pollinators and flowers in bloom. We sampled insects during three sampling rounds in each year: the first sampling round occurred during the bloom of early-flowering plants (e.g., *Gaultheria shallon, Mahonia aquifolium*, *Rubus ursinus*) and the final sampling round coincided with the end of the blooming period for most late-flowering plants in the region (e.g., *Anaphalis margaritacea, Cirsium* spp.). Prior to sampling, we established three 20 × 3 m belt transects radiating from the plot center that were used for hand netting insects and quantifying floral resources. We randomly selected an azimuth to place the first transect and established the other two transects 120° and 240° from the initial azimuth to maximize coverage while minimizing bias.

We conducted sampling between 08:00 h and 16:00 h during conditions with no precipitation, wind speeds < 3.5 m/s, and ambient temperature $> 16°$ C. During each sampling period, we walked a single pass down the center of each belt transect for 10 min and hand-netted any insects observed visiting flowers in bloom, for a total of 30 min. We retained each captured individual for identification and recorded the plant species from which it was netted. In the rare event that an insect could be identified without lethal collection (e.g., honey bees [*Apis mellifera*]), we recorded the insect-flower interaction without retaining the specimen. We did not count time spent processing insects toward the time allotted for netting. For retained specimens, we pinned and identified them to the lowest possible taxon using dichotomous keys. Bees were then further identified to species whenever possible using keys that were available for local genera (e.g., *Agapostemon* [Stephen et al. 1969], *Ceratina* [Discoverlife.org], *Bombus* [Williams et al. 2014], *Halictus* [Roberts 1973]). L. Best (Oregon State University) validated all identifications and categorized remaining specimens to species or morphospecies using regional synoptic collections.

Data Analysis

We performed all statistical analysis using R Statistical Software (v4.4.2; R Core Team 2024). To assess networks relative to stand age, we classified stands into three age classes that represent ecologically distinct early seral conditions that occur during following harvest. Specifically, we categorized our sites as young early seral stands (1–5 years post-harvest), intermediate early seral stands (6–10 years post-harvest), and mature early seral stands (≥ 11 years post-harvest). We established these categories based on the distribution of average canopy cover within sites; mature stands represent the point where stands average ≥ 75% canopy cover (see Zitomer et al. 2023). We first examined the entire community of floral visitors by constructing networks from observations of the four major pollinator groups we observed (i.e., bees, flies, wasps, beetles, and butterflies), followed by examining networks for bees only. In both analyses, we categorized host plants observed within networks as 'native' or 'non-native' using the USDA Plants database (Natural Resources Conservation Service 2025; Supplement T1).

We used the 'bipartite' package (Dormann et al. 2008) to generate quantitative network variables on plant-bee interactions only. We chose to examine only bee-flower interactions via quantitative analysis because bees, which are known to be an essential pollinating group (Neff & Simpson 1993; Klein et al. 2007), are abundant in managed conifer forests (Rivers & Betts 2021; Zitomer et al. 2023), and could be identified to the species/morphospecies level in our study. For this analysis of network structure, we included all plant-bee interactions observed over the course of a year at each stand to represent a network (rather than combining stands by age categories). Because of the limited number of observations made in stands after canopy closure, we assessed quantitative characteristics of bee-flower network structure in stands < 15 years after harvest. Several network variables can be influenced by network size and completeness, making direct comparisons among sampled communities potentially misleading (Rivera-Hutinel et al. 2012). Therefore, we used null models to generate standardized z-scores to compare modularity, connectance, and robustness across the stand age continuum and reflect the deviance of network variables from random expectation while controlling for network size. We generated null models using proportional probabilistic resampling, which preserves marginal totals of bipartite matrices while randomizing their internal structure (Patefield 1981). We generated 1,000 null models per web for all variables except robustness, which we calculated from a subsample of 100 null models per web due to its higher computational demands.

After calculating network variables for plant-bee networks, we compared network structure across the stand age gradient using linear mixed models in the 'lme4' package (Bates et al. 2014). We evaluated each of the network variables in a separate model with stand age (continuous) as a fixed effect and stand identity as a random effect. We verified model fit and dispersion by evaluating simulated model deviance residuals (package 'DHARMa'; Hartig 2024). Models of the number of bees and the number of plants in each network were fitted using Poisson mixed models with a log link. The remaining models were fitted with linear mixed models with an identity link. We computed 95% confidence intervals (CIs) for fixed effect variables using likelihood profiles (package 'broom.mixed'; Bolker and Robinson 2022).

