Forest bees benefit from compositionally diverse broadleaf canopies

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ABSTRACT

Forests provide critical habitats for pollinating insects, including forest-dependent and habitat generalist species, yet it is unknown how these assemblages are shaped by overstory tree composition. We sampled bees in closed canopy plots in the southeastern United States representing a continuum of forest age and tree composition, from younger conifer-dominated forests to older forests dominated by deciduous broadleaf trees. Species-specific responses of bees to forest composition, and the influence of their traits on responses, were estimated using a joint species distribution model. Additionally, we investigated species richness trends of nesting, sociality, and phenological traits. Forest composition greatly influenced bee species occurrence: 48\% of species had positive relationships with the diversity of insect-pollinated broadleaf trees and 46\% had negative relationships with the proportion of conifer basal area. Bee species with early phenological activity drove these responses and richness patterns supported these trends. Our results indicate that phenology is an important factor determining bee species’ forest dependency and sensitivity to forest composition in this region. We conclude that diverse broadleaf forests are crucial to maintaining bee diversity by providing floral resources that support forest-dependent species even in closed canopy conditions. Conifer forests can also provide valuable habitat to bee pollinators when restored to open canopy conditions. However, because no traits are indicative of conifer forest dependency and bee species respond to understory flora rather than tree attributes, open conifer forests may more strongly favor habitat generalists than forest specialists.

1. Introduction

Declines in insect numbers or shifts in their communities pose a growing threat to ecosystem stability and human society (Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). Worldwide, approximately 87\% of plant species and 35\% of human crop production rely on pollinators (Klein et al., 2007; Ollerton et al., 2011), creating concern that declining pollinator communities may threaten ecosystem integrity and food supply (Barendregt et al., 2022; Forister et al., 2010; Powney et al., 2019). Bees are perhaps the most effective pollinators in most ecosystems (Willmer et al., 2017), yet declines are occurring at multiple spatial and temporal scales (Burkle et al., 2013; Koh et al., 2016; Ulyshen and Horn, 2023). These declines, coupled with major shifts in regional bee composition over the last century (Bartomeus et al., 2013), may be linked to the widespread degradation of their preferred habitats by anthropogenic land-uses (Ellis et al., 2010). Maintaining suitable habitat is thus essential to both conserving bee biodiversity and promoting their pollination services (Garibaldi et al., 2011).

Found on every continent except Antarctica, forests occupy roughly 31\% of global land area (FAO, 2020; Olson et al., 2001). Despite being a historically undervalued habitat for bees, these ecosystems provide important resources that promote pollination services in forests and adjacent land-uses (Ulyshen et al., 2023). It is clear from some regions that forests support unique bee assemblages including many forest-dependent species (Harrison et al., 2018; Winfree et al., 2007). However, forests are highly variable both among and within regions and it remains unclear how these differences in stand composition affects bee pollinator communities. Beyond the variation in tree composition that occurs naturally, anthropogenic drivers are increasingly important determinants of forest composition globally. Climate change (Esquivel-Muelbert et al., 2019; Rosenblad et al., 2023), altered disturbance regimes (Close et al., 2009; Nowacki and Abrams, 2008), invasive species (Potter et al., 2023; Rojas-Sandoval et al., 2022), and their interactions (Jolly et al., 2015; Liu et al., 2017) are all contributing to
forest compositional shifts. Moreover, to meet the resource needs of growing populations, forests managed for timber production or other economic incentives are becoming increasingly common worldwide (FAO, 2020), and these are often characterized by monocultures of fast-growing tree species (Fox et al., 2007; Turnbull, 1999).

Because the tree species present in forest canopies strongly influence ecological communities and their associated ecosystem functions (Peng et al., 2022; Sobek et al., 2009; Tinya et al., 2021; Vivanco and Austin, 2008), understanding how bees respond to forest composition is necessary for biodiversity conservation and sustainable ecosystem management. Particularly relevant are the influences that forest composition may have on the availability of floral resources, which may explain divergent patterns reported in the literature on forest-bee associations. For example, bee diversity tends to be low in closed canopy conifer forests (Favorito et al., 2023; Rhoades et al., 2018; Rivers and Betts, 2021; Zitomer et al., 2023), whereas distinct bee communities and forest specialist species occur in broadleaf forests (Aguiar et al., 2015; Gutiérrez-Chacón et al., 2018; Harrison et al., 2018). In closed canopy broadleaf forests, canopy trees provide floral resources for bees (Ramalho, 2004; Saunders, 2018; Urban-Mead et al., 2021, 2023) and, in deciduous regions, these may be supplemented with herbaceous understories before annual leaf expansion (Mola et al., 2021; Motten, 1986). However, in closed canopy conifer forests, these floral resources may be largely absent (Ovington, 1955).

