VARIATION IN BUMBLE BEE FORAGING NETWORKS ACROSS A GRADIENT OF FOREST CANOPY

by

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Land use change, invasion of non-native species, and other modes of habitat loss contribute to native bee population declines. A key decline factor may be a loss of nutritional resources, especially when landscapes have reduced floral diversity and abundance. Increasing floral resources may mitigate future declines and forest ecosystems may offer necessary food and nesting opportunities for native bees. However, it is unclear whether and how forest management practices influence the capacity of forests to fulfill these roles. My research advances our understanding of bumble bee nutrition as a function of plant community structure by examining it within a forest ecosystem. I focused on foraging patterns of bumble bees across a gradient of canopy openness in the Oregon Coast Range. With the understanding that bumble bees prefer warm, sunny, fair-weathered spaces with abundant floral resources, I hypothesized that there would be a positive relationship between floral diet breadth and canopy openness. I further predicted that increased canopy cover would result in less floral richness, and greater niche overlap among bumble bee species. My research provides information that could assist in conifer forest management practices to better provide for wild bumble bee community restoration and conservation.

Variation in bumble bee foraging networks across a gradient of forest canopy.

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Abstract

Land use change, invasion of non-native species, and other modes of habitat loss contribute to native bee population declines. A key contribution to population decline may be a loss of nutritional resources, which can occur when landscapes have reduced floral diversity and abundance. Increasing floral resources may mitigate future declines and forest ecosystems may offer necessary food and nesting opportunities for native bees. However, it is unclear whether and how forest management practices influence the capacity of forests to fulfill these roles. Our research advances the field's understanding of bumble bee nutrition as a function of plant community structure by examining it within a forest ecosystem. To do this, we focused on foraging patterns of bumble bees across a gradient of canopy openness in the Oregon Coast Range. With the understanding that bumble bees prefer warm, sunny, fair-weathered spaces with abundant floral resources, we hypothesized (1) there would be a positive relationship between floral diet breadth and canopy openness. We further predicted (2) increased canopy cover would result in less floral richness, and greater niche overlap among bumble bee species. Our results support the first hypothesis for two of our most abundant species but not the third. Moreover, floral richness was indeed lower with greater canopy cover, but responses in niche overlap varied across our three most abundant species. This demonstrates that different bumble bees have varying responses in foraging behavior to forest canopy structure. This research provides information that could assist in conifer forest management practices to better provide for wild bumble bee community restoration and conservation.

Introduction

The population decline of bees has amassed considerable scientific and public attention due to their impact on ecosystem functions, such as improved plant reproductivity. One group of bees, known as bumble bees (genus *Bombus*), garners special attention because of its role as North American native and charismatic generalist providing early and late season pollination services (Xerces Society). Threats to bumble bee populations include a combination of habitat loss, pathogen exposure, agricultural intensification, pesticide use, and climate change (Potts et al. 2010; Vaudo et al. 2024). These threats often co-occur and their negative effects exacerbate each other in reducing floral resource availability, nesting habitat, and overall population health.

Habitat loss is one of the largest drivers of pollinator biodiversity loss worldwide and can take on many forms including landscape simplification driven by the invasion of nonnative species out-competing native floral resources, land-use intensification, and urban and other anthropogenic developments. Mass-flowering events associated with agriculture and invasive species homogenize the resources available to pollinators, thus decreasing diet breadth within bumble bee foraging networks (Watrous et al. 2019). Decreased floral richness may also lead to greater overlap in foraging patterns (Ponisio 2020). These degraded and fragmented habitats are less able to support persistent pollinator communities (Ponisio et al. 2019a). Meanwhile, climate change is driving phenological shifts in bee foraging activity and flowering time such that the two become mismatched and their interactions scarce (Watrous et al. 2019).

While these factors negatively impact all pollinators, bumble bees suffer greater nutritional stress as these two trends in floral resource decline compound. This is due to bumble bees' requirement for a well-rounded diet acquired from diverse and abundant floral resources. Nectar, mostly sugar, fuels the energetic demands of flight, buzz pollination, and internal temperature regulation (Woodard and Jha 2017). Pollen offers necessary protein, lipids, and micronutrients critical to larval development and metabolic and immune health throughout all bumble bee life stages (Woodard and Jha 2017; Vaudo et al. 2024). A shortage of either or both resources can induce nutritional stress within bumble bee populations. Previous research on nutritional stress found that less abundant and less diverse floral resources contribute significantly to the decline of the bumble bee population (Woodard et al. 2019). Further research shows that greater floral diversity and generalist species, such as bumble bees, can help resist overall population and community decline (Ponisio et al. 2019a).