Results

Insect-Flower Interactions

We recorded 928 insect-flowering plant interactions in 41 of the 60 stands we sampled (Fig. 1). Despite equal sampling effort per stand, we observed interactions in all young stands (16 of 16), nearly all intermediate stands (15 of 17), and less than half of mature stands (10 of 27). Despite the greater number of mature stands sampled, most insect-flower interactions were observed on young stands ($n = 539$; 58%), followed by intermediate stands ($n = 318$; 34.3%), with very few were observed on mature stands ($n = 71$; 7.7%).

Bees were the most observed floral visitors overall, representing 75.8% ($n = 703$) of recorded plant-visitor interactions. Flies were the second most common visitors at 14.4% ($n = 134$), followed by wasps (5.2%; $n = 48$), beetles (1.9%; $n = 18$), and butterflies (0.4%; $n = 4$). We excluded 21 visits from the analysis that comprised 12 visits from non-focal groups (i.e., Hemipterans, Neuropterans, and Orthopterans; 1.3%) and 9 visits (1.0%) by unidentified floral

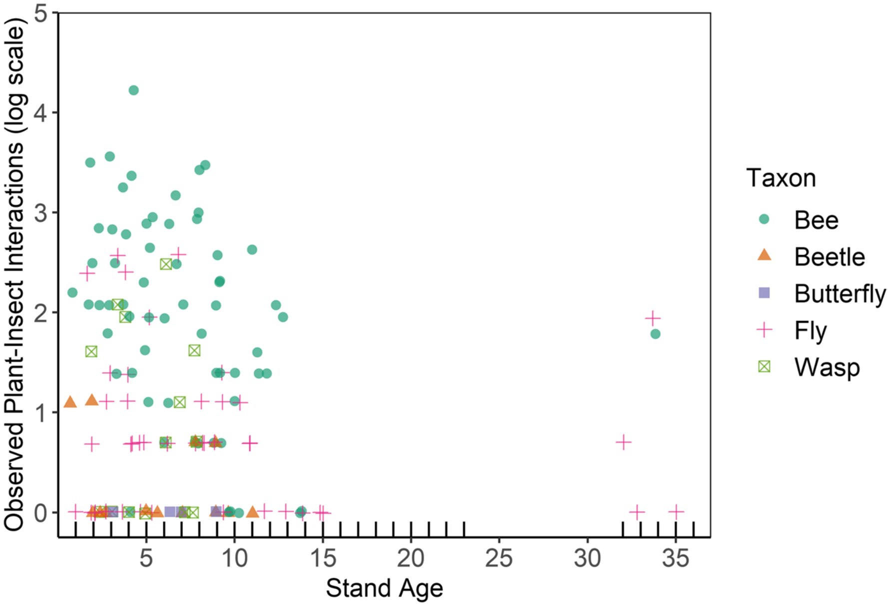

Fig. 1 Number of observed plant–insect interactions by stand age across $n=60$ regenerating Douglas-fir stands. Each sampling point represents the log-transformed total number of interactions in each stand pooled across all sampling periods per year (2018 and 2019). Different symbols represent the taxa of insect visitors. Points are jittered. Rug plot shows ages of sampled stands; most ages are represented by multiple stands. Non-transformed observations, including 'zero' observations where no plant–insect interactions occurred, can be found in the supplementary information (S2)