Forest dependency or specialization of bee species may arise from adaptations to resources unique to forests, such as nesting within wood, excavated cavities, or tree hollows (Fortuin and Gandhi, 2021; Glenny et al., 2023; Roubik, 1979). Moreover, forest specialization may be attributed to reliance on the uniquely-timed floral availability within deciduous broadleaf forests. To capitalize on these seasonally-constrained resources, forest specialist bees within deciduous broadleaf systems are primarily active in the spring (Harrison et al., 2018; Smith et al., 2021). However, to our knowledge, no traits have been specifically linked to conifers or dependency on conifer-dominated forests. This suggests that most bees utilizing conifer forests may be habitat generalists rather than forest specialists. As conifers are naturally dominant in some parts of the world (Olson et al., 2001), are invasive in others (Essl et al., 2010; Simberloff et al., 2010), and are the predominant taxa used in intensive timber production (FAO, 2020), these compositional patterns likely have broad implications on bee biodiversity and its management.

In this study, we use a trait-based approach to investigate how forest composition influences bees within mature forests in the Piedmont region of the southeastern United States. Forests in this region vary naturally from conifer dominant (primarily pines, Pinus spp.) to deciduous broadleaf dominant (Spooner et al., 2021). We sampled bees from two broad age classes of mature forests equally distributed along a forest cover gradient: younger (regrown after 1938, generally with larger amounts of conifers) and older (mature in 1938, generally with less or no conifers). As bee traits are important predictors of their reliance on mature forest habitat (Fortuin and Gandhi, 2021; Harrison et al., 2018), we considered the influence of bee traits on species-specific responses and the contribution of certain trait groups to overall richness patterns. We specifically investigated 1) if bee species occurrence and richness were negatively related to the conifer proportion of stand basal area and 2) if responses of species occurrence and richness to forest composition were driven by bee traits.

Fig. 1. A) Map of the study location in the southeastern United States, with inset showing forest cover and study sites in Clarke County, Georgia. Forest cover is from the National Land Cover Database (Dewitz, 2023). B) Proportion of basal area in younger and older mature forest sites split into three groups for viewing: conifer (predominantly Pinus spp.), oak (Quercus spp.), and other (29 non-oak broadleaf genera).
2. Methods

2.1. Study setting and site selection

This study was conducted in Clarke County, Georgia, USA, in the Piedmont region of the southeastern United States (Fig. 1A). Natural forest composition in the Piedmont ranges from conifer dominant (primarily pines) to deciduous broadenleaf dominant (Spooner et al., 2021), with many stands of mixed composition, and the amount of conifers negatively correlated with increasing stand age (Nicholson and Monk, 1974; Oosting, 1942). Historic farming throughout the Piedmont cleared virtually all forest at some point and degraded the region’s soils (Trimble, 1974; Van Lear et al., 2004). Widespread farm abandonment allowed the Piedmont region to regain forest cover over the mid to late 1900s (Ramankutty et al., 2010; Sohl et al., 2016), much of which came from the natural regeneration and planting of native pines (Nicholson and Monk, 1974; Van Lear et al., 2004). Contemporary forests in the Piedmont are generally closed canopy, consisting primarily of oaks (Quercus spp.) and pines with other trees also occurring according to moisture levels (e.g., hickories (Carya spp.) on xeric sites and maples (Acer spp.), tuliptree (Liriodendron tulipifera), and sweetgum (Liquidambar styraciflua) in mesic conditions). Modern forest conditions today are likely more mesic, dense, and shaded than historical forests due to fire suppression and resulting changes in stand dynamics and species composition (Spooner et al., 2021). In addition, recent regional population growth has witnessed increasing urban and suburban land-uses, resulting in extensive fragmentation of today’s forests (Drummond and Loveland, 2010; Wear, 2002).

Today, Clarke County is 53% forested but only a third of that forest has existed since the 1930s, suggesting recent regrowth consistent with regional trends (Traylor et al., 2023). Areas with low forest cover are either urban-suburban or agricultural (Dewitz, 2023). We selected 40 sites that differed in broad age conditions (relatively old versus relatively young) and the amount of forest in the surrounding landscape (using Dewitz (2019)). Old forests are those that were mature in 1938 and have persisted since, whereas young forests have regrown since 1938. Age was assessed with forest cover maps provided by the local government (Athens-Clarke County Unified Government, 2019), which used historical and repeated aerial photography to evaluate stand persistence over time. Supporting this assessment, composition of sampled stands matched expected age trends (old forests had larger quantities of oaks whereas young forests had larger quantities of pine; Fig. 1B and (Traylor et al., 2023)). Forest composition also varied according to a moisture gradient, with mesic sites having larger quantities of Liriodendron and especially Liquidambar. Aside from composition, few structural differences existed between the age classes in terms of tree diversity, basal area, and gap fraction, although trees were on average larger in old forests (refer to Traylor et al. (2023) for more details). Old and young forests were both scattered throughout the county, and thus there was no difference in the amount of forest cover at multiple spatial scales between the age groups (Traylor et al., 2023).