Forests and woodlands can meet critical nutrition needs by hosting understory plants with early-season pollen crucial for queens establishing nests and rearing larvae as well as later-season resources before overwintering (Mola et al. 2021; Woodard et al. 2019). Open and intermediate canopies, such as those of patchwork logging, offer greater benefits to bumble bees because they allow sunlight to reach the forest floor and provide warmth, light, and abundant understory floral resources (Mola et al. 2021); logging and thinning regimes may also create these conditions (Zitomer et al. 2023). Moreover, as climate change introduces heat waves and other extreme weather events that are metabolically costly for bumble bees, wooded landscapes are becoming increasingly important refuges from wind, rain, extreme heat, and drought (Mola et al. 2021). At a landscape scale, variations in forest canopy and subsequent plant community structure may elicit differing benefits for pollinator communities.

As generalists, bumble bees are important to study because they can help maintain plant-pollinator metacommunities, offer resilience, and support biodiversity across time and space (Ponisio et al. 2019; Resasco et al. 2021; Vaudo et al. 2024). Interaction networks depicting the visitation of bumble bees to plants can help elucidate what plants are available and used for forage. Bumble bees' mutualistic relationships with a wide array of flowering plants leverage their interaction networks as insight into the overall health of an ecosystem, especially in response to changing climate and anthropogenic disturbances (Soares et al. 2017). Our research investigates the efficacy of forest ecosystems in providing refuge from these pressures by comparing foraging networks of bumble bees across a gradient of forest canopy openness. We inquired: (1) How does the diet breadth of bumble bee foraging networks vary across different canopies? And (2) How does plant species richness relate to bumble bee foraging niches across different canopies?

With the understanding that greater canopy openness contributes to warmer temperatures and greater sunlight for flowering plants, we expect that (1) Bumble bee diet breadth, or the number of different plants visited, will increase with canopy openness. With the same reasoning, we expect (2) the plant richness will increase with canopy openness, leading to less overlap of floral resource use with greater canopy openness. Understanding how pollinators respond to forest composition at a landscape scale, especially across patchworks of successional timelines, is critical for developing management techniques that restore and conserve pollinator community resources (Rivers et al. 2018a).

Methods

Data was collected over the spring and summer of 2020-2022. The study area was located within conifer forests of various ages, ownerships, and management in the Oregon Coast Range, an area of low-elevation mountains between the Pacific Ocean to the west and the temperate Mediterranean-climate Willamette Valley to the east (Franklin & Dyrness 1988). The region experiences temperate dry weather during the summer months and 150 to 300 cm of precipitation between November and May (Franklin & Dyrness 1988). Forests here are dominated by the conifers western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*), creating a mosaic of mono-aged commercial stands within mixed-age federal forests (Franklin & Dyrness 1988) Other tree species within this landscape include western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), bigleaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*) (Franklin & Dyrness 1988).

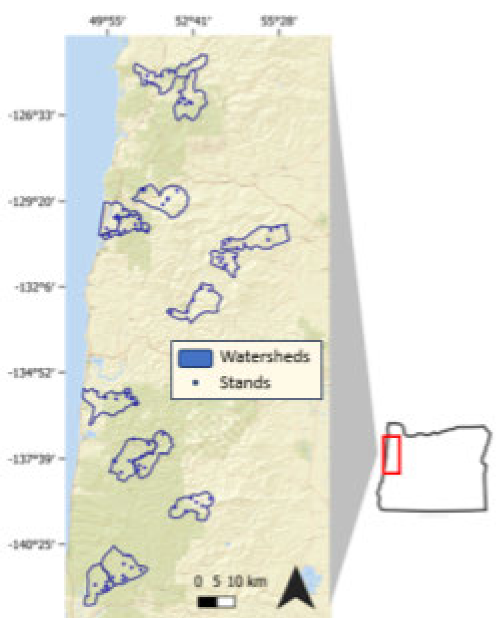

Figure 1: Map of the study area with watersheds and sampled stands. The red box delineates the region of Oregon within which our study occurred (figure modified from Fan Brown et al. *in prep*).

We collected specimens using a standardized, sterile netting procedure. We surveyed across 68 stands; age and management type were homogeneous within each stand, but variable at a landscape scale. Within each stand, three pairs of 32m transects were surveyed (total of 192m of transect), as well as an additional 32 m transect along the road to account for roadside effects (Rivers et al. 2018b). We caught bees using hand netting techniques along these transects to limit data to only the insects that were actively foraging and pollinating. We conducted surveys during optimal bee foraging weather (above 65F, little-no rain, low wind) on both sides of the 32m transect. Surveys lasted for 10 active minutes and the plant species each specimen was observed pollinating was recorded.