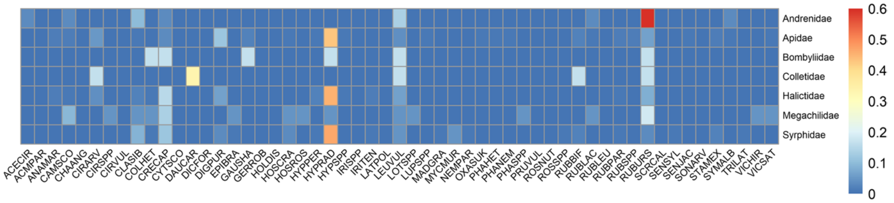

Fig. 2 Heatmap showing the proportion of visits to each flower species by the five bee families (Apidae, Andrenidae, Colletidae, Halictidae, and Megachilidae) and two fly families (Bombyliidae and Syrphidae) that accounted for 86.7% of plant–insect interactions observed in the study

visitors. The most visited flowers were *Hypochaeris radicata*, *Crepis capillaris*, *Rubus ursinus*, *Digitalis purpurea*, and *Lucanthemum vulgare*. These flowers accounted for a large proportion of the observed visits across several of the most common visitor families (Fig. 2).

The composition of insects and their host plants varied across the three networks (Fig. 3). We observed a similar number of interactions between young and intermediate stands; young stands had five insect groups (bees, flies, beetles, wasps, and butterflies) interacting with 36 plant taxa whereas

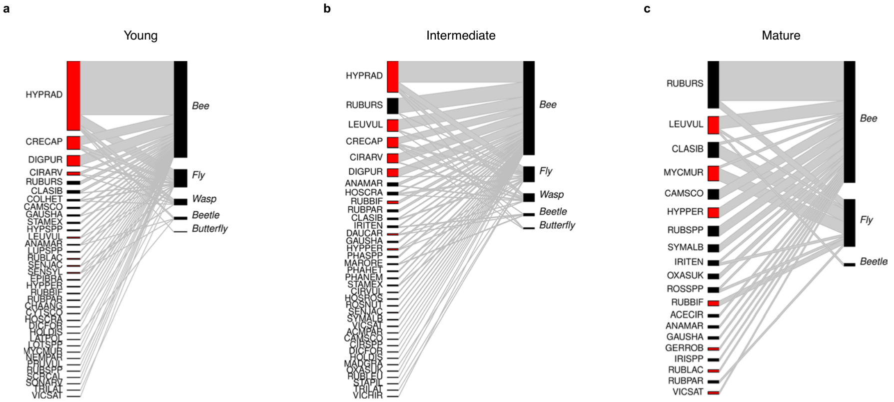

Fig. 3 Plant–insect visitor networks in **a**) young (1–5 years post-harvest; left); **b**) intermediate (6-10 years post-harvest; middle), and **c**) mature (≥ 11 years post-harvest; right) stands. Sampled from n = 16 early stands, n = 17 intermediate stands, and n = 27 mature stands. Plant codes are defined in Supplement T2

intermediate stands had the same five insect groups interacting with 37 flowering plant taxa. In contrast, we observed interactions between only three insect groups (bees, flies, and beetles) and 20 flowering plant taxa in mature stands. Bees were the most common insect visitor in all age categories. In young stands, the four most common floral hosts were *Hypochaeris radicata*, *Crepis capillaris*, *Digitalis purpurea*, and *Cirsium arvense*. In intermediate stands, the four most common floral hosts were *Hypochaeris radicata, Rubus ursinus*, *Leucanthemum vulgare,* and *Crepis capillaris*. In mature stands, *Rubus ursinus*, *Leucanthemum vulgare, Claytonia sibirica, and Mycelis muralis* were the most common floral hosts. Overall, 71% of the insects we recorded were observed visiting non-native plants in bloom, with 40.1% of all recorded visits occurring to *Hypochaeris radicata*.

Bee-Flower Interactions

Of the 19 bee genera recorded in this study, the most common floral visitors were *Bombus* ($n=240$), *Lasioglossum* ($n=157$), *Apis* ($n=113$), *Halictus* ($n=69$), and *Ceratina* ($n=45$; Supplementary T1). Non-native western honey bees (*Apis mellifera*) accounted for 16% of observed bee-flower interactions. We collected bees from 36 flowering plant genera, representing 52 flower species (eight plants were identified to genus only; see Supplementary T2). The most common floral hosts on which bees were observed were *Hypochaeris radicata (*$n=379$ visits*), Rubus ursinus* ($n=73$ visits)*, Digitalis purpurea* ($n=65$ visits), *Leucanthemum vulgare* ($n=44$ visits), and *Cirsium arvense* ($n=41$ visits).