2.2. Insect sampling and forest measurements

At each site, we randomly chose a forested sampling location on the property within 200 m of a road to facilitate access. We sampled bees at this location using a flight intercept trap consisting of clear, cross-vaned window panes (each 30.5 × 20.5 cm) held over a white bucket (3.78 L) (see Traylor et al. (2022) for details). Because bee communities in temperate forests are stratified vertically and vertical patterns shift throughout the year (Ulyshen et al., 2010), we suspended the trap at 5 m aboveground to collect an intermediate sample of bees preferentially flying near the ground vs. higher in the canopy (Ulyshen et al., 2020). Traps were placed in the field from 9 March–9 September 2020, pro-pylene glycol was used as a preservative between collection dates, and trap contents (samples) were collected every two weeks. Bees were dried, pinned, and identified. Counts of each species were pooled per site across all collections. We excluded the European honey bee, Apis mellifera, from all further analyses because this species is domesticated in the region and reliant on human maintained colonies.

We inventoried forest structure and composition from a 0.1-ha plot centered at each sampling location (refer to Traylor et al. (2022) for details). For this inventory, we measured the diameter at breast height (DBH) and recorded the genus of all living trees at least 10 cm in DBH; we then calculated plot-level basal area (m²) overall and for each genus. We summarized tree composition by performing a non-metric multidimensional scaling (NMDS) ordination on a site × genus basal area matrix. Each site was then given coordinates on three axes, which roughly corresponds to forest age and conifer basal area (axes 1 and 3) and presumably moisture conditions (axis 2; positive values indicate more mesic sites while negative values indicate more xeric sites) (refer to Traylor et al., 2022). The proportion of conifer basal area was calculated as the summed basal areas of pine and red cedar (Junipers) divided by the total basal area. We also calculated the diversity of insect-pollinated trees at each site by counting the number of tree genera with flowers known to be visited by insects (Acer, Alnus, Albatia, Broussonetia, Cornus, Diospyros, Halesia, Ilex, Liriodendron, Magnolia, Melia, Nyssa, Oxycardium, Paulownia, Prunus, Pyrus, Robinia, Tilia). We acknowledge that pollinators also regularly visit flowers of wind-pollinated trees (Saunders, 2018), but we were interested in the specific contribution of typical insect-pollinated genera to habitat quality. Additionally, we calculated the total volume of deadwood pieces >10 cm diameter at each site (excluding standing dead trees; refer to (Traylor et al., 2022) for more details). Finally, to get a better sense of light availability at each site, we used a hemispherical camera held at trap height to photograph the overhead canopy after full leaf-expansion, and calculated gap fraction as the proportion of open sky pixels. Mean ± SD, median, and ranges of stand structure and composition variables, and their correlations, are shown in Supplementary Tables S1 and S2, respectively.

2.3. Bee traits

We compiled trait and taxonomic information for all bee species collected using 45 references (Supplementary Table S3) and open-source data on Global Biodiversity Information Facility (GBIF; www.GBIF.org). Taxonomic ranks included family, subfamily, genus, subgenus, and species. Traits include phenology, body size, nesting, and sociality. Phenology is thought to correspond to a species’ dependence on forests in deciduous broadleaf systems (Harrison et al., 2018; Smith et al., 2021) with other traits indicating nesting or resource requirements (e.g., so-ciality). Body size may be related to bee dispersal ability and/or foraging range (Kendall et al., 2022).

To increase reproducibility and reduce the chance of irregular phenological observations that may occur within a single year, we used bee species phenology determined by the month when occurrence records peak on GBIF in the southeastern United States (a box from −75 to −95 longitude and 28–36 latitude; this area excludes peninsular Florida). For simplicity in linear models, we grouped species according to their phenology into early season bees (with peak phenology occurring in May or earlier) and late season bees (with peak phenology occurring in June or later). This distinction is in alignment with the majority of native insect-pollinated trees blooming in spring and early summer (e.g., Acer, Cornus, Diospyros, Halesia, Ilex, Liriodendron, Magnolia, Prunus) and prior to or occurring with leaf-expansion (Motten, 1986).

A species’ body length was determined as the value given (or mean length of a given maximum and minimum) from descriptions of females in taxonomic literature (Supplementary Table S3), rounded to the nearest 0.1 mm. Nesting and sociality traits were determined from the literature when available or presumed from what is known for the genus or subgenus. A species’ nesting trait was categorized as either above-ground or belowground, with the following subcategories used for aboveground (decaying wood; pre-made cavities; stems/pith) and
belowground (soil; leaf-litter). A species’ sociality was classified as social, solitary, or parasitic, with subcategories provided for social (sub-social; eusocial) and solitary (solitary; communal). Trait and taxonomic information for all species can be found in Supplementary Table S4.

