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Compositional attributes of invaded forests drive the diversity of insect functional groups

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ABSTRACT

Forest canopies are important habitats for animal biodiversity globally. The structural and compositional components of canopies influence biodiversity, and recent advancements in remote sensing have given insight to these relationships. As invasive shrubs alter both the structure and composition of forests, we use handheld, mobile LiDAR to relate these elements and the over-arching tree composition to insect biodiversity in Georgia, USA. Both LiDAR-derived structural metrics (vegetation density and Shannon vertical complexity index) were related to invasive shrub cover. We sampled four insect functional groups using two methods: woodboring beetles, mycophagous beetles, and bees were sampled using flight intercept traps 5 m aboveground, while litter-foraging ants were sifted from leaf-litter. From our generalized linear models, we found that tree composition strongly influenced all groups, though responses varied among functional groups. Woodboring beetles were negatively influenced more strongly by invasive shrub cover than vegetation density and also responded positively to tree and deadwood diversity. By contrast, bees and mycophagous beetles were unaffected by both the structure and composition of invasive shrubs, but were sensitive to tree composition. In the leaf-litter, ants were negatively influenced by invasive shrub cover and were sensitive to tree composition. Thus, the composition of forests is an important driver of insect diversity in our system, but with idiosyncratic responses among functional groups. Our results demonstrate the utility of LiDAR in clarifying the relationship between structure and composition on biodiversity in forest canopies, especially in regards to invasive plants.

1. Introduction

Forest canopies are the “last biotic frontier” (Erwin, 1983), with countless unique microhabitats providing resources and residence for an abundance of animal biodiversity globally (Erwin, 2001). The forest canopy is a complex three-dimensional realm consisting of all aboveground plant structures and the spaces between them (Didham and Fagan, 2004; Nadkarni et al., 2001). The amount and

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distribution of vegetation within this diffuse aerial zone varies greatly among forests depending on the composition of the plant community, local environmental conditions, management history, and invasion by non-native plants. These differences are thought to have important implications for the diversity, distribution and movement patterns of animals, and various canopy components are expected to differently influence functional and trophic guilds (Heidrich et al., 2020; Tinya et al., 2021). This is particularly true for insects, which exhibit immense diversity in terms of species number, but also life strategies and resource use. For example, differences in tree composition may promote the diversity of some insect groups while reducing or not influencing others (Leidinger et al., 2021). This may be linked to specific resources or abiotic conditions provided under certain canopy types, such as deadwood objects used by saproxylic insects (Seibold and Thorn, 2018), foraging and nesting habitats for pollinators (Hanula et al., 2015), or warm sunny conditions favoring ants (Grevé et al., 2018).

For decades, ecologists have suspected that structural elements of canopies were important for biodiversity (e.g., MacArthur and MacArthur, 1961). Yet, quantifying the structural components of the canopy has not always been easy or even possible. However, the advancement of remote sensing technologies has allowed for a deeper understanding of the influence of canopy structure on biodiversity. Of these, light detection and ranging (LiDAR) has proven to be most applicable and versatile (Davies and Asner, 2014), and airborne LiDAR can effectively quantify numerous forest structure metrics (0.5–1 m² resolution) across a landscape (e.g., Müller and Brandl, 2009). More recently, the implementation of LiDAR scanning from the ground (i.e., terrestrial or mobile LiDAR) has proven especially useful in characterizing lower canopy layers at cm-scale resolution (Lovell et al., 2003; Hilker et al., 2012; Crespo-Peremarch et al., 2020), but generally at smaller spatial extents compared to airborne scanning (i.e., within a single plot or tree; Newnham et al., 2015; Dassot et al., 2011). The use of LiDAR has provided new insights into how canopy structure influences insect biodiversity. Similar to composition, there is no single aspect of canopy structure that promotes overall insect biodiversity, with different functional or taxonomic groups responding to specific structural elements (Davies and Asner, 2014; Schuldt et al., 2019). However, the complexity of the canopy (as defined by multiple vegetation layers, heterogeneously distributed vegetation, or similar classifications) seems to generally support overall higher insect abundance (Knuff et al., 2020) and correspondingly higher species richness as well (e.g., Müller et al., 2018). This is supported for multiple taxa, including Lepidoptera (both moths and butterflies), Diptera, Hemiptera, and saproxylic Coleoptera (Heidrich et al., 2020; Müller et al., 2018; Zellweger et al., 2016). Importantly, flying insects are expected to be more sensitive to forest structure than flightless or ground-dwelling insects (Davies and Asner, 2014). For example, the species richness of ants and beetles sampled in the leaf-litter were not influenced by canopy complexity or heterogeneity in previous studies (Janssen et al., 2009; Grevé et al., 2018; Heidrich et al., 2020).

An advantage of LiDAR is the ability to disentangle the structural and compositional effects of forest canopies on biodiversity (e.g., Müller et al., 2010). This might prove to be especially useful in assessing the ecological impacts of invasive plant species, where the effects of an invader's identity are rarely disentangled from its contribution to forest structure. For example, dense mid-story thickets formed by invasive shrubs are often reported to suppress insect diversity near the forest floor (e.g., Hanula and Horn, 2011a, 2011b; Ulyshen et al., 2010a; Ulyshen et al., 2020a). Yet, whether these effects are driven by invasive shrub properties or by merely creating a dense canopy environment remains unknown. There is evidence that dense vegetation can impede insect flight and obstruct resource detection (Verdeny-Vilalta et al., 2014; Geroff et al., 2014; Randlkofer et al., 2010; Beyaert and Hilker, 2014). Furthermore, dense stands may change abiotic conditions related to insect movement, and lower insect diversity has been found when entire stands are dense (Müller et al., 2014). By contrast, many insect groups may instead benefit from a dense canopy within a single shrub or tree due to increased structural complexity and associated resource concentration (Müller et al., 2014). This may occur even within the canopy of non-native shrubs (Loomis and Cameron, 2014). Overall, the effects of vegetation density on insect communities is linked to the life history of the investigated groups and the spatial extent used to measure canopy structure (Müller et al., 2014, 2012). Such findings suggest that insect communities may be responding to the dense canopy environment created by invasive shrubs rather than inherent plant properties. If this is the case, biodiversity overall may be less sensitive to invasive plants than commonly assumed, which would increase the need for taking structural metrics such as vegetation density into account.

