Evergreen Abundance Drives Ground Beetle Diversity And Density In Eastern Temperate Forests

Janey R. Lienau (janey.lienau@yale.edu)
Center for Tree Science, The Morton Arboretum https://orcid.org/0000-0002-4681-235X
Robert W. Buchkowski
Western University https://orcid.org/0000-0001-6381-8609
Meghan G. Midgley
Center for Tree Science, The Morton Arboretum https://orcid.org/0000-0002-1195-1608

Research Article

Keywords: Aboveground-belowground interactions, community ecology, forest ecosystems, functional groups, invertebrates, National Ecological Observatory Network, ground beetles, diversity,

Posted Date: December 16th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-1132825/v1

Version of Record: A version of this preprint was published at Pedobiologia on January 11th, 2024. See the published version at https://doi.org/10.1016/j.pedobi.2024.150930.

Abstract

Purpose: Soil insects mediate plant-soil interactions by fragmenting and decomposing litter that forms the base of soil food webs and through predator-prey interactions. Plant communities, in turn, shape soil insect communities via the quality, availability, and diversity of their litters. However, these drivers have rarely been examined in concert even though describing soil insect community patterns is critical for mitigating the effects of global environmental changes.

Methods: Here, we evaluated the effects of tree diversity, density, and functional groups on ground beetle (*Carabidae*) diversity, density, and community composition in four eastern temperate forest sites in the National Ecological Observatory Network. *Results* Though we expected that higher tree diversity and density would, respectively, lead to higher diversity and density ground beetle communities, we found little evidence to support this hypothesis. Instead, evergreen tree abundance strongly shaped ground beetle diversity, density, and community composition. Specifically, evergreen plots as defined by National Land Cover Database hosted lower density ground beetle communities than deciduous plots. Similarly, ground beetle Shannon diversity and density decreased as the relative abundance of evergreen tree species increased.

Conclusions: Although further study is needed to explicitly link litter quality with soil insect communities, the resource environments created by trees with varying leaf habits appear to be a dominant force driving ground beetle community diversity and density patterns.

Introduction

Soil insects play a central role in aboveground-belowground interactions (Bardgett and van der Putten 2014). By modifying tree litters and consuming soil biota, soil insects mediate decomposition, nutrient cycling, and carbon storage (Hättenschwiler et al. 2005, 2017; McCary and Schmitz 2021; Wardle c2002). However, environmental changes, such as pollution and climate change, are resulting in rapid insect diversity and abundance loss globally (Seibold et al. 2019), destabilizing food webs (Hooper et al. 2005; Lister and Garcia 2018). As such, identifying the drivers of soil insect diversity and abundance patterns is essential to mitigate the risks of environmental changes.

Tree communities shape soil insect diversity and abundance via the diversity and abundance of their litters (Sylvain and Wall 2011). A common hypothesis in ecology is “diversity begets diversity," (MacArthur and Levins 1964; Tilman 1986; Siemann 1998; Maynard et al. 2017) that soil insect diversity is greatest in high diversity plant communities. This hypothesized relationship has been observed across systems. For instance, in experimental grasslands, both nematode and insect diversity track plant diversity (Eisenhauer et al. 2011; Schuldt et al. 2019). Similarly, in subtropical forests where litter quality was consistent across stands, plant diversity predicted fungal community diversity (Chen 2019). Just as “diversity begets diversity” insect density may also be greatest in high density plant communities (Schuldt et al. 2019). Litter abundance has a significant effect on insect abundance and ecosystem function (Hooper et al.

2005), and springtail and ant abundance increases with leaf litter and root biomass across forested ecosystems (Manhães et al. 2013; Potapov et al. 2017). As plants and the litter they produce form the base of the soil food web, increased plant and litter diversity and biomass might lead to increased soil insect diversity and abundance in forests.