### 2.4. Landscape data and spatial scale

All analyses were performed in R v4.3.0 (R Core Team, 2023). We used USGS 2021 National Land Cover Database (NLCD; Dewitz, 2023) to estimate the amount of forest surrounding our sites at multiple spatial scales. NLCD maps the land cover of the USA at a resolution of 30 m, and includes 20 categories of land cover. Using the ‘raster’ package (Hijmans, 2023), we combined categories 41 (deciduous forest), 42 (evergreen forest), 43 (mixed forest), and 90 (woody wetlands) to make a forest/non-forest map of the study region (all other categories were grouped as non-forest). Using the `getfunc` function of the ‘rgeos’ package (Sivand and Rundel, 2021), we calculated the proportion of forest in the landscape surrounding each site at 10 spatial scales (from 200 to 2000 m, using 200 m increments), hereafter referred to as landscape forest cover (LFC). These spatial scales are appropriate for bee community responses to multi-scale landscape factors (Janvier et al., 2022) and are within accepted distances of bee dispersal and foraging (Kendall et al., 2022; Zurbuchen et al., 2010). We used Pearson correlation between species richness and LFC at all scales to determine the optimal “scale of effect” (Holland et al., 2004; Jackson and Fahrig, 2015) or the spatial scale at which most species respond (Supplementary Table S5). The highest correlation with richness was at 400 m (r = −0.367), but this scale was highly correlated to 2000 m (r = 0.668). As we were interested in multi-scale responses (i.e., one small and one large scale; Janvier et al., 2022), we instead chose to use the 200 m scale (with a similar correlation with richness, r = −0.362) and 2000 m (correlation with richness r = −0.095), which were less correlated with each other (r = 0.570). These scales will hereafter be referred to as LFC 200 and LFC 2000 to indicate the proportion of landscape forest cover measured at 200 m and 2000 m radii, respectively.

### 2.5. Joint species distribution modelling

We used a joint species distribution model (JSDM) in the hierarchical modelling of species communities (‘HMSC’) package (Tikhonov et al., 2020) to assess species-specific responses to local forest conditions and multi-scale LFC, and the role of traits in determining species’ responses. The model uses Bayesian inference to fit a multivariate, hierarchical generalized linear mixed model to a community matrix of abundance or occurrence. In this framework species are modelled jointly with a hierarchical layer in the model, which allow for better parameter estimation, particularly for less frequently collected species (Ovaskainen and Abrego, 2020). For each covariate included, the model estimates a species’ response (β parameter; i.e., a regression coefficient), which describes the relationship between a species occurrence and a covariate, and posterior support for positive or negative responses. Across all species, the influence of traits on species responses (γ parameter) is also estimated for each trait-covariate combination. This parameter assesses the relationship between β parameters and trait values for all species, and can indicate if different responses within a community are related to traits. Additionally, the amount of residual phylogenetic structure in the model (ϕ parameter) is estimated and can be thought of as the variation in phylogenetically linked responses that are not accounted for by the included traits.

We created a site × species presence-absence matrix composed of species occurring at five or more sites. Species occurring at fewer than five sites cannot be modelled effectively (Ovaskainen and Abrego, 2020) (n = 56) and we similarly chose to exclude the commonest species occurring at >90% of sites which lack absence information (n = 3). We fit a presence/absence JSDM on a matrix of 50 species at 40 sites with a Bernoulli distribution and probit link function. We included four traits: nesting (categorical: aboveground, belowground), sociality (categorical: social, solitary, parasitic), phenology (peak activity in the southeastern United States, 1–12, log-transformed to reduce skewness), and mean body size (log-transformed to reduce skewness). The model included seven fixed-effect covariates: the conifer proportion of basal area, log-transformed gap fraction, log-transformed diversity of insect-pollinated trees, log-transformed deadwood volume, Tree NMDS Axis 2 (describing tree composition, from Traylor et al., 2023; hereafter “Tree Axis 2”), LFC 200, and LFC 2000. Tree NMDS Axes 1 and 3 were not used as covariates because of their relationship to the conifer-broadleaf gradient. Transformations were done to increase linearity. These traits and covariates had acceptable levels of multicollinearity (maximum variance inflation factor = 1.428 for traits, 1.702 for covariates; checked with VIF in (Vanegas et al., 2023). We lacked a phylogeny that included all of our species, so we instead included a taxonomic correlation matrix into the model in order to account for similar responses and traits between closely related species. We created a tree based on hierarchical taxonomic relationships (using the levels of family, subfamily, genus, subgenus, and species; Supplementary Table S4) with all branch lengths equal to 1 in the ‘ape’ package (Paradis and Schliep, 2019). Taxonomic trees are suitable when no phylogeny is available, although deep divergences and recent divergences are underestimated, respectively (Ovaskainen and Abrego, 2020). Genera without formal subgenera were given dummy subgeneric names (e.g., “Colletes” for Colletes) in order to keep all species equidistant from the root (Supplementary Table S4). Finally, we accounted for spatial autocorrelation in species occurrences and covariates by including a spatially-structured random effect at the site-level.