Across 68 stands, there were 58 different levels of canopy openness, ranging from 10.5% to 96%. Canopy openness was calculated using a spherical densiometer. The number of open points on the instrument was recorded at each stand for North, East, South, and West directions. These points were then averaged and converted to a percentage for each stand.

From field surveys over three years, we caught 422 bumble bees of eight species: *Bombus caliginosus* (194), *B. vosnesenskii* (120), *B. sitkensis* (69), *B. flavifrons* (15), *B. mixtus* (14), *B. fervidus* (5), *B. melanopygus* (4), and *B. vandykei* (1).

To investigate questions concerning bumble bee foraging breadth, plant richness, and niche overlap, we began by using the bipartite package in R version 4.4.0 to create bipartite networks for each stand (Dormann et al. 2008; Dormann et al. 2009). Bipartite networks consist of all of the bumble bees caught at a given stand and the plants they were observed visiting. We then calculated a rarefied degree for each stand's networks using Chao2 (Chao, Colwell, Lin, and Gotelli 2009). Rarefied degree, a measure of diet breadth, approximates the number of different plant species a bumble bee would have visited if more sampling had occurred (Ponisio 2020). Next, we calculated niche overlap using Jaccard's similarity index, $J(A, B) = \frac{A \cap B}{A \cup B}$, wherein A and B are community samples; the intersection divided by the union of them (Ponisio et al. 2019b). Niche overlap is a measure of competition or sharing of resources, such that a value closer to 1 indicates greater niche overlap and therefore greater competition and/or sharing of resources (Ponisio et al. 2019b).

We created scatterplots using ggplot2 in R 4.4.0 depicting the calculated metrics rarefied degree and niche overlap at each stand (Wickham 2016). Individual scatterplots were made for both metrics of each of the three most abundant bumble bee species (*B. vosnesenskii, B. sitkensis,* and *B. caliginosus*) across a gradient of canopy openness associated with the mean canopy cover for each stand. We visualized floral richness within networks across the canopy gradient as a scatterplot using ggplot2 in R 4.4.0 (Wickham 2019). The number of unique plant species present in foraging networks at each stand was plotted corresponding to the mean canopy at each stand. We fit a linear model to test the relationship between canopy openness and the species richness within foraging networks. This provides necessary context for understanding the relationships between bees' niche overlap metric and canopy openness, as we hypothesized that an increase in canopy openness would lead to greater floral resource availability, and thus lower niche overlap.

To test whether canopy cover has an impact on bumble bee diet breadth, we fit linear mixed models using the package lme4 (Bates, Mächler, Bolker, & Walker 2015) in R version 4.4.0. Canopy cover remained a fixed effect and diet breadth and canopy openness response variables. We included an interaction between canopy openness and bumble bee species (*B. vosnesenskii, B. sitkensis,* or *B. caliginosus)* to model differences in their responses to the canopy. We included a random effect of stand identity to account for the multiple surveys at each stand. We fit similar mixed linear models to test whether niche overlap is affected by canopy openness, replacing the response variable diet breadth with that of niche overlap, and keeping the remainder of the model the same.

Results

Foraging networks of different bumble bee species in the forests of the Oregon Coast Range respond differently to increased canopy openness. For instance, greater canopy openness correlates with greater foraging network breadth for *B. vosnesenskii* and *B. sitkensis* while the foraging network breadth of *B. caliginosus* decreased. A similar diverging pattern occurred for the relationship between network niche overlap and canopy openness for these three bumble bee species.