Forests in the southeastern United States are continuously altered by the invasion and dominance of invasive shrub species (Miller, 2003; Wang and Grant, 2012; Ward, 2002), providing an opportunity to investigate the compositional and structural effects of shrubs on insect communities. Here, we relate the compositional and structural aspects of the shrubs, and the overarching tree community, to the diversity of four insect functional groups in the southeastern United States: woodboring beetles, mycophagous beetles, pollinators (bees) and litter-foraging ants. We used vegetation density and Shannon vertical complexity index as structural metrics that relate to shrub cover. Because canopy structure is likely to be most important for flying insects (Davies and Asner, 2014; Zellweger et al., 2016), we predicted that dense thickets created by shrubs would have negative effects on the diversity of woodboring beetles, mycophagous beetles, and bees by impeding their movement and disrupting resource detection methods (Verdeny-Vilalta et al., 2014; Geroff et al., 2014; Randlkofer et al., 2010; Beyaert and Hilker, 2014). Oppositely, we predicted litter-foraging ants would be impacted by invasive shrubs altering the leaf-litter (Weand, 2020; Mitchell et al., 2011) and impacting prey populations (Woodworth et al., 2020; Clark and Seewagen, 2019; Mahon et al., 2019; Nguyen et al., 2016) rather than by creating a dense canopy. Because invasive plants are expected to disproportionately impact rare species (Wagner and van Driesche, 2010), we used Hill numbers (Hill, 1973; Chao et al., 2014) to compare effects on richness weighted towards rare, common and dominant species. Finally, we predicted that tree composition would have group-specific responses based on divergent life history strategies (Leidinger et al., 2021; Tinya et al., 2021; Heidrich et al., 2020).

2. Methods

2.1. Study location and site selection

This study was conducted within a 310 km² landscape comprising Athens-Clarke County, Georgia, USA (Fig. 1) with all data collected in 2020. The county resides in the Piedmont region, approximately 244 m above sea level. It has a humid subtropical climate, with an average temperature of 17 °C and average rainfall of 1177 mm (National Centers for Environmental Information, 2019). Within Athens-Clarke County, GA, we used detailed forest maps (ACCUG, 2019; Dewitz, 2019) to select potential sites of varying age and then contacted owners for permission to sample on their property. In total, we sampled 40 sites including 16 and 24 on public and private property, respectively. At each site, one sampling location was chosen at random, so long as it was positioned within 25–200 m of a known road, trail, or parking area. These criteria were established to control for edge effects but maintain easy access for visiting every site within a day. Randomization was done using the “Create Random Points” command in ArcMap 10.4 (Esri, Redlands, California), where one point was created on each property following the rules above. All sampling locations were separated by at least 1 km.

2.2. Insect trapping and functional group identification

To sample flying insects, a flight intercept trap (Fig. 2A) was hung 5 m above the ground at each site. We suspended each trap from a rope thrown over branches so that it hung away from tree trunks and could be raised and lowered unobstructed. The traps consisted of two intersecting clear-window panes (30.5 cm height, 20.5 cm width) tied with wire to a 3.78 L, white bucket (20 cm diameter). This trap design was found to be effective at collecting both beetles and bees in previous studies (Ulyshen and Hanula, 2007; Ulyshen et al., 2010b). We drilled two, 8 mm holes on opposite sides near the top of the bucket and installed 0.5 mm wire-mesh windows to allow for overfill without losing any of the sample. To attract woodboring and mycophagous beetles (Bouget et al., 2009), traps were baited with low-release ethanol lures (Synergy Semiochemicals, Delta, British Columbia, Canada) that were replaced every 4 weeks. Traps were active from 9 March 2020–9 September 2020, and samples were collected every two weeks. In order to preserve the