We ran the JSDM using the default priors in the ‘HMSC’ package (Tikhonov et al., 2020). We used four Markov chain Monte Carlo (MCMC) chains to sample the posterior distribution, each running for 145,000 iterations. The first 20,000 iterations were discarded as burn-in and thereafter the posterior was sampled every 500 iterations for a total of 250 samples per chain (1000 samples total). Convergence of the MCMC chains was checked with potential scale reduction factors (Gelman and Rubin, 1992) and sample independence with effective sample sizes (ESS). Explanatory power of the model was averaged across all species using Tjur R². Predictive power was estimated by performing 10-fold cross validation (each site randomly assigned to one of 10 folds), and each fold was used for validation based on predictions from the other nine folds. Again, Tjur R² was averaged across all species and validation folds to assess predictive power of the model.

### 2.6. Generalized linear models of species richness

To investigate the responses of bee richness (overall and for all trait groups) to local forest conditions and multi-scale LFC, we performed generalized linear models using a Poisson distribution and a log link function. Response variables included richness of all bees, aboveground nesters, belowground nesters, social bees, solitary bees, parasitic bees, early season bees, and late season bees. We did not have separate models for subcategories of nesting or sociality groups because richness of these groups was either low overall or each dominated by a single subcategory (see Supplementary Table S6). Predictor variables were the same as in the JSDM, including transformations. However, because forest age is highly correlated with the amount of conifers, we additionally ran each model with a categorical age variable (old, young) replacing the conifer proportion of basal area. These competing models were compared with AICc (calculated with ‘AICcmodavg’ package, Mazerolle, 2023), and the best model was reported (see Results). Each selected model was checked and had acceptable levels of dispersion (max = 1.420; checked using c_hat with the ‘AICcmodavg’ package, Mazerolle, 2023). Models displayed non-significant amounts of residual spatial autocorrelation (checked using Moran’s I (Moran.I) from the ‘ape’ package, Paradis and Schliep, 2019).
2.7. NMDS analysis of community composition

Finally, we investigated the influence of multi-scale LFC and local forest conditions on bee community composition. We first created a site × species presence-absence matrix after removing species present at fewer than 3 sites (and thus too rare to be informative), which left 67 species to be included in the following analysis. We used the vegdist function of the ‘vegan’ package (Oksanen et al., 2022) to calculate a distance matrix using the Sørensen coefficient, which calculates dissimilarity of qualitative data (Sørensen, 1948). To first test if community composition of bees differed between young and old forests, we performed a PERMANOVA on the Sørensen distance matrix using the adonis2 function in the ‘vegan’ package (Oksanen et al., 2022). Significance was tested with 9999 permutations. To relate community composition with continuous covariates, we first used the Sørensen distance matrix to create six NMDS ordinations differing in the number of resulting axes (one to six) using the metaMDS function of ‘vegan’ (Oksanen et al., 2022). The stress of each ordination was compared, and we chose to further use the ordination with three axes in the next step to balance acceptable levels of stress with ease of interpretation. With this ordination, we performed an envfit analysis with 9999 permutations (Oksanen et al., 2022), which uses multiple regression to fit continuous covariates onto the ordination and permutations to test the significance of correlations between covariates and the NMDS axes. Covariates were the same as in linear models, but we additionally included the richness of each trait group (including subcategories) to better understand how community composition may be driven by specific traits.

3. Results

3.1. Joint species distribution model of bees

We collected 4157 bee individuals comprising 110 species in 27 genera, of which 50 species in 14 genera were included in the JSMD. The explanatory power of the JSMD was fair (Tjur R² = 0.175; values averaged across all species in the model). The predictive power of the model was lower but better than random (Tjur R² = 0.026; values averaged across all species and cross-validation folds) and predictive values were strongly correlated to explanatory values (Pearson’s r = 0.835; Supplementary Figure S1). Twenty-nine species had predictive Tjur R² > 0, and predictive Tjur R² was not correlated to species prevalence (Pearson’s r = −0.012; Supplementary Figure S1). Residual phylogenetic structure in the model (mean p parameter = 0.826) indicates a large amount of phylogenetic signal in species responses (β parameters) not accounted for by traits.

Species’ responses (β parameters) indicate idiosyncratic relationships with forest and landscape covariates, yet general patterns are visible for both the entire species list and specific genera (Fig. 2; refer to Supplementary Table S7 for mean estimates, 95 % credible intervals, and posterior support). With >85 % posterior probability (pp), 23 species (46 % of those modelled) responded negatively to the proportion of conifer basal area, 24 species (48 %) responded positively to insect-pollinated tree diversity, and 15 species (30 %) responded positively to gap fraction. Each of these covariates also had a single species (2 % of those modelled) respond in opposite direction to the general trends. Species driving these patterns were typically in Andrena, Colletes, Eucera, Hylaeus, and Nomada (as well as sporadic species in Bombus, Ceratina, and Osmia), although five species of Lasioglossum also responded positively to insect-pollinated tree diversity. Notably, 15 species (30 %) responded both negatively to conifer basal area and positively to insect-pollinated tree diversity. Responses to Tree Axis 2 were mixed (positive: 13 species, 26 %; negative: 10 species, 20 %), although some genera appear to respond similarly (positive: Bombus, Nomada, Osmia; negative: Andrena). Responses to deadwood appear sporadic.