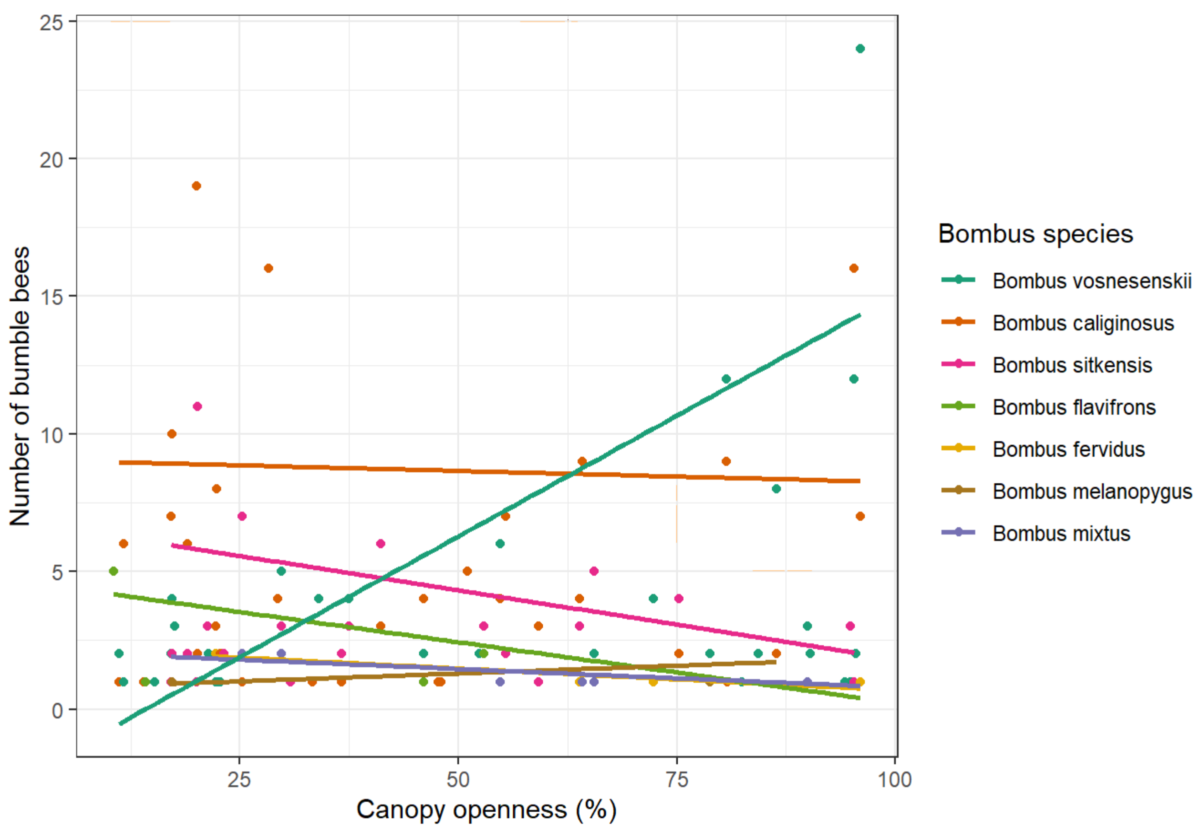

Figure 2: Trends in bumble bee abundance across a gradient of canopy openness.

The eight species present display varying changes in prevalence across the canopy gradient, though not all changes are statistically significant. A linear regression shows that *B. vosnesenskii*'s abundance increases as the canopy becomes more open (R-value: 0.64, p-value: 4.6×10^{-15}). The abundances of four species decreases: *B. sitkensis* (R-value: -0.36, p-value: 0.0025), *B. flavifrons* (R-value: -0.76, p-value: 0.0063), *B. fervidus* (R-value: -0.93, p-value: 0.021), *B. mixtus* (R-value: -0.68, p-value: 0.016). *B. vandykei* was excluded due to sample size. There was no significant decrease in abundance for *B. caliginosus* (R-value: -0.04, p-value: 0.58) or *B. melanopygus* (R-value: 0.66, p-value 0.34).