The composition of bees and their host plants varied across the three networks (Fig. 4). In young stands, we observed interactions between 57 bee taxa and 33 flowering plant taxa. Within intermediate stands, we observed interactions between 46 bee taxa and 33 flowering plant taxa. Within mature

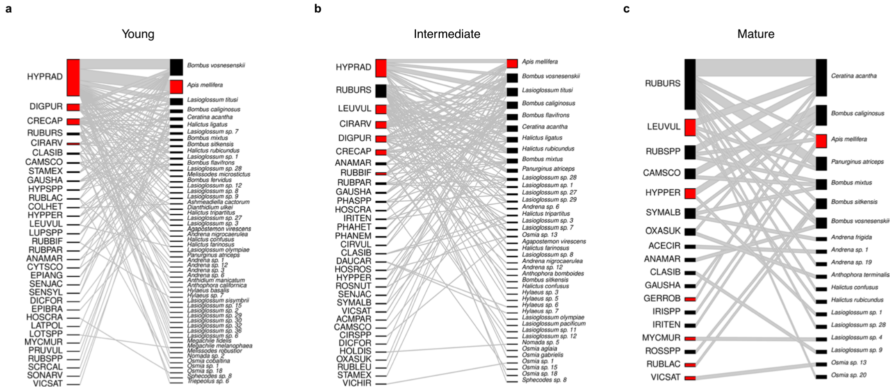

Fig. 4 Plant-bee visitor networks in **a**) young (1–5 years post-harvest); **b**) intermediate (6-10 years post-harvest); and **c**) mature (≥ 11 years post-harvest) stands. Sampled from $N = 16$ early stands, $N = 17$ intermediate stands, and $N = 27$ mature stands. Plant codes are defined in Supplement T2

stands, we observed interactions between 21 bee taxa and 18 flowering plant taxa. *Bombus vosnesenskii* was the most common bee visitor in the young stands, representing 24% of observations within that age category. *Apis mellifera* was the most common bee visitor in intermediate stands, representing 10% of observations within that age category. For the mature stands, the most common bee visitor was *Ceratina acantha,* representing 22% of observations within that age category.

Network Characteristics Across the Stand Age Gradient

Bee-flower network characteristics varied with stand age within the first 15 years after harvest (Table 1). When controlling for random effects, every year of stand age was associated with an 8% decrease in the mean number of bee species relative to the previous year (95% CI: −13%, −3%; marginal R^2 of 0.19; Fig. 5a). We did not detect a relationship in the number of flower species per network across the stand age gradient; each additional year of stand age was associated with a 2% decrease in the mean number of flower species but the confidence interval overlapped with zero (95% CI: −6%, 2%). We found that there were more diverse plant-bee interactions in younger stands; there was a 0.073 decrease in mean interaction diversity in plant-bee networks for every year increase in stand age (95% CI: −0.132, −0.013; marginal $R^2 = 0.09$; Fig. 5b). However, mean interaction evenness did not change meaningfully with stand age (mean = 0.002 (95% CI: −0.009, 0.013; marginal R^2 of 0.002).

We assessed $n = 41$ interaction networks against a null model; $n = 21$ networks were eliminated from the analysis because they were either too small to calculate meaningful metrics or because no variation was generated in the null model (leading to undefined z-scores). We found no evidence for a change in modularity, an indicator of how clustered interactions are within a network, with stand age ($\beta = -0.001$, 95% CI [−0.172, 0.174]; marginal $R^2 < 0.001$).

Table 1 Results of generalized linear mixed models, including beta estimates (β) for the effect of stand age on each response variable with associated 95% confidence intervals, averaged over random effect levels. Results for models with a log link are back-transformed. Bold values represent confidence intervals that do not overlap with zero

Response variable	Distribution	Link	df	Effect of Age (β)	95% CI
Number of bee species	Poisson	Log	58	**0.92**	**0.87, 0.97**
Number of flower species	Poisson	Log	58	0.98	0.94, 1.02
Interaction diversity	Normal	Identity	58	**−0.07**	**−0.13, −0.01**
Interaction evenness	Normal	Identity	51	0.002	−0.009, 0.013
Connectance	Normal	Identity	41	0.035	−0.114, 0.186
Modularity	Normal	Identity	41	−0.001	−0.172, 0.174
Robustness (consumer level)	Normal	Identity	41	0.005	−0.132, 0.142
Robustness (producer level)	Normal	Identity	41	0.035	−0.152, 0.082