Studying the relationships between functional groups is a practical approach for understanding how diversity might beget diversity, because functional relationships include information about the mechanisms behind species interactions. For example, litter quality influences soil insect diversity and abundance via changes in resource availability. Plant functional groups with higher litter quality (e.g., lower lignin:N and C:N litters) create environments that support high diversity nematode communities (Cesarz et al. 2013). Trees are often divided into functional groups based on leaf habit and mycorrhizal association. Evergreen trees generally produce lower quality leaf litters than deciduous trees (Augusto et al. 2015). Similarly, in temperate and boreal forests, trees associated with arbuscular mycorrhizal fungi (AM trees) typically have higher quality leaf litters than those associated with ectomycorrhizal fungi (ECM trees) (Keller and Phillips 2019). Thus, forests dominated by deciduous and AM trees may support higher insect diversity and density than forests dominated by evergreen and ECM trees. However, the relationships among litter quality, soil insect communities, and the forests above them have been largely overlooked (Hättenschwiler et al. 2005; Bardgett and van der Putten 2014).

Beetles (*Coleoptera*) are the largest taxa of described organisms on earth. The ground beetle family (*Carabidae*) are the most numerous among them, with an estimated 40,000 species *(Insect Biodiversity* 2017). Ground beetles are considered key community indicators because of their large family size, multiple trophic levels, and high family-level diversity (Koivula 2011; Hoekman et al. 2017). Therefore, we used ground beetles to explore our leading question: Do litter quality, quantity, and diversity drive insect community composition, diversity, and density patterns in forest systems? We hypothesized that increased tree species diversity and litter quality would lead to increased ground beetle diversity. Additionally, we hypothesized that ground beetle density would be greatest in stands dominated by trees with high-quality litters and in stands with high tree density.

Materials And Methods

Site Selection and Characteristics

We used long-term ground beetle and vegetation records curated by the National Ecological Observatory Network (NEON) to evaluate relationships between tree vegetation metrics and ground beetle diversity, density, and community composition (National Ecological Observatory Network (NEON) 2021a, b). NEON collects and publishes continual open-source ecological data to facilitate understanding of aquatic and terrestrial ecosystem change across North America (Thorpe et al. 2016). Of NEON's 47 terrestrial sites, 20 are core (permanent) sites and 27 are relocatable (temporary) sites. Each terrestrial NEON site contains 40 m × 40 m distributed sampling plots which are chosen to represent the composition of National Land Cover Database (NLCD) vegetation types found at the site. While up to 20 distributed plots are used for vegetation sampling in a given site, only 10 are used for ground beetle sampling in a given year. Eighteen of the 47 terrestrial sites are largely dominated by upland forest (>75% of the beetle-sampled plots are classified as deciduous, mixed, or evergreen forests). Of these 18, six sites contain only evergreen forest plots and five contain only deciduous forest plots. As our goal was to assess the effects of forest stands with varying leaf habits on ground beetle metrics, we used four sites that had sufficient forest cover and variability in classification for our analyses. These sites contain a relatively even distribution of deciduous, mixed, and evergreen forest plots: Bartlett Experimental Forest (BART), Harvard Forest (HARV), Jones Ecological Research Center (JERC), and Talladega National Forest (TALL) (Table 1).

Table 1. Site-level characteristics of the four NEON sites examined in this study from NEON's field site documentation (https://www.neonscience.org/field-sites/explore-field-sites).

	BART	HARV	JERC	TALL
State	New Hampshire	Massachusetts	Georgia	Alabama
Site Type	Relocatable	Core	Relocatable	Core
Latitude	44.063889	42.53691	31.194839	32.95047
Longitude	-71.287375	-72.17265	-84.468623	-87.393259
Mean Elevation (m) and range	274 (230-655)	348 (160-415)	47 (29-55)	166 (63-179)
Mean Annual Temperature (°C)	6.2	7.4	19.2	17.2
Mean Annual Precipitation (mm)	1325	1199	1308	1383
Average Green Days	180	210	220	255
Mean Canopy Height (m)	23	26	27	25
Soil Classification	Aquic Haplorthods	Oxyaquic Dystrudepts	Arenic Kandiudults	Typic Hapludults
Upland Forest Plots (%)	100	100	91.67	100
Deciduous Plots (%)	30.8	41.67	27.27	30
Mixed Plots (%)	46.15	33.33	27.27	30
Evergreen Plots (%)	23.08	25	45.45	40
Dominant Plant Species	*Fagus grandifolia,Tsuga canadensis, Acer rubrum*	*Osmunda cinnamomea, Quercus rubra,Tsuga canadensis*	*Aristida beyrichiana, Quercus falcata,* *Pinus palustris*	*Quercus montana, Liriodendron tulipifera, Cornus florida*