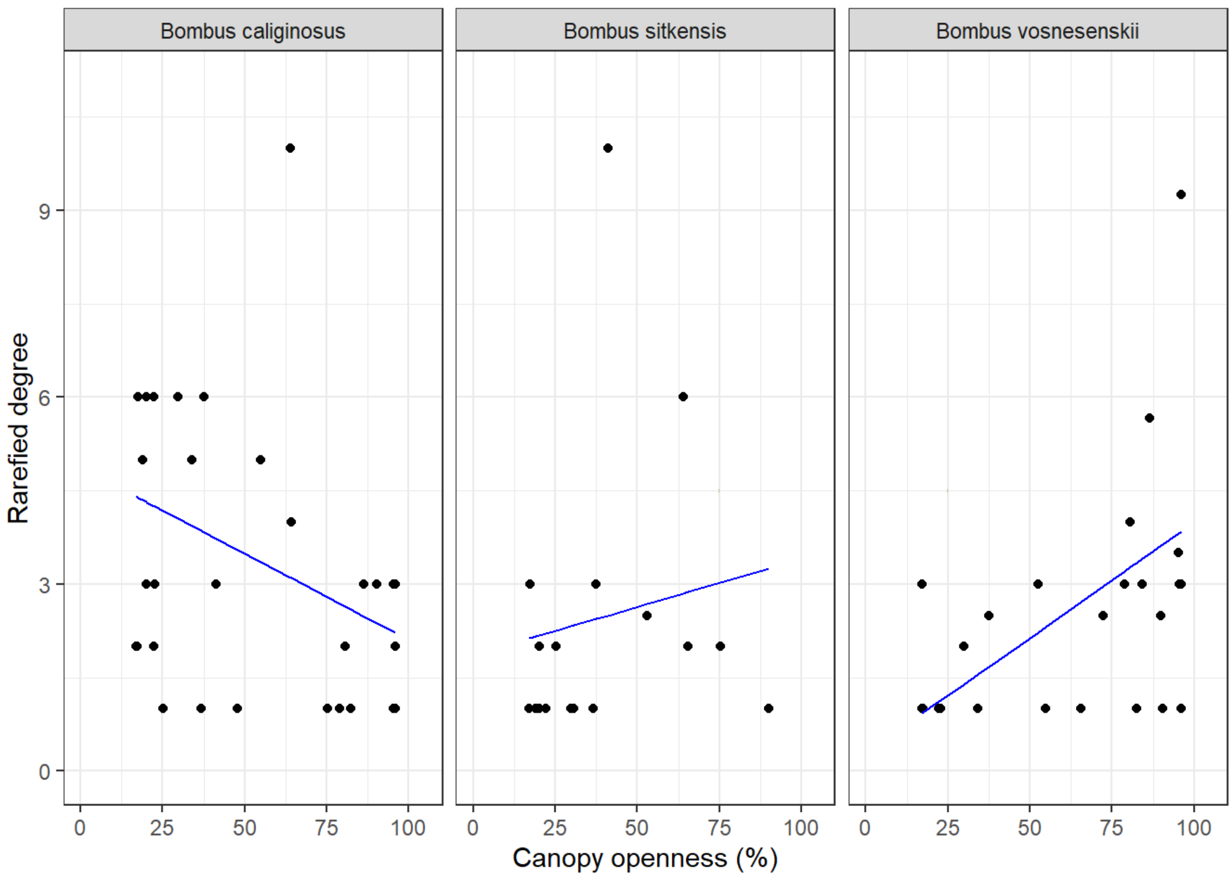

Figure 3: Rarefied degree trends across a gradient of canopy openness from 10.5% to 96% open for *B. vosnesenskii, B. sitkensis,* and *B. caliginosus.*

A mixed linear model controlling for the fixed effects of canopy openness and bumble bee species and the random effect of stand reveals that as the canopy becomes more open, the rarefied network degree for *B. caliginosus* decreases while that of both *B. sitkensis* and *B. vosnesenkii* increases. Due to insufficient data, the other bumble bee species were eliminated from analysis.

Bombus	*intercept*	*std. error*	*d.f.*	*t-value*	*p-value*
caliginosus	3.416	± 0.334	60.22	9.495	$8.42*10^{-12}$ ***
sitkensis	2.605	±0.561	99.50	8.915	0.018 *
vosnesenskii	2.241	± 0.413	84.11	6.505	0.0055 **
Bombus	**slope**	**std. error**	**d.f.**	**t-value**	**p-value**
caliginosus	-0.812	± 0.334	59.17	10.24	0.0181 *
sitkensis	0.450	±0.635	97.64	12.22	0.04998 *
vosnesenskii	1.085	± 0.387	80.28	15.13	$4.98*10^{-6}$ ***

Table 1: Coefficients, standard error, degrees of freedom, t-value, and p-values for the intercept and slope of mixed linear models for *B. caliginosus, B. sitkensis* and *B. vosnesenskii.* Canopy cover was a fixed effect and diet breadth and canopy openness were response variables; stand remained a random effect.