Similarly, we did not find evidence for a change in mean connectance (β = 0.035, 95% CI: [−0.114, 0.186]; marginal $R^2 = 0.005$). We also did not find evidence for a change in robustness with stand age at the consumer (β = 0.005, 95% CI: [−0.132, 0.142]; marginal $R^2 < 0.001$) or producer (β = 0.035, 95%CI: [−0.152, 0.082]; marginal $R^2 < 0.01$) levels.

Discussion

Our hypothesis that fewer insect-plant interactions would be detected with increasing time since harvest was supported, as we observed the greatest number of insect visitors in young and intermediate stands when examining both the community of insect visitors and bees alone. Of note, these differences were found despite sampling in fewer younger stands. Our study also illustrated changes in the composition of floral visitors and the plants they used as stands aged. Although bees were the most common insect visitors across the stand age continuum, flies accounted for a greater proportion of visits in mature stands. Flies are often more abundant in habitats with greater canopy cover (Woodcock et al. 2003; McCabe et al. 2019), and here we show that the importance of flies as floral visitors increases within closed-canopy habitats, as well. Although flies are often under-studied as pollinators (Kearns 2001; Dunn et al. 2020), their role in networks in this study adds to increasing evidence that groups such as hoverflies (Syrphidae) contribute pollination services in forests.

For bee visitors specifically, our prediction that networks would become less diverse as stands aged was also supported. This result contrasts with other studies that have observed lower interaction diversity in more disturbed habitats and it adds to evidence that land management can increase network diversity in systems where reducing canopy cover creates habitat for forbs (Davies et al. 2023; Thapa-Magar et al. 2023; Pérez-Gomez et al. 2024). Our findings did not support the hypothesis that networks would be more modular in older stands. Lower

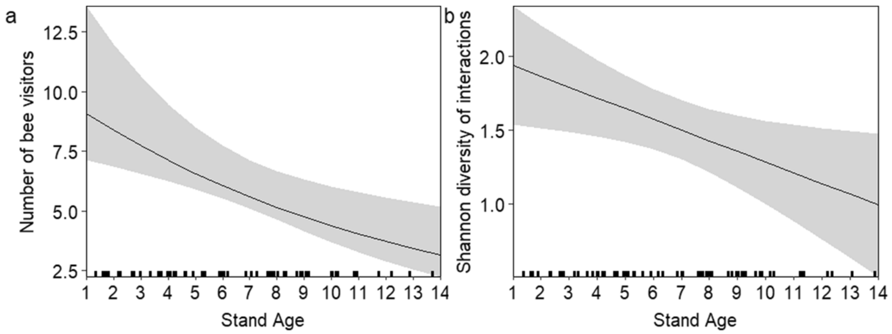

Fig. 5 Predicted mean values for **a**) the number of bees and **b**) interaction diversity of networks across the stand age gradient, averaged across random effect levels. In each plot, estimated relationship is shown as a solid line with 95% CI shown as a ribbon. Rug plot shows stand age where bee-plant interactions were observed, jittered

modularity is expected in smaller networks (Oleson et al. 2007), so the lack of evidence for a change in modularity is interesting given the few interactions observed as stands aged. Furthermore, non-native species were abundant in the youngest stands, which can increase generalist interactions and decrease modularity (Larson et al. 2016).

We found no change in the evenness or connectance of the networks along the age gradient in regenerating conifer forests. Greater values of connectance can indicate network stability but may also occur due to lower species richness and/or a more generalized network with fewer specialists (Soares et al. 2017). Networks were also equally robust across the stand age gradient, indicating that for both bees and flowering plants, the tolerance of a system to the extinction of its component species was equal as the canopy closed and the networks became smaller.