Tree Data and Indices

Every five years, NEON technicians collect tree vegetation data from the distributed plots at a site (Meier et al.). Sampling bouts are triggered by senescence; sampling begins after at least 50% of the deciduous canopy at a site has begun to senesce and is completed before growth begins the following season. Throughout each plot, all trees with diameter at breast height (DBH; 130 cm height) greater than or equal to 10 cm are tagged and marked with geolocation and expertly identified.

Within each site, we focused on plots in which woody plant and ground beetle data were co-located. At the time of our analyses, woody plant vegetation data had not been collected from distributed plots at BART and JERC, so our more refined forest-beetle analyses are limited to HARV and TALL. For HARV and TALL, we used woody plant data from the most recent sampling campaign: 2019 for HARV and the initial survey data from 2014 and 2015 for TALL. Trees were defined as single- or multi-bole live trees greater than to equal to 10 cm DBH. Plots were excluded if they contained less than three trees at least 10 cm in diameter.

We used forest composition metrics as indices of litter quality, quantity, and diversity. The relative abundance of evergreen and ECM trees in a plot were used as indices of litter quality. Percent evergreen tree cover was calculated based on the total basal area of evergreen trees divided by the total basal area of all trees in a plot. The same method was used to calculate percent ECM tree cover in a plot. Mycorrhizal associations were assigned based on Averill et al. (2019). Tree density was used as an index of litter quantity. We used two metrics of tree density: the number of trees in a plot and the total basal area of trees in a plot. Finally, we used tree diversity as an index of litter diversity. Both Shannon and Simpson diversity indexes were calculated based on both tree basal area or the number of stems in a plot using the vegan package in R (Oksanen et al. 2020).

Ground Beetle Data and Metrics

Within a site, NEON field technicians survey ground beetle communities biweekly from 10 distributed sampling plots using pitfall traps (Hoekman et al. 2017; LeVan). Pitfall traps are a common ground beetle collection technique where a small cup (11 cm diameter, 7 cm deep) with a diluted amount of propylene glycol preservative is placed flush with the soil surface. A 20 × 20 cm plastic cover is placed overhead to keep out rain and falling debris. Each site had a total of 40 pitfall traps; from 2013 - 2017, each 40 × 40 plot had four traps in each cardinal direction 20 meters from the plot center. In 2018, the trap number was reduced to three per plot for a total of 30 traps per site. After green up and minimum ambient temperature averaged 4℃ for 10 days, a sampling bout begins at a site. Sampling ends when temperature falls below 4℃. NEON sites have an average of 11 biweekly sampling bouts per year. NEON technicians then sort and identify ground beetles to species and morphospecies, with a subset pinned or pointed and sent off for expert identification. Non-pinned or pointed specimens are stored in 95% ethanol and archived by site. 97% of carabid species identified by technicians are correct at the species level, and 99% are correct at the genus level. Further details can be found in NEON documentation (Ground Beetles | NSF NEON).

We analyzed the ground beetle data collected from pitfall traps from 2014 to 2019 after removing samples with disturbed cups or lids. We also excluded samples collected from plots that were sampled < 3 times or data from years with interrupted sample collection. Ground beetles were collected at each site during a sampling bout. Individual samples that were expertly identified to the subspecies level were grouped to their species-level identification. For each plot, we aggregated ground beetle data for each collection year and assessed density and diversity. Density was calculated as the number of individuals collected divided by the number of cups that were sampled in a given plot in a given year. We also calculated yearly plot-level density for the five most abundant species at HARV and TALL following a similar protocol. We used the vegan package in R to calculate ground beetle diversity using the Shannon and Simpson indices.