General responses to LFC occurred at the 200 m scale but not the larger 2000 m scale (Fig. 2). Thirteen species (26 % of those modelled) responded negatively to LFC 200, whereas 5 species (10 %) responded positively. Negative responses were largely from Andrena and Lasioglossum, however, positive responses included Lasioglossum coerulescens and varied other species. Responses to LFC 2000 were mixed (positive: 9 species, 18 %; negative: 7 species, 14 %), and generic patterns were not present except for four Lasioglossum species responding positively. Four species also showed multi-scale responses, which were always in opposite directions.

We found evidence of nine relationships (γ parameters) indicating that traits influenced species’ responses with >85 % pp (Fig. 3A; refer to Supplementary Table S8 for mean estimates, 95 % credible intervals, and posterior support), although only one of these was with high support (>95 % pp). Sociality influenced species’ responses to forest gap fraction and Tree Axis 2, and phenology influenced responses to insect-pollinated tree diversity. In the case of sociality, responses (β parameters) of solitary and parasitic species to Tree Axis 2 were higher than social species. Phenology’s negative relationship with insect-pollinated tree diversity indicates that occurrence probability of earlier occurring bees increases with increasing diversity of insect-pollinated trees more than those occurring later in the season (Fig. 3B). Although positive in direction, phenology did not significantly influence responses to conifer proportion of basal area (Fig. 3).

Two traits positively influenced responses to LFC at the 200 m scale with high support (>95 % pp): nesting and body length. In the case of nesting, responses to LFC 200 (β) for aboveground nesters were higher compared to belowground nesters. Given the mean β values (Fig. 2), belowground nesters had more negative responses whereas aboveground nesters had more neutral values (i.e., closer to 0). Similarly, the relationship with body size indicates that β increased with body size, and thus larger species had more neutral responses to LFC 200 whereas smaller species had more negative responses. A weaker positive relationship between phenology and LFC 200 was also found. At the 2000 m scale, sociality and body length showed positive and negative influences on species responses, respectively, with weaker support.

3.2. Bee richness

Generalized linear models containing the proportion of conifer basal area generally had lower AICc values than models containing forest age, either substantially so (difference in AICc > 2) or slightly so (difference in AICc between 0 and 2). An exception was for aboveground nesting bees where the age model had lower AICc with a difference > 2 (Supplementary Table S9). Thus, we report the model with proportion conifer for overall richness and all groups excluding aboveground nesters.

Bee richness responded to local forest conditions, and overall trends were generally driven by specific trait groups (Fig. 4; Table 1; full model summaries in Supplementary Table S10). Overall bee richness had a negative response to the proportion of conifer basal area and a positive response to the diversity of insect-pollinated trees. Negative responses to the conifer proportion of basal area were from belowground, solitary, and early season bee groups (Fig. 4A). Positive responses to insect-pollinated tree diversity were driven by the same groups, although aboveground nesting also showed marginal positive trends (Fig. 4B). Tree Axis 2 had a positive influence on aboveground nesters and nest parasites, and gap fraction showed a marginal positive influence on early season bees. However, these trends did not appear in the overall richness. Additionally, aboveground nesters, which were better explained by a forest age model, showed a marginal negative response to forest age, meaning slightly higher richness in older forests.

Similarly, bee richness was influenced by the amount of forest in the landscape, with certain trait groups responding more or less strongly (Fig. 4C; Table 1; full model summaries in Supplementary Table S10).
Fig. 2. Estimates of β parameters (regression coefficients) from the joint species distribution model, indicating species responses to covariates. Positive (red) and negative (blue) responses indicate that a species’ occurrence probability increases or decreases, respectfully, with an increase in the focal covariate. Shading indicates amount of support (posterior probability, pp), with the highest supported relationships (>95% pp) having the darkest shading. Mean estimates and 95% credible intervals of β can be found in Supplementary Table S7. Species’ categorical traits are also shown, but note that phenology in the model was continuous (1–12), with early species denoted as those with phenology <6. Insect-poll. tree div. = Insect-pollinated tree diversity.
Richness of all bees declined with increasing forest cover at the 200 m scale, and this was largely due to negative responses by ground nesting bees and marginal negative responses from social bees and late season bees. Richness of aboveground nesters, early season bees, and all other sociality levels showed no responses to forest cover (Fig. 4C; Table 1; Supplementary Table S10). No richness responses to forest cover at the larger 2000 m scale were found overall or for any trait group.