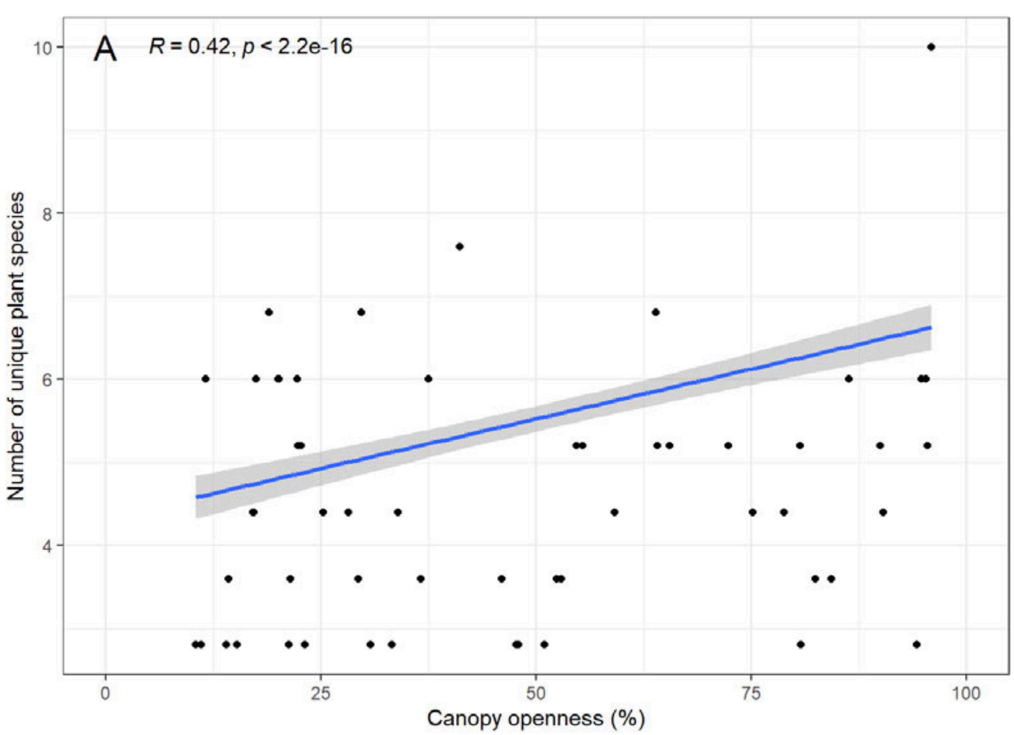

Figure 4a: The plant species richness of bumble bee foraging networks across a gradient of canopy openness.