Statistical Analyses

We used linear mixed effects models to evaluate the effects of forest stand properties on ground beetle diversity and density. For analyses conducted using data from all four sites (BART, HARV, JERC, and TALL), we used NLCD class as a fixed effect and nested plot ID within site ID as a random effect. For more detailed analyses using woody plant vegetation data from HARV and TALL, we created six models. All models contained evergreen tree abundance and ECM tree abundance as fixed effects and nested plot ID within site ID as a random effect. To evaluate the effects of litter quality and diversity on ground beetle diversity, we ran four models: tree Shannon diversity based on stems or basal area to predict beetle Shannon diversity and tree Simpson diversity based on stems or basal area to predict beetle Simpson diversity. Similarly, we ran two models to evaluate the effects of litter quality and density on ground beetle density; separate models were run for tree density based on number of stems and tree density based on basal area. We conducted Shapiro-Wilk Normality tests on residuals to select models with equal variances and log-transformed data when appropriate although this did not change model interpretation.

For community composition analyses at HARV and TALL, we created NMDS ordination plots to visualize differences in ground beetle communities across plots at each site. For statistical analysis, we conducted a PERMANOVA using the Bray-Curtis method in the vegan package in R to evaluate the effects of evergreen tree abundance on ground beetle community composition. To assess the extent to which abundant species drove variability in total abundance and community composition, we used linear mixed effects models with plot ID as a random effect to evaluate the effects of forest stand properties on ground beetle abundance for the top five most abundant species. We conducted these analyses on HARV and TALL data and performed Shapiro-Wilk Normality tests on residuals to assess distributions.

Results

A total of 7,331 ground beetle individuals were collected and identified from the four forested sites in our study. Across the four sites, BART had the highest Shannon diversity, Simpson diversity, and density of ground beetles while JERC had the lowest (Table 2).

Table 2. Ground beetle community characteristics at BART, HARV, JERC, and TALL.

	Shannon diversity (ave across plots per year ± SE)	Simpson diversity (ave across plots per year ± SE)	Density (ave individuals/cup across plots per year ± SE)	Dominant species (relative abundance)
BART (*n*=57)	1.95 ± 0.04	0.81 ± 0.01	2.24 ± 0.15	*Synuchus impunctatus (19%), Pterostichus tristis (16%), Pterostichus pensylvanicus (12%), Pterostichus rostratus (8%), Pterostichus coracinus (8%)*
HARV (*n*=60)	1.73 ± 0.04	0.76 ± 0.01	1.33 ± 0.10	*Carabus goryi (21%), Synuchus impunctatus (21%), Sphaeroderus stenostomus (13%),* *Pterostichus tristis (9%), Sphaeroderus canadensis (7%)*
JERC (*n*=48)	0.88 ± 0.09	0.46 ± 0.05	0.46 ± 0.04	*Pasimachus subsulcatus (20%), Anisodactylus merula (13%), Cyclotrachelus sigillatus (10%), Cyclotrachelus laevipennis (8%), Cyclotrachelus ovulum (7%)*
TALL (*n*=40)	1.40 ± 0.09	0.65 ± 0.03	0.63 ± 0.06	*Cyclotrachelus convivus (26%), Anisodactylus merula (10%), Selenophorus opalinus (8%), Anisodactylus haplomus (7%), Dicaelus dilatatus (6%)*

Tree characteristics also varied between sites (Table 3). For both diversity indices, TALL had greater tree species diversity than HARV. HARV had lower tree density based on the number of stems present and basal area. The relative abundance of evergreen trees had a larger range at both sites than the relative abundance of ECM-associated trees metric. At HARV, plots were dominated by *Pinus strobus* L., *Quercus rubra* L., and *Acer rubrum* L. tree species while at TALL, plots were dominated by evergreen trees of the *Pinus* genus, including *Pinus taeda* L. and *Pinus palustris* Mill..