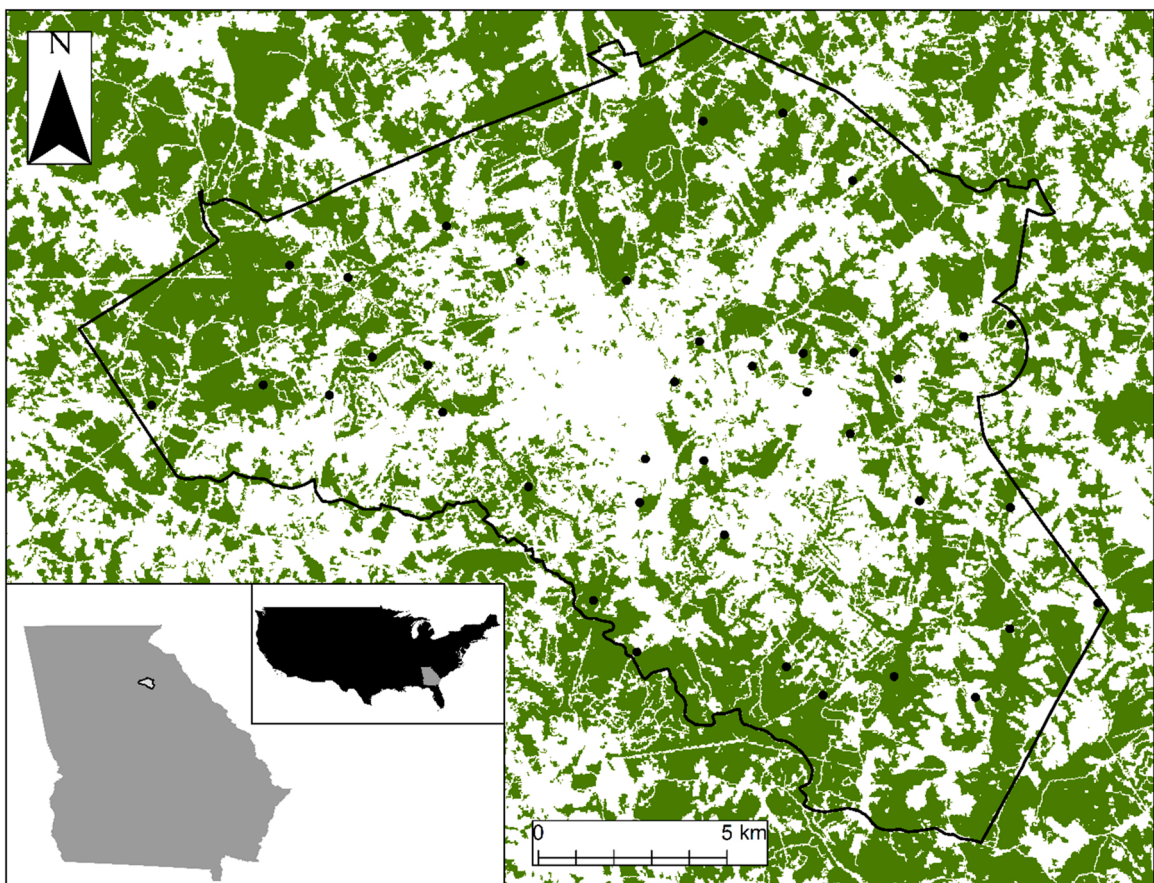


Fig. 1. Placement of sampling locations in Athens-Clarke County, Georgia, USA. Black dots are sampling locations, green represents forest cover from Dewitz (2019).

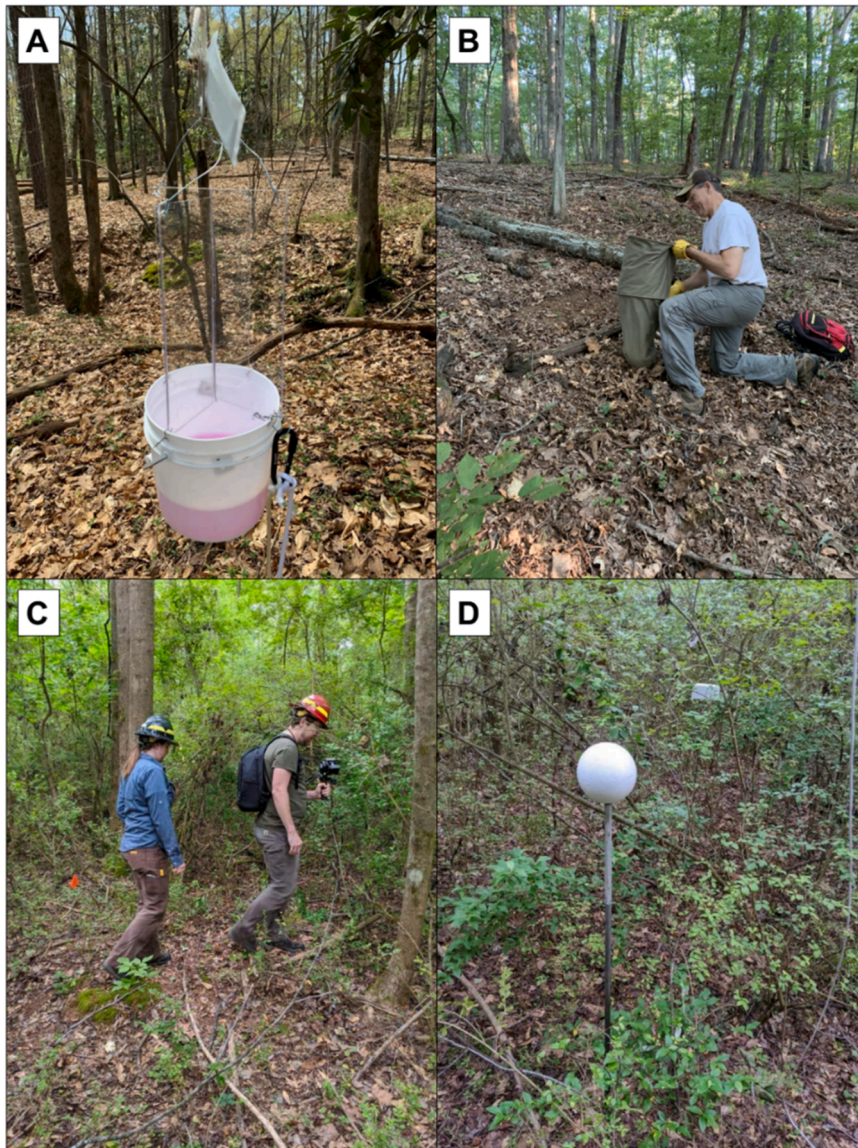


Fig. 2. A) Window panel trap used to sample flying insects. B) Sifting leaf-litter at a site with low vegetation density. C) Using the mobile LiDAR scanner (in hand) at a heavily invaded and dense site. D) Reference objects used to orient the LiDAR scans, at the same site as C. Distance between reference objects is 3 m.

samples in the field between collections, the buckets were filled with propylene glycol with a drop of dish detergent. To sample ants, we collected leaf-litter samples using a sifter with 1.25 cm mesh (Fig. 2B), resulting in samples that were approximately 1 L each. During each of three sampling periods (June, July, and August 2020), we collected a litter sample from each site. We sifted litter approximately 5 m away from the trap by taking 5 paces to the south, east, and west for the first, second, and third collection periods, respectively.