Our previous work highlighted the high bee diversity and floral resource availability in the years following timber harvest (Rivers and Betts 2021; Zitomer et al. 2023); the network approach in this study goes beyond those findings by providing evidence for changes in plant-pollinator interactions as stands age. Bees were the most frequent visitors across the stand age gradient, but in mature stands with closed canopies, bee genera *Ceratina* and *Panurginus* had relatively larger roles in the network; similarly, flies had a more pronounced role in the plant-pollinator networks as stands aged. Further study is needed to compare the plant-pollinator networks in what we categorized as 'mature' early seral stands (up to 35 years old) to bee communities in older forests, such as late successional and old-growth stands that are expected to have canopy gaps due to windfall and other finer-grained disturbances over time, and therefore may be a closer match to the more diverse and specialized networks expected in less 'disturbed' habitats (Devoto et al. 2012).

Plant-pollinator networks in our study were dominated by non-native flowering plants across the stand age continuum, but the relative frequency of visits to non-native plants was especially high in young and intermediate stands. In young stands, the four most common floral host plants (i.e., *Hypochaeris* *radicata*, *Crepis capillaris*, *Digitalis purpurea*, and *Cirsium arvense*) are classified as non-native species. In intermediate stands, three of the four most common floral hosts were non-native, with *Rubus ursinus* being the only native species. In mature stands, two of the four most common floral hosts were non-native, with *Rubus ursinus* and *Claytonia sibirica* the two most common native plants. The prominence of non-native plants as floral hosts is notable given that forest management actions can promote invasive forbs in clearcuts (Stokely et al. 2020). If non-native species account for a large proportion of interaction diversity in plant-pollinator networks, resource competition between native and non-native species may be high, potentially compromising the stability of the network or quality of pollination services (Kaiser-Bunbury & Bluthgen 2015). By dominating the pollination networks in young stands, non-native host plants may be impacting which pollinator species are sustained through canopy closure and therefore available to forage in more sparsely resourced older stands.

Non-native species may also alter the temporal availability of resources. For example, in our study, native species that accounted for many of the visits by bees and flies were early-blooming species such as *Rubus ursinus.* In contrast, non-natives that accounted for the greatest proportion of visits included late-blooming species like *Hypochaeris radicata* and *Cirsium arvense.* Furthermore, although non-native plants can serve as a food source for pollinators, they often vary in the nutrients they provide, which may have negative consequences for pollinator health (Stout and Tiedeken 2017; Vanbergen et al. 2017a). For example, the most common non-native plant in this study was *Hypochaeris radicata*, an invasive species in the Asteraceae family (Dennehy et al. 2011). Some species in this family have relatively high protein content in their pollen that may attract more pollinators relative to native flowers (Russo et al. 2019); further research is needed to understand whether such species provide adequate food resources to native pollinators when they replace native flora (Vanbergen et al. 2017a). Additional research is also needed to understand the specific management activities (e.g., herbicide application rates) that may alter the composition of flowering plants available to insect pollinators in regenerating stands.

The non-native western honey bee (*Apis mellifera*) was among the top floral visitors in each age class in our study. The presence of this species may be an additional driver of network structure as honey bees compete with native bees for resources (Thomson 2004; Valido et al. 2019; Davis et al. 2025). Honey bee presence also has implications for resource availability, as the reduction in pollen and nectar due to honey bee foraging could be significant enough in some cases to potentially reduce native bee fitness (Cane & Tepedino 2017). Furthermore, non-native bees can be vectors for parasites or diseases when foraging on the same flowers as native bees (Goulson 2003; Fürst et al. 2014). Although previous work conducted in these stands showed a weak negative relationship between floral resource availability and the prevalence of some parasites in this system (Ponisio et al. 2024), additional work is needed to understand how frequent visits from honey bees might influence these patterns.

Conclusion

We found evidence for more – and more diverse – plant-insect interactions shortly after harvest within intensively managed conifer plantations. Bees were the dominant insect visitor across managed forest stand ages, and the extent of flies in plant-pollinator networks increased as stands moved towards canopy closure. Plant-bee network interactions in particular tend to be less diverse with time since harvest, which coincides with pollinator species loss as the canopy closes. Non-native plants and insects play an outsized role in networks across the stand ages, highlighting the impact of these species within managed forest habitats. Managers looking to provide pollinator habitat should consider the potential loss of resources from removing blooming non-native plants, and if possible, retaining with native species that have similar characteristics to the species that are removed.

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Declarations

Competing Interests None declared.

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