Table 3. Forest stand characteristics at HARV and TALL. Diversity and density metrics are plot level averages and standard errors. Evergreen and ECM tree abundances are in percentages based on basal area. Density and diversity metrics are based on both basal area (BA) and number of stems.

	HARV (*n*=12)	**TALL** (*n*=8)
Div (Shannon, BA)	0.94 ± 0.087	1.21 ± 0.21
Div (Shannon, stem)	1.17 ± 0.074	1.31 ± 0.24
Div (Simpson, BA)	0.51 ± 0.046	0.60 ± 0.09
Div (Simpson, stem)	0.62 ± 0.036	0.62 ± 0.10
Density (BA)	12820.2 ± 1983.4 cm^2	16642.2 ± 4265.1 cm^2
Density (stem)	16.9 ± 2.1	28.8 ± 8.7
%evergreen (range)	0 - 91	0 - 100
%ECM (range)	31-100	44 - 100
Dominant species and relative abundance (BA)	*Pinus strobus (43%), Quercus rubra (29%)*	*Pinus taeda (24%), Pinus palustris (23%)*
Dominant species and relative abundance (stem)	*Pinus strobus (31%), Acer rubrum (25%)*	*Pinus taeda (27%), Pinus palustris (18%)*

While there were clear differences in ground beetle diversity and abundance across sites, ground beetle diversity did not vary much with forest cover type when stands were classified broadly as deciduous, mixed, or evergreen (Fig. 1). Ground beetle diversity tended to be lower in the evergreen plots than in the deciduous plots, but these differences were not statistically significant ($P \geq 0.66$; Fig. 1a-b). In contrast, ground beetle density varied across forest cover classes ($P = 0.02$); ground beetle density was lower in evergreen forests than in deciduous forests ($P = 0.04$; Fig. 1c).

Differences in ground beetle community were more apparent when analyzed using detailed data on stand composition (i.e., at HARV and TALL). Ground beetle Shannon diversity tended to decrease as evergreen abundance increased (Fig. 2; $P < 0.09$). This relationship was less clear when Simpson diversity was used as an index of ground beetle diversity ($P > 0.11$). In contrast, the relative abundance of ECM-associated trees was a poor predictor of ground beetle diversity ($P \geq 0.28$), and tree diversity indices had little to no effect on ground beetle diversity ($P \geq 0.68$).

Ground beetle density also decreased as evergreen abundance increased ($P < 0.01$; Fig. 3). However, neither the relative abundance of ECM-associated trees ($P > 0.11$) nor tree stand density ($P > 0.87$) had significant effects on ground beetle density.

Ground beetle community composition varied with evergreen abundance at TALL ($P = 0.043$) but not HARV ($P = 0.12$; Supplemental Fig. 1). However, we found no effect of evergreen abundance on densities of the top five most abundant species at TALL ($P \geq 0.46$; Fig. 4f-j). In contrast, one of the most abundant ground beetle species at HARV, *Synuchus impunctatus*, decreased in density as the relative abundance of evergreen trees increased ($P = 0.04$; Fig. 4b). The most abundant species at HARV, *Carabus goryi*, did not tend to have lower density in evergreen stands ($P \geq 0.12$; Fig 4a) and the relative abundance of evergreen trees also had no effect on other abundant beetle species examined ($P \geq 0.33$; Fig. 4c-e). We found no effects of tree basal area or ECM-associated tree abundance on the densities of abundant ground beetle species at TALL ($P \geq 0.59$) or HARV ($P \geq 0.19$).

Discussion

Resource diversity, abundance, and quality shape soil communities and food webs. In this study, we evaluated the effects of tree diversity, density, and traits on ground beetle diversity, density, and community composition. Rather than increased resource diversity and abundance leading to increased beetle diversity and abundance, we found that tree traits shaped ground beetle diversity and density. Specifically, as the relative abundance of evergreen trees increased, ground beetle diversity and density declined. As such, our study demonstrates that tree leaf habit has a greater influence on ground beetle communities than stand diversity or tree density.