We mounted and identified taxa known to belong to the focal functional groups in the canopy and leaf-litter, limiting our scope to certain taxa that are well known for each function: pollinators (Hymenoptera: Anthophila), wood-boring beetles (Coleoptera: Cerambycidae), mycophagous beetles [Coleoptera: Anthribidae, Cerylonidae, Endomychidae, Erotylidae, Laemophloeidae, Monotomidae, Mycetophagidae, Silvanidae, Tenebrionidae: Diaperinae: Diaperini, Tetratomidae, Zopheridae (including Colydiinae)], and generalist leaf-litter predators (Hymenoptera: Formicidae). From the mycophagous beetle group, we included only taxa having an association with fungi that grow on or in deadwood. Therefore, we excluded taxa that have no association with fungi (e.g., Anthribidae: *Ormiscus* spp), are thought to feed on molds or decaying vegetation rather than fungi on or under the bark of deadwood (e.g., Erotylidae: Xenoscelinae, Zopheridae: *Hyporhagus punctulatus*, Mycetophagidae: *Litargus tetraspilotus*), or are thought to be predaceous in bark beetle galleries (e.g., Laemophloeidae: *Dysmerus* spp, Zopheridae: *Colydium lineola*). Mycophagous beetles found in leaf-litter

samples were not included here, as we were only interested in species caught while flying.

2.3. Forest stand data

We first established a 0.1 ha circular plot around each intercept trap using a Haglöf DME ultrasound distance measurer (Haglöf, Langsle, Sweden). This plot size has a radius of 17.84 m, within the 20 m of accuracy guaranteed for this device. Within the plot, we measured stand and deadwood characteristics. We recorded the diameter at breast height (DBH) and genus of each stem > 10 cm as an attempt to characterize the mature trees in the plots. From this data and for each site, we calculated Shannon's Diversity (Shannon, 1948) of trees, total basal area, and median tree diameter. We further calculated the diversity and total basal area separately for tree genera known to be pollinated by insects (*Acer*, *Ailanthus*, *Albizia*, *Broussonetia*, *Cornus*, *Diospyros*, *Halesia*, *Ilex*, *Liriodendron*, *Magnolia*, *Melia*, *Nyssa*, *Oxydendrum*, *Paulownia*, *Prunus*, *Pyrus*, *Robinia*, *Tilia*), which may be important for bees.

We characterized deadwood pieces > 10 cm in diameter as either snags (standing dead trees), downed logs, or stumps (the standing base of fallen trees with a measurable height). Each deadwood piece was given a decay class (1–5 with 1 = freshly dead and 5 = heavily decayed) (Spetich et al., 1999). This classification differentiates decay severity between logs vs. snags, and stumps were treated as logs in this study. For each piece, we recorded the genus (or hardwood/softwood/unknown for heavily decayed pieces or those missing bark) and estimated the volume based on its shape. On stumps, the height and the diameter at the mid-height were recorded, and volume was calculated as a cylinder. If a stump was rectangular, we also measured the depth and calculated volume as a rectangular prism. For all downed deadwood pieces with an end diameter > 10 cm, we measured the longitudinal length and diameters at the basal and apical ends. If a deadwood piece was partly outside of the plot, we measured the diameter where it crossed the plot boundary instead of at the end located outside the plot. If a piece was flat instead of round, we measured the thickness as well. The volume of downed logs was calculated using the formula for a narrowing cylinder (round piece) or a trapezoidal prism (flattened piece). The DBH of snags > 10 cm was measured but volume could not be estimated. The total volume of deadwood was summed for each site. Using the Siitonen Index (Siitonen et al., 2000), we also calculated deadwood diversity as the number of unique deadwood pieces based on position (snag, downed, stump), genus, decay class, and size class. Size classes were determined using a scale based on the diameter at mid-height (stump), largest end (downed logs), or DBH (snags) as follows: 1 for a diameter 10–20 cm, 2 for 20–30 cm, 3 for 30–40 cm, and so on.

After leaf expansion, hemispherical photos were taken at trap height in each plot by removing the trap temporarily and pulling a hemispherical camera into position (as described in Sheehan et al., 2019). We used WinSCANOPY (Regent Instruments Inc., Quebec, Canada) to calculate gap fraction in each photo as the percentage of open-sky vs. canopy cover pixels.

2.4. Invasive shrub surveys

We characterized invasive shrub cover along four 10 m transects in the cardinal directions from the plot center. At 1 m increments along each transect, we created circular subplots 0.1 m diameter, totaling 40 subplots per site. At each subplot, we recorded any invasive shrubs > 1 m tall. From this, we calculated the invasive shrub cover as the number of subplots containing invasive shrubs at heights > 1 m. The species included in this metric were *Elaeagnus* spp, *Ligustrum* spp, and *Lonicera* spp, which all form dense thickets in the canopy (Miller, 2003). Only above this height would we consider shrubs to be mature (bush-like rather than a single stem), which has been shown to have the largest effects on invertebrates (Nguyen et al., 2016).

2.5. Mobile LiDAR scanning

We used a ZEB Revo (GeoSLAM, Nottingham, United Kingdom) handheld, mobile LiDAR scanner to estimate the understory vegetation density in our plots (Fig. 2C). In short, these scanners capture 2D laser scan data, which is combined with inertial measurement unit data in the simultaneous localization and mapping (SLAM) algorithm to create 3D point clouds. In each plot, we placed three foam shapes on poles to be used as reference points for point cloud and directional orientation (Fig. 2D). We scanned plots by slowly walking in back-and-forth transects offset by 2–3 m from one side of the plot to the other, then performing a set of transects perpendicular to the first set. We circled around and between large trees and dense thickets in order to lower the amount of 3D space hidden from the laser's view (Watt and Donoghue, 2005; Dassot et al., 2011). We started and ended a scan at the same location. Scans were performed either in the early dawn or in overcast conditions in order to reduce the effect of sun exposure on laser performance. In total, each scan took approximately 20–25 min, and we performed two scans in each of 31 plots. In the remaining nine plots, we performed one longer scan (usually 30–40 min) due to rough terrain, dense vegetation, or suboptimal weather conditions.