3.3. Bee community composition

The NMDS with three axes resulted in an ordination with stress = 0.201. The envfit analysis suggests that changes in community composition is related to forest composition and LFC (Supplementary Figure S2; full envfit results in Supplementary Table S11). In particular, the proportion of conifer basal area was significantly related to bee composition ($r^2 = 0.235$, $p = 0.021$), and LFC at both 200 and 2000 m scales were also significantly correlated to NMDS axes (200 m: $r^2 = 0.369$, $p = 0.001$; 2000 m: $r^2 = 0.215$, $p = 0.030$). The species richness vectors of trait groups all had strong correlations with the NMDS axes ($r^2 = 0.323–0.648$, $p < 0.003$), indicating that shifts in overall community composition may be driven by trait group responses (Supplementary Table S11 and Figure S2). Most trait groups respond similarly and were directed away from increasing conifer proportion of basal area. Although forest age is related to the amount of conifer basal area (young forests have more pine; Traylor et al., 2023), community composition of bees did not differ between forest age groups (PERMANOVA $F_{1,38} = 1.390$, $p = 0.152$).

4. Discussion

Biodiversity and associated ecosystem functioning are sensitive to forest composition; however, very little is known about bee responses. In a system that naturally varies from conifer to broadleaf dominant forests, we found that bee occurrence and richness declined with increasing proportions of conifer basal area. Furthermore, we found widespread positive responses of bee occurrence and richness with increasing diversity of insect-pollinated broadleaf trees. These responses were linked to traits, indicating specific adaptations of bees to deciduous broadleaf but not conifer forests. Our findings suggest that diverse broadleaf forests play a key role in maintaining regional pollinator diversity, and
provide insight for the management of bee communities in forested regions. Our results indicate that bees respond to forest composition under closed canopy conditions (i.e., >85 % canopy cover) and benefit most from diverse broadleaf forests. These results bridge two contradictory themes surrounding bee-forest relationships: negative associations with closed canopy conifer forests (Favorito et al., 2023; Rhoades et al., 2018; Rivers and Betts, 2021; Zitomer et al., 2023) and distinct bee communities with forest specialists in broadleaf forests (Aguiar et al., 2015; Gutiérrez-Chacón et al., 2018; Harrison et al., 2018). A simple explanation is that closed canopy conifer forests offer few foraging resources compared to those available in closed canopy broadleaf forests. Tree blooms in broadleaf canopies provide abundant pollen that is readily collected and used in nesting provisions, as well as nectar (Ramalho, 2004; Saunders, 2018; Ulyshen et al., 2023). In temperate regions, leafless canopies in the spring additionally allow for herbaceous growth and floral resources in the understory (Chase et al., 2023; Mola et al., 2021; Morten, 1986; Urban-Mead et al., 2021). It is evident that bees do not rely on conifer trees or forests to the same degree, as the use of conifer pollen is considered incidental from it coating other flowers or vegetation (Rust, 1987). Moreover, as many conifer forests, especially plantations, are continuously closed canopy, understory resources may be diminished or absent (Wray and Elle, 2015; Zitomer et al., 2023). Our results indicate that diverse broadleaf canopies have widespread benefits to bee occurrence and richness, likely due to heterogeneity in bloom timing or species’ pollen preferences (Bertrand et al., 2019; Heinrich, 1976; Inari et al., 2012). Further work may investigate if particular broadleaf forest types equally support bee pollinators and the relative importance of canopy and understory resources.

Although lists of forest dependent bee species are unavailable in most regions, species’ traits may be a useful predictor. For example, forest dependency in bees is driven by a reliance on resources unique to forests, such as nesting in deadwood, pre-excavated cavities, or tree hollows (Fortuin and Gandhi, 2021; Glenny et al., 2023; Roubik, 1979). In temperate regions, forest dependency may also arise from a phenological overlap with uniquely-timed floral resources (Harrison et al., 2018). For instance, in deciduous broadleaf forests of eastern North America, many forest dependent bee species are spring-active (e.g., many Andrena, Nomada, and Osmia; Smith et al., 2021), and our results support this with these and other spring-active genera (e.g., Colletes, Eucera, Hylaeus) being responsive to forest composition. In fact, we found that species active earlier in the season responded more positively to insect-pollinated tree diversity than those active later (Fig. 3B). Negative responses to conifers were additionally driven by early season species (Andrena, Colletes, Eucera, and Hylaeus), whereas late season species were unresponsive (e.g., most Lasioglossum). However, the relationship
Table 1

<table>
<thead>
<tr>
<th>Trait</th>
<th>Model Coefficients (p &lt; 0.10)</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenology</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>0.452 (0.018)</td>
<td>0.017</td>
</tr>
<tr>
<td>Late</td>
<td>-2.983 (0.003)</td>
<td>0.009</td>
</tr>
<tr>
<td>Nesting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aboveground</td>
<td>0.226 (0.013)</td>
<td>0.017</td>
</tr>
<tr>
<td>Belowground</td>
<td>0.448 (0.038)</td>
<td>0.048</td>
</tr>
<tr>
<td>Sociality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solitary</td>
<td>0.230 (0.014)</td>
<td>0.017</td>
</tr>
<tr>
<td>Parasitic</td>
<td>0.230 (0.049)</td>
<td>0.143</td>
</tr>
</tbody>
</table>

Forest Ecology and Management 566 (2024) 122051
C.R. Traylor et al.