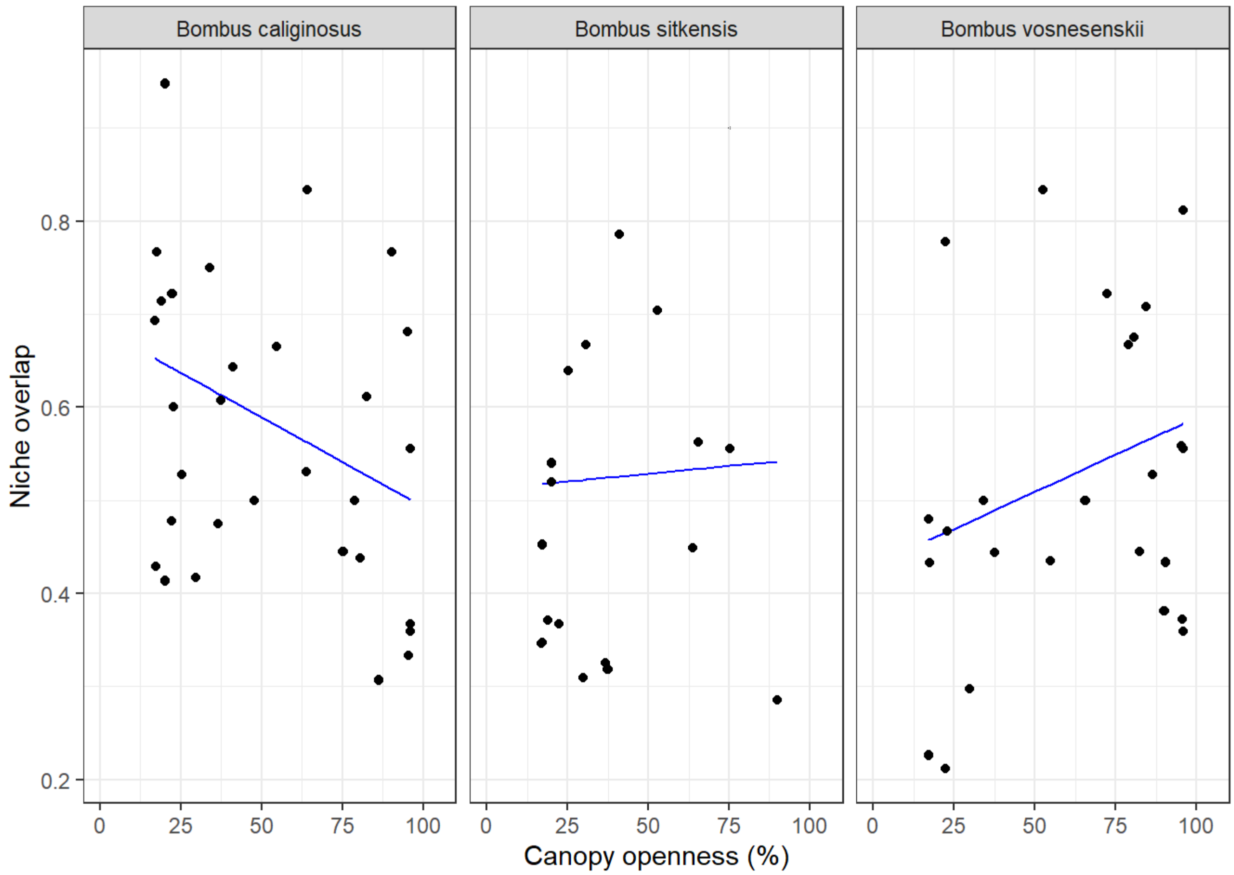

Figure 4b: As the canopy becomes more open, the niche overlap for *B. caliginosus* decreases, while that of *B. sitkensis* and *B. vosnesenskii* increases.

As the canopy becomes more open, the plant species richness within bumble bee foraging networks increases. A linear model shows that for every 10% more open the canopy is, there is an average of 4.2 more unique plant species within bumble bee foraging networks (p-value $2.2x10^{-16}$). A mixed linear model controlling for the fixed effects of canopy openness and bumble bee species and the random effect of stand reveals that as the canopy becomes more open, the niche overlap for *B. caliginosus* decreases while that of *B. vosnesenkii* increases; the relationship for *B. sitkensis* is not significant. Due to insufficient data, the other bumble bee species were eliminated from analysis.

Bombus	***intercept***	***std. error***	***d.f.***	***t-value***	***p-value***
caliginosus	0.584	± 0.026	50.64	22.34	$2*10^{-16}$ ***

sitkensis	0.530	±0.037	90.80	20.86	0.1441
vosnesenskii	0.514	± 0.026	78.50	19.67	0.0092 **
Bombus	**slope**	**std. error**	**d.f.**	**t-value**	**p-value**
caliginosus	-0.056	± 0.026	48.67	18.99	0.0369 *
sitkensis	0.0097	±0.037	88.50	23.97	0.1171
vosnesenskii	0.0468	± 0.026	75.47	25.66	$7.8*10^{-5}$ ***

Table 2: Coefficients, standard error, degrees of freedom, t-value, and p-values for the intercept and slope of mixed linear models for *B. caliginosus, B. sitkensis,* and *B. vosnesenskii.* Canopy cover was a fixed effect and niche overlap and canopy openness were response variables; stand remained a random effect.

Discussion

This study explores changes in bumble bee foraging networks across a gradient of canopy openness to better understand the implication of varying forest types on floral visitation patterns of bumble bees. The eight bumble bee species observed within this heterogeneous coniferous forest landscape had differing relationships with canopy openness. Two species' abundances increased with increased canopy openness, five species' abundances decreased, and one species was represented by only one specimen, though not all relationships between bumble bee species abundance and canopy cover were statistically significant. This unexpected variance in the strength of the relationship between abundance and canopy indicates that bumble bees are likely responding to managed coniferous forests' structures in differing ways. This emphasizes the need for further research and conservation of forest habitats used by native pollinators.

Hypotheses that more open-canopied forest ecosystems are likely to provide greater abundance and diversity of floral resources (Zitomer et al. 2023) provide that the corresponding network degree, or diet breadth, of bumble bees in these systems would be greater. Overall, there is mixed support for this hypothesis. The diet breadth only increased with greater canopy openness for *B. sitkensis* and *B. vosnesenskii*, while it decreased for *B. caliginosus* and there was not enough data to conclude any significant relationship for the other five species examined. The foraging network breadths of *B. caliginosus* and *B. vosnesenskii* present diverging relationships with canopy openness although they share many traits such as having large bodies, near-identical coloration, and wide foraging ranges (Fisher et al. 2022). We also hypothesized that there would be a positive correlation between plant species richness as the canopy became more open. Subsequently, we predicted that the greater plant species richness would correlate with decreased niche overlap as the canopy became more open since a greater array of floral resources would allow for less competition. Again, there is mixed support for this hypothesis. The plant species richness did indeed increase as the canopy became more open, but niche overlap only decreased for *B. caliginosus.*

For each respective species, the niche overlap and diet breadth shared parallel trends across the canopy gradient. The rarefied degree was highest when the niche overlap was also highest, and vice versa. This echoes speculation from Ponisio et al. 2019 that greater competition, or niche overlap, may induce greater inter-species diet breadth as individuals within the population are driven to specialize in floral visitation. This increased niche overlap may lead to redundancy and therefore resilience within a plant-pollinator community (Ponisio 2020). For *B. caliginosus* this occurs when the canopy is most closed, while for *B. sitkensis* and *B. vosnesenskii*, it is when the canopy is most open.