2.6. Data analysis

The laser return data were processed into a point cloud using the GeoSLAM software, Geo SLAM Hub v4.1.1 (GeoSLAM, Nottingham, United Kingdom). Point clouds were imported into R version 4.0.4 (R Core Team, 2021) and further processed with the *TreeLS* package (de Conto, 2020). Each point cloud was first cropped using the *tlsCrop* function to standardize the scanned area (962 m²) before applying a nearest neighbor filter to remove isolated returns (*nnfilter* function, search radius = 0.1 m, number of neighbors = 2). Ground returns were then classified and used to normalize (i.e., flatten) the point clouds so that each ground point corresponded to zero meters with the *tlsNormalize* function. The point cloud data were then voxelized using side lengths of 10 cm to homogenize the point-density distribution of lidar returns. We calculated the total number of voxels per 1 m height then summed these

counts for each height, hereafter referred to as vegetation density. Furthermore, we calculated a measure of canopy vertical complexity with Shannon's entropy using the voxelized data (Shannon, 1948; Pretzsch, 2008). Although we scanned some sites twice, we only used data from the first scan to calculate these metrics.

We characterized the tree composition of each site by performing a nonmetric multidimensional scaling (NMDS) analysis using Bray-Curtis distances in PC-ORD (Wild Blueberry Media LLC) on the basal area represented by each tree genus per site with the "autopilot" settings. NMDS was used because the basal area data were non-normal. Genera only present at a single site were removed before conducting the ordination ($n = 10$ removed; $n = 22$ used in ordination). This resulted in an ordination consisting of two axes with a stress of 13.122 after 46 iterations, the values of which were then used as predictor variables in our models of insect response (see below). Correlations between tree genera and both axes are provided in [Supplementary Table S1](#).

The abundance of each insect species was pooled per site. We estimated species richness for each site using Hill numbers, which allow for comparisons between species richness estimates allotting more weight to rare ($q = 0$), common ($q = 1$), and dominant ($q = 2$) species (Chao et al., 2014). Hereafter, Hill number estimates will be referred to as species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) as recommended in a recent review (Roswell et al., 2021). Our samples were standardized by coverage, a measure of how completely a community has been sampled based on the number of singletons, doubletons, and the total abundance (Chao and Jost, 2012). Using coverage as a standardization process allows for fairer comparisons of communities' true diversity, rather than what was sampled, which is highly dependent on how many rare species there are and how rare they are in a community (Chao and Jost, 2012; Roswell et al., 2021). We used the lowest observed coverage for each functional group to standardize the dataset and interpolate the estimated diversity for all sites. The lowest coverage was 0.6832 for bees, 0.6467 for woodboring beetles, 0.6250 for mycophagous beetles, and 0.6694 for ants. For mycophagous beetles, we chose to remove four sites that had coverage lower than 0.6000, as low coverage provides inaccurate richness estimates (Chao and Jost, 2012). To estimate Hill numbers, we used the estimateD function in the *iNext* package (Hsieh et al., 2016) in R (R Core Team, 2021). The maximum abundance for an ant species per site was set to 20. In cases where Hill numbers could not be estimated for ants because we only observed 1 species at a site ($n = 6$), we set the value as 1 for all q values.

We performed generalized linear models for each functional group and Hill number combination to investigate the relationships between insect biodiversity and canopy structure and composition. Because Hill estimates are continuous, we used Gaussian distributions (identity link) when our richness estimates were normally distributed (woodboring beetle Shannon and Simpson diversities) and Gamma distributions (log link) when they were right-skewed (all else). The models included these variables: vegetation density,