Table 1: Summarized results from generalized linear models of bee richness. A separate model was used for overall bee richness and for each category of three traits: phenology (early season, late season), nesting (belowground, aboveground), sociality (social, solitary, parasitic). Significant z-values (p < 0.05), but marginally significant results (0.10) are discussed in the text. Full model coefficients and standard errors can be found in Supplementary Table S1. R is deviance based.

Historically, many conifer ecosystems were dependent on frequent surface fires that maintained open canopies with herbaceous understories (Greenberg and Collins, 2021; Hanberry et al., 2023, 2018). Over the past century, fire suppression, silvicultural practices favoring dense plantations over naturally regenerated ecosystems, the loss of large herbivores, and encroachment by mesic species (mesophication) has resulted in more closed conifer overstories, denser midstories, and diminished herbaceous communities (Fox et al., 2007; Hanberry et al., 2023, 2018; Laughlin et al., 2011). These changes have taken place across most of the southeastern United States, especially the Piedmont where our study took place (Sponser et al., 2021). Although broadleaf forests across the eastern United States have likewise changed over time to become denser and with greatly diminished understories (Hanberry et al., 2020; Nowacki and Abrams, 2008), these forests still provide floral resources in the canopy and understory that allow a seasonally constrained assemblage of bee species (Chase et al., 2023; Urban-Mead et al., 2021).

Conifer-dominated ecosystems provide essential habitat to a wide
range of endemic plants and animals, many of which are threatened or endangered. However, conifers are also planted or invasive in areas historically dominated by broadleaf forests or where forests do not grow naturally (Essl et al., 2010; Pérez-Gómez et al., 2024; Simberloff et al., 2010). Our results suggest that the displacement of broadleaf forests by conifer stands in such areas may negatively impact forest-dependent bees. Where conifers naturally occur, it is clear that restoring open canopy conditions in conifer forests through clearing, thinning, and burning will benefit bee richness by establishing herbaceous understories and exposing soil (Favorito et al., 2023; Gelles et al., 2023; Hanula et al., 2015; Moylett et al., 2020; Zitomer et al., 2023). However, the bee communities in these restored conifer forests are thought to respond to changes in the understory flora rather than to the overstory (Dixon et al., 2022; Hanula et al., 2015; Ulyshen et al., 2022), suggesting that they may not be dependent on tree- or forest-specific resources and habitat. Moreover, our results and those of others (Fortuin and Gandhi, 2021; Zitomer et al., 2023) provide no indication that bees have traits adapted to unique resources provided by conifer trees or forests. Although many wood-nesting bees inhabit open canopy conifer forests when wood is available (Ulyshen et al., 2024), the bee species primarily benefitted by clearing, burning, and thinning are typically active late in the season, nest in soil, and are social (Fortuin and Gandhi, 2021; Galbraith et al., 2019; Lazarian et al., 2016; Moylett et al., 2020; Odanaka et al., 2020; Ulyshen et al., 2021). Species in these same trait groups are typically habitat generalists that may also occur in agricultural and developed land-uses (Harrison et al., 2018; Smith et al., 2021); in our study, they were unresponsive to forest conditions but declined with increasing forest cover. Once our current understanding of bee forest-dependency, it is unclear as to what extent these management practices will benefit forest-dependent bees rather than habitat generalists. Thus, further research is needed to determine if the bee species inhabiting restored, open conifer forests depend on those forests or if they are also found in other land-uses that provide similar habitat. Regardless of what future endeavors find, our results demonstrate that broadleaf trees are important habitat components that support a unique fauna of forest-dependent bee species.

5. Conclusions

Maintaining suitable forest habitat is integral to ensuring bee biodiversity and promoting their pollination services. However, not all forests are of equal value to bee species, some of which are habitat generalists and others that are forest specialists. We found that nearly half of bee species (46%) declined in mature forests with increasing amounts of conifers, whereas even more species (48%) benefitted from forests with a diverse canopy of insect-pollinated broadleaf trees. These relationships were driven by bee species with an early phenology that overlaps with flower availability in deciduous broadleaf forests, indicating that broadleaf forests play a key role in supporting regional pollinator diversity and forest specialist species. Conifer forests, which today are often denser and more shaded than they were historically, may support richer bee communities after prescribed burning or thinning. However, these relationships may also benefit habitat generalists rather than forest specialists. Silvicultural treatments intended to restore, improve, and maintain pollinator habitat should therefore be designed with these relationships in mind.

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CRediT authorship contribution statement

Don C. Bragg: Writing – review & editing. Michael D. Ulyshen: Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. Clayton R. Traylor: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Joseph V. McHugh: Writing – review & editing, Resources, Methodology, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data and code used in this study are publicly available at https://doi.org/10.5281/zenodo.10689005.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122051.

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Athens-Clarke County Unified Government (ACCUG), 2019. Data from: Legacy Forest Project.