Tree traits better predict ground beetle diversity and density than stand diversity and density

Data from HARV and TALL did not support our hypotheses that higher tree diversity and density would support higher ground beetle diversity and density. Instead, ground beetle diversity and density consistently responded to tree traits; as the relative abundance of evergreen species increased, ground beetle diversity and density decreased. Similarly, across all four NEON sites, ground beetle density was lower in evergreen than deciduous forests. Tree species identity is often more important than tree diversity in predicting soil food web diversity (Cesarz et al. 2013; Eissfeller et al. 2013; Mueller et al. 2016). For instance, while increased tree diversity enhanced soil macrofauna diversity at coarse taxonomic resolution, tree functional types alone shaped diversity at fine taxonomic scale (e.g., species of *Carabidae*) in experimental plantings (Ganault et al. 2021). Similarly, in subtropical forests where litter quality was consistent across stands, plant diversity did not predict bacterial diversity (Chen 2019). Thus, resource quality may generally be a better predictor of soil community properties than resource diversity and density.

Leaf habit is a better predictor of ground beetle diversity and density than mycorrhizal association

As the relative abundance of evergreen trees decreased, ground beetle diversity and density increased, supporting our hypothesis that low litter quality negatively affects ground beetle diversity and density. This is consistent with the findings of Mueller et al. (2016) who found that soil invertebrate diversity generally and ground beetle diversity specifically were lower in evergreen tree monocultures than in deciduous tree monocultures. Similarly, ground beetle species richness decreases as soil N content decreases (Vician et al. 2018), which is common in evergreen stands. Evergreen trees typically produce litter with high lignin content and create acidic soils (Augusto et al. 2015). High lignin litters and low soil pH are generally associated with low net N mineralization (Scott and Binkley 1997). These harsh environmental conditions may favor specialist organisms, resulting in low diversity and density soil communities (Büchi et al. 2014). While these conditions may also prevent competitive exclusion, other properties of evergreen stands outweigh these effects resulting in less diverse ground beetle communities in evergreen forests than those found in deciduous forests.

Deciduous stands might have a larger resource base resulting in a broader range of niches to support a more diverse ground beetle community. An alternative explanation is that deciduous canopies increase litter diversity which begets beetle diversity directly by fostering diverse food resources for ground beetles. Our data support the former hypothesis given that deciduous forests clearly correlated with higher ground beetle abundance and diversity while tree species diversity had no effect on ground beetle diversity. Overall, leaf habit was an important driver of ground beetle diversity and density likely due to high evergreen abundance creating lower resource quality environments.

In contrast, mycorrhizal association was not a significant predictor of ground beetle diversity or density. Deciduous and AM species have high litter quality and soil N availability, while evergreen and ECM forests are associated with low soil inorganic N, high lignin content, and acidic soils (Augusto et al. 2015; Keller and Phillips 2019). However, along a spectrum of litter quality, we expect AM deciduous trees to have the highest quality litters, ECM evergreen trees to have the lowest quality litters, and ECM deciduous litter to be of intermediate quality. Therefore, differences in litter quality between deciduous and evergreen trees may be greater than those found between mycorrhizal types (Cornelissen et al. 2001). Leaf habit appears to be a more important driver of ground beetle community density and diversity than mycorrhizal association.