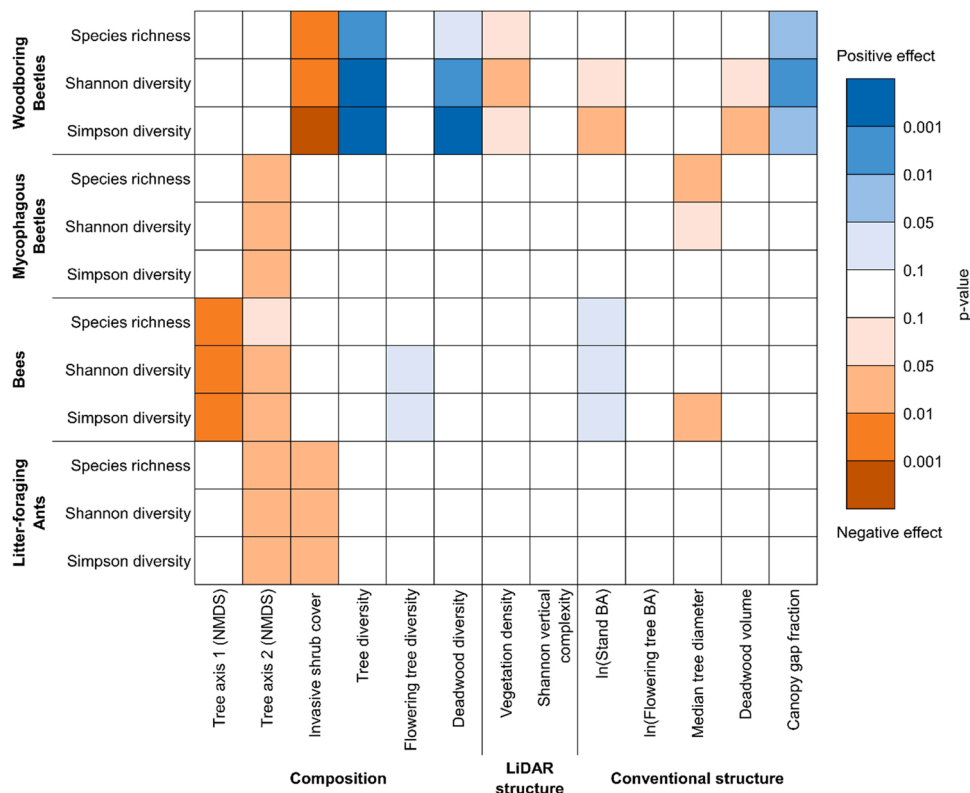


Fig. 3. Significance and effect direction of explanatory variables in the generalized linear models for species richness, Shannon diversity, and Simpson diversity of each insect functional group. Explanatory variables are grouped as either compositional, structural from remotely-sensed LiDAR, or structural from conventional forestry measurements.

Shannon vertical complexity index, invasive shrub cover, tree NMDS axes 1 and 2, deadwood volume and diversity, gap fraction, median tree diameter, tree diversity, and natural log of stand basal area. For bees, we also included flowering tree diversity and natural log + 1 of flowering tree basal area. Gap fraction was not included in ant models because we took canopy photos at 5 m, which is above the shrub layer. Invasive shrubs reduce light availability on the forest floor (Cash et al., 2020), which would make our estimates of gap fraction inaccurate for the leaf-litter. Natural logs were used to reduce skewedness of our predictor variables. We checked for multicollinearity between predictor variables with variance inflation factors (VIF), using the `vif` function in the *faraway* package (Faraway, 2016). We tested for the assumption of spatial independence for the response variables and full model residuals using the Moran.I function in the package *ape* (Paradis and Schliep, 2019). For models using the Normal distribution, we checked normality of the residuals with a Shapiro-Wilks test and inspected residual vs. fitted plots for heteroskedasticity. We also tested for influential observations using the `cooks.distance` function in the *stats* package (R. Core Team, 2021).

3. Results

In total, we collected 80 species (2304 individuals) of woodboring beetles, 57 species (1085 individuals) of mycophagous beetles, 111 species (4223 individuals) of bees, and 36 species (3755 individuals) of ants (Supplementary Table S2). We recorded a total of 32 tree genera, ranging between 2 and 13 species per site. Shannon's diversity of tree genera ranged between 0.189 and 2.197 (mean = 1.299). Invasive shrub cover ranged between 0 subplots containing shrubs ($n = 20$) and 35 subplots (mean = 5.9, standard deviation = 9.23). Out of the invasive shrubs, *Ligustrum* spp (privet) was the most common (found at 15 sites and 118 subplots), followed by *Elaeagnus* spp (olive, 12 sites and 97 subplots) and *Lonicera* spp (honeysuckle, 7 sites and 46 subplots). Shannon vertical complexity index ranged from 0.445 to 0.587 (mean = 0.523, standard deviation = 0.034). Vegetation density of the entire canopy ranged from 4831 to 7784 filled 10 cm³ voxels (mean = 6474.6, standard deviation = 735.8).

Invasive shrubs were linked to structural differences in forests sampled in our study. Invasive shrub cover was marginally correlated to the vegetation density of the entire canopy (Pearson's coefficient = 0.292, $p = 0.067$) and significantly correlated with the Shannon vertical complexity index (Pearson's coefficient = -0.539 , $p = 3.29 \times 10^{-4}$). With increasing shrub cover, forests were generally denser and vertical vegetation heterogeneity was lower. Shannon vertical complexity index was not significantly correlated with vegetation density (Pearson's coefficient = 0.182, $p = 0.261$).

The generalized linear models explained the majority of deviance for woodboring beetles (65.3–69.5%), almost half for bees (47.0–49.7%), but explained less for mycophagous beetles (33.6–38.7%) and litter-foraging ants (29.1–33.8%), indicating our models lacked important explanatory variables for these latter groups. No spatial autocorrelation was detected, nor were there outlier observations detected (all Cook's distances < 1). Overall, we found idiosyncratic responses among functional groups to various aspects of forest composition and structure (Fig. 3; Supplementary Tables S3, S4, S5, S6). In general, compositional effects were more important than structural effects for all insect groups investigated, and there were only minor differences when weighting towards rare species (species richness), common species (Shannon diversity), or dominant species (Simpson diversity). First, we found a strong negative effect of Tree Axis 2 on the richness and diversities of ants, bees, and mycophagous beetles (except bee species richness, which was a weak negative trend). In our NMDS, this axis correlated highly with the tree *Liquidambar styraciflua* (Pearson's coefficient = -0.822) (Supplementary Table S1). Tree axis 1 had a strong negative influence on bee richness and diversities and was highly correlated with *Pinus* spp. (Pearson's coefficient = 0.828) and *Quercus* spp. (Pearson's coefficient = -0.749) (Supplementary Table S1). While the tree composition had no direct effect on woodboring beetles, the richness and diversities of woodboring beetles significantly increased with more diverse forest stands. Similarly, there was a weak positive trend of the diversity of flowering trees on bee diversities (but this was reduced without the NMDS axes in the model). For invasive shrubs, woodboring beetle and ant richness and diversities decreased with increasing shrub cover. Structural components related to shrub cover were largely uninfluential, except for woodboring beetles. In this case, Shannon diversity decreased significantly with increasing vegetation density (richness and Simpson diversity also had a weak negative trend). Bees and mycophagous beetles had no response to invasive shrub cover, vegetation density, or Shannon vertical complexity.