The niche overlap and floral visitation patterns might be complicated by the prevalence of non-native invasive plants throughout the entire gradient of canopy openness. In many disturbed landscapes, including managed forests, invasive species readily outcompete native plants and can homogenize the floral resources available for bumble bees. Less diverse foraging networks and niches may emerge as non-native plants become the preferred floral resource for bumble bees (Mola et al. 2021; Watrous et al. 2019). Indeed, there is a consistent prevalence of invasive flowering plants across all canopies in our study system. Although these plants provide some floral resources, their detrimental effect on floral diversity can be costly to the overall health of bumble bee colonies (Mola et al. 2021).

Of the 422 bumble bees caught and analyzed, 46% of them were *B. caliginosus*, 28% were *B. vosnesenskii,* and 16% were *B. sitkensis*. Five other species made up the other 9% of the bumble bees surveyed. The data is thus limited in its applications, only having significant results for the most abundant of the bumble bee species surveyed. Given the variability in foraging networks across the canopy gradient, it is possible that the other five species were under-surveyed because their use of forest floral resources is incongruent with the sampling techniques used. For instance, they could be more reliant on forest floral resources during the months prior to or following the spring and summer surveys conducted; or more reliant on flowering trees which are more difficult to sample using hand-netting methods.

The difference in relationships amongst these bumble bee species echoes speculation from Mola et al. (2021) that different bumble bee species may use forested ecosystems differently. The gaps in understanding and support for our hypotheses indicate a need for more robust surveys and analyses of the ways that bumble bees use floral resources within forest ecosystems. The abundance of *B. caliginosus*, not typically the most abundant bumble bee in Oregon pollinator surveys, throughout the gradient of canopy and especially in areas with a more closed canopy, suggests that this species in particular relies on forested landscapes. The strong positive correlation between *B. vosnesenskii's* presence and canopy openness suggests that thinned forests are important resources for this species. The significant correlations between the foraging breadth, niche overlap, and canopy openness supports the notion that canopy differences play a role in structuring the foraging networks of bumble bees. The lack of significance in this relationship for five of the species surveyed indicates that much is still unknown about how an ecologically and economically critical genus is using wide swaths of managed landscapes in Oregon.

A more heterogeneous forest landscape may correlate with greater diversity in the pollinator community as each species capitalizes on a different section of the forest gradient (Mola et al. 2021). Forest management such as thinning or gap creating may benefit bumble bee species such as *B. vosnesenskii* and *B. sitkensis*, whose diet breadth increases and potentially community resilience with greater canopy openness. However, these same practices would be detrimental to the diet breadth of *B. caliginosus*. Because foraging breadth is a critical component of overall bumble bee colony health (Watrous et al. 2019), management practices that maintain a heterogeneous landscape are likely best for conserving and restoring bumble bee populations. In particular, forest management should prioritize preserving patches of old-growth forests in order to provide adequate habitat for *B. caliginosus*, which is classified as threatened, and prefers more closed-canopy forests (Fisher et al. 2022).

Conclusion

As habitat loss and climate change compound negative effects on pollinator populations, refuges of resources and shelter, such as forested ecosystems, become even more important. Until recently, it has largely been unknown how pollinators such as bumble bees are using forest ecosystems. Because forest systems across the U.S. and in Oregon especially are managed for a diversity of priorities, a greater understanding of how forest management practices impact the resources available and bumble bees using them is extremely important. Our research suggests that different bumble bees are using forested ecosystems in different ways, such that *B. caliginosus* has the greatest diet breadth and niche overlap in more closed-canopy systems, while the opposite is true for *B. sitkensis* and *B. vosnesenskii*. We also found that canopy cover plays a role in structuring the floral resources available and thus the associated plant-pollinator networks. For the three most abundant bumble bee species in our study (*B. caliginosus, B. vosnesenskii,* and *B. sitkensis*), there were differing relationships between network degree, niche overlap, and canopy openness. Forest management styles that yield a heterogeneous landscape with a mosaic of canopy covers may present the best chance of providing for the most abundant and diverse pollinator communities. However, a lack of significant evidence for the other five bumble bee species in our study highlights the need for more research to best optimize forest management practices for conserving and restoring pollinator populations.

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