Other forest composition and structure variables were also important for functional groups (Fig. 3, Supplementary Tables S3, S4, S5, S6). Increasing amounts of deadwood reduced woodborer Simpson diversity and slightly so for woodborer Shannon diversity. Conversely, increasing diversity of deadwood significantly elevated diversities of woodborers, and slightly so for richness. Lower richness of mycophagous beetles and Simpson diversity of bees were found with larger median tree diameters. Higher stand basal area reduced Simpson diversity of woodboring beetles (and slightly so for Shannon diversity), but there was also a significant positive effect of canopy gap fraction for this group. Bee richness and diversities slightly increased with higher basal area.

4. Discussion

With the increasing availability of remote sensing technology to characterize and quantify structural elements in forest canopies, our understanding of the relationship between canopy structure and biodiversity has grown. For example, many insect groups benefit from an increased complexity in canopy structure (Knuff et al., 2020; Müller et al., 2018; Heidrich et al., 2020; Zellweger et al., 2016), a metric that was challenging to quantify before the use of LiDAR (Davies and Asner, 2014). Furthermore, without this technology, it would be nearly impossible to investigate some basic ecological questions, such as the independent roles of canopy composition and structure on biodiversity (e.g., Müller et al., 2010). This technology may be especially useful in understanding and responding to the effects of plant invasions, which continue to alter the structure and composition of forests worldwide. The main purpose of this study was to use mobile LiDAR to investigate the structural and compositional elements of invaded forest canopies on insect communities.

Because invasive shrubs often create thick mid-story layers of vegetation, we were specifically interested in testing whether these species affect insect communities by creating dense canopy environments or through properties inherent to the plants themselves. We expected flying insect groups (woodboring beetles, mycophagous beetles, and bees) would decline in dense canopies while ground-dwelling insects (litter-foraging ants) would be uninfluenced by the structure (Grevé et al., 2018; Heidrich et al., 2020; Janssen et al., 2009). Furthermore, we expected the impacts on rare species would be greater than on dominant ones (Wagner and van Driesche, 2010). As discussed below, we found that the composition of invaded forests strongly influenced insect richness in this study, and structural elements related to invasive shrubs had little if any effect. Overall patterns varied greatly among insect functional groups but varied little within a functional group when rare and dominant species were weighted differently.

Congruent with previous studies (Leidinger et al., 2021; Grevé et al., 2018), we found that the physically dominant plants in forests, trees, exert a strong compositional influence on insect diversity. Most notably, mycophagous beetles, bees, and litter-foraging ants were all negatively associated with Axis 2 of our tree composition NMDS, an axis negatively correlated with the tree species *L. styraciflua*. This species grows widely but is particularly abundant in previously disturbed riparian or poorly-drained areas (Kormanik, 1990). Due to riparian forests being more humid than uplands (Ulyshen and Hanula, 2009), fungi may be more prevalent there and support a higher diversity of mycophagous beetles (Brunet and Isacson, 2010). Similarly, the association of litter-foraging ants with a high basal area of *L. styraciflua* might be indicative of higher richness in previously disturbed forests (Palladini et al., 2007). Disturbances typically open the canopy, creating warmer conditions beneficial to ant communities (Grevé et al., 2018). Along with Axis 2, bees were also negatively associated with tree NMDS Axis 1, which was positively correlated with *Pinus* and negatively correlated with *Quercus* basal area. Additionally, bees showed a slight positive relationship with flowering tree diversity. This adds to our understanding of differences in bee diversity among forest types within the region. Although open pine-dominated forests often yield more bee individuals and species on average than closed hardwood-dominated forests (Hanula et al., 2015), our results suggest that hardwood forests with high flowering tree diversity and previous disturbances may be of high value to these insects, though the importance of flowering tree diversity deserves further investigation. Finally, woodboring beetles did not respond to composition directly, but instead responded positively to tree diversity, as demonstrated in other studies (Meng et al., 2013; Noguera et al., 2018). This trend is likely explained by the high host specificity exemplified by many xylophagous species (Wende et al., 2017; Ramos-Robles et al., 2020), a conclusion supported by the positive association between woodborers and deadwood diversity in this study (Fig. 3).

Aside from trees, woodboring beetles and litter-foraging ants also responded negatively to invasive shrub cover. Despite our intention to investigate the compositional effects of the invasive shrubs, it is unclear if these patterns were driven directly by inherent plant properties of the shrubs or reflect differences in disturbance histories among our plots. For example, invasive shrubs found in this study thrive in urban environments (Kuhman et al., 2010), regenerating forests (Ward, 2002; Wang and Grant, 2012), and recently disturbed forests (Hagan et al., 2014). For woodboring beetles, younger forests often provide less quality habitat (i.e., deadwood amount) than older forests and host correspondingly fewer species as well (Stenbacka et al., 2010; Grove, 2002). Additionally, although forest disturbances may provide a temporary pulse of woody resources, the diversity of woodborers decline over time as the wood decomposes (Thibault and Moreau, 2016). Similarly, ant communities in urban settings are often homogenized (Thompson and McLachlan, 2007; Sanford et al., 2008) and dominated by invasive ants (Holway and Suarez, 2006). In our study, we commonly collected an invasive ant, *Brachyponera chinensis*. While native ants decline in the presence of *B. chinensis*, this species is not restricted to urban or disturbed forests (Guénard and Dunn, 2010) and its relation to invasive plants is not known, making its effect in our study not well understood. Such relationships may therefore be responsible for the negative relation of these two functional groups and invasive shrubs. However, it is also possible that invasive shrubs have direct negative effects on these taxa through compositional effects. For example, thickets formed by invasive shrubs are known to prevent sunlight from reaching the forest floor (Cash et al., 2020) and have been shown to alter wood decomposition rates (Ulyshen et al., 2020b). These effects can be expected to reduce the heterogeneity of deadwood (Pouska et al., 2016), an important factor in driving woodboring beetle diversity (Seibold and Thorn, 2018; Seibold et al., 2016; Vodka et al., 2009). Therefore, the response of woodboring beetles to invasive shrubs may be due to a local reduction in larval habitat heterogeneity. Similarly, invasive thickets exclude herbaceous vegetation (Hanula et al., 2009; Maynard-Bean and Kaye, 2019) and alter the composition and nutrient cycling dynamics of leaf-litter (Weand, 2020; Mitchell, 2011). Depending on the species, invasive leaf-litter can be easily decomposed and has been shown to promote invertebrate detritivores (Bush et al., 2018; Woodworth et al., 2020; Utz et al., 2018; Lalk et al., 2021) and their predators (Mahon et al., 2019). However, these effects may be temporary, and invaded sites host less stable leaf-litter arthropod communities than native sites, especially late in the season (Woodworth et al., 2020). This may explain why studies sampling early in the growing season have found that ant richness is higher under invasive shrubs (Mahon et al., 2019), but studies sampling later in the season find a decline in richness (Clark and Seewagen, 2019). Overall, the relationship between leaf-litter invertebrates and invasive shrubs is likely complex and dynamic through a single season (Hartshorn, 2021; Woodworth et al., 2021) and over many years (Nguyen et al., 2016). Because we sampled late in the season (June–August), it is plausible that trophic cascades under the canopies of invasive shrubs are responsible for the reduction of ant richness and diversity found in our study.

In line with our prediction, we found negative effects of vegetation density on woodboring beetles. This finding aligns with those from Müller et al. (2014), where xylophagous beetles declined in spruce canopies of dense stands. It is possible that these effects are linked to dense vegetation impeding flight or disrupting resource and mate detection via olfactory cues (Verdeny-Vilalta et al., 2014; Randlkofer et al., 2010; Beyaert and Hilker, 2014). This seems likely, given that woodboring beetles (family Cerambycidae in our study) are well known for their use of semiochemicals, especially pheromones, to locate mates and oviposition sites (Millar and Hanks, 2017). However, contrary to our prediction, the other flying functional groups (mycophagous beetles and bees) had no response to increased vegetation density. This finding opposes results from Müller et al. (2014), which found the richness of all sampled flying insects declined in dense stands, regardless of body size, feeding guild, or host specificity. Furthermore, nocturnal flies and moths have

been found to increase in abundance with more vegetation density (Müller et al., 2012). It is likely that differences among studies may be attributed to differences in life-history between the targeted insect groups, but also a result of experimental design. For example, Müller et al. (2014) controlled for differences in tree community composition by only sampling in spruce canopies. In contrast, we were interested in an effect of tree community composition and our sampling sites reflected this interest. Importantly, the cover of invasive shrubs in our study was related to both LiDAR-derived structural variables, and generally more invaded forests had higher vegetation density and a less heterogeneous distribution of vegetation vertically. Yet, neither of these structural elements had strong effects on any of the functional groups compared to either the composition of the shrubs or the tree communities (Fig. 3). Although some structural characteristics are known to be highly important for insect diversity (e.g., Knuff et al., 2020; Müller et al., 2018), the relative importance of composition over structure for some insect groups has been recognized in other studies (e.g., Schaffers et al., 2008). From our results, it appears that forest composition (including trees and invasive shrubs) is driving the richness patterns for the insect groups investigated. The structure imposed by the shrubs may be less important overall for the investigated groups, or may have greater influence in certain canopy types than others (i.e., another form of “context dependency” as proposed by Müller et al., 2014). Future experimental investigations may give insight to the nuances between structure and composition, for example, log colonization experiments for saproxylic beetles in dense and open canopies with variable tree composition or between native and non-native shrub canopies.

Unexpectedly, bees and mycophagous beetles did not respond to either invasive shrub cover or vegetation density in this study. The lack of effects from these related features may be due to strong effects of the tree composition or the context dependency hypothesis as stated above. Many of the studies documenting insect declines in invaded forests were conducted in a riparian forest type (Hanula and Horn, 2011a, 2011b; Ulyshen et al., 2010a; Ulyshen et al., 2020a), which loosely corresponds to Axis 2 from our NMDS. In our study, this forest composition had a positive impact on bee and mycophagous beetle richness (Fig. 3). Additionally, the lack of effects may be due to vertical stratification. Previous work shows that bee and beetle communities are vertically stratified in forests, resulting in decreased richness below invasive shrub cover but not above it (Ulyshen et al., 2020a, 2010a). Our trap was placed 5 m aboveground, a height that was uninfluenced by shrub presence in these previous studies. Therefore, the influence of the shrubs both compositionally and structurally is likely small or absent on some insect groups at this height.

5. Conclusions

This study joins the growing body of literature using LiDAR to disentangle the influences of canopy composition and structure on insect biodiversity. We found only a small negative relationship between woodboring beetle diversity and vegetation density, whereas the other three functional groups examined in this study were unaffected by structure. As suggested by other studies, not all insect groups are expected to respond similarly to the same structural metrics (e.g., Schuldt et al., 2019; Knuff et al., 2020; Davies and Asner, 2014) or responses may be dependent on spatial scale (Müller et al., 2014). Regardless, our findings suggest that in our system, the structure imposed by invasive shrubs is less influential on insect biodiversity than compositional effects of the trees and shrubs. Consistent with recent reviews (Lalk et al., 2021; Litt et al., 2014; Schirmel et al., 2016), the effects of invasive shrub cover were similarly variable among functional groups, being important for woodboring beetles and litter-foraging ants only. Importantly, our results support the notion that invasive shrubs in forests have only negative or neutral effects on insects through both inherent plant properties and physical structure. This suggests that efforts to eradicate invasive shrubs will improve both the structure and composition of forests for maintaining diverse insect communities.

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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.

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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.gecco.2022.e02092](https://doi.org/10.1016/j.gecco.2022.e02092).

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