Ground beetle diversity and density patterns are not driven by shifts in community composition

While we detected shifts in community composition at TALL and some species-level preferences for deciduous-rich sites at HARV, general relationship between ground beetle diversity and density do not appear to be driven by ground beetle species composition or preferences. Past studies have suggested that leaf palatability traits have a larger effect on detritivore and carnivore community composition than leaf litter diversity (Brousseau et al. 2019). We observed that *Synuchus impunctatus* (496 total individuals) at HARV tend to prefer deciduous forests, which may contribute to general ground beetle density trends. However, other species at both HARV and TALL show little preference for deciduous or evergreen stands. In fact, while two of the five most abundant species at TALL, *Cyclotrachelus convivus* and *Dicaelus dilatatus*, tended to decrease in density as the relative abundance of evergreen trees increased, *Anisodactylus merula*, *Selenophorus opalinus*, and *Anisodactylus haplomus* seemed to favor mixed forest stands. The most abundant species found at HARV and TALL have been documented in past studies in all forest types with thick leaf litter (Lariviere and Larochelle 2003), which may be found across stands varying in leaf habit. Furthermore, the most abundant species in our study are omnivores and carnivores, feeding on larva, smaller insects, and seeds; as such, species-level habitat preferences may be limited.

Caveats and Future Directions

Our study suggests strong relationships between tree leaf habit and soil community density and diversity. However, our ability to extrapolate our results and identify the drivers underlying these patterns are limited by site characteristics and data availability. While we attempted to survey a total of four Eastern temperate forest sites that met our criteria, two datasets were incomplete. As such, our more detailed analyses were limited to HARV and TALL. Additionally, evergreen trees are largely *Pinus* at both HARV and TALL which may not be broadly representative of all evergreen tree species. However, general trends across all four sites based on stand-level NLCD classifications suggest that ground beetle diversity and density are generally lower in evergreen sites than deciduous sites. Future studies should leverage newly collected NEON vegetation data with additional litter and soil property measurements to assess the generality of our findings.

In addition to sample size limitations, the observational nature of this study limits our ability to disentangle potential stand-level drivers. We used stand-level tree metrics as indices of litter diversity, density, and quality, but litter properties are not the only factors that vary between evergreen and deciduous stands. For instance, light availability - commonly lower in evergreen forests than deciduous forests - has been shown to strongly shape ground beetle diversity across forest stands (Mueller et al. 2016). Increased light availability under deciduous trees may lead to increased soil temperature and understory plant diversity, thereby increasing resource availability and diversity. As such, studies that directly manipulate tree communities and assess the environmental conditions created by these communities will facilitate linking tree communities to soil insect communities in a mechanistic way (Mueller et al. 2016; Ganault et al. 2021).

Conclusion

Insects are essential to human life. Understanding soil insect density and diversity patterns across forests is key to mitigating the effects of global insect biodiversity loss. Across North America, ground beetle communities vary on a latitudinal gradient (Hoekman et al. 2017). Our study shows that ground beetle diversity, density, and community composition also vary within sites. In particular, tree leaf habit and associated resource quality strongly drives variation in ground beetle diversity and density. More than tree diversity and density, leaf habit has a significant effect on soil insect communities which may mediate observed variation in ecosystem functions across forests.

Abbreviations

NEON (National Ecological Observatory Network), N (Nitrogen), C (Carbon), BART (Bartlett Experimental Forest), HARV (Harvard Forest), TALL (Talladega National Forest), JERC (Jones Ecological Research Center), AM (Arbuscular Mycorrhizal), ECM (Ectomycorrhizal), NLCD (National Land Classification Database)

Statements And Declarations

Funding

Funding for this project was provided by the National Science Foundation (REU Award No. 1851961) and the Center for Tree Science at The Morton Arboretum. The National Ecological Observatory Network is a program sponsored by the National Science Foundation and operated under cooperative agreement by Battelle. This material is based in part upon work supported by the National Science Foundation through the NEON Program.

Conflicts of interest

The authors have no relevant financial or non-financial interests to disclose.

Availability of data

Data used in this research were obtained through the NEON Assignable Assets program.

Data Product ID	Data Product Name	DOI	Site IDs	Date Range
DP1.10220.001	Ground beetles sampled from pitfall traps	https://doi.org/10.48443/tx5f-dy17	BART, HARV, JERC, TALL	2013 - 2018
DP1.10098.001	Woody plant vegetation structure	https://doi.org/10.48443/e3qn-xw47	HARV, TALL	2014 - 2019

Code availability

All data and accompanying analysis code are available on GitHub at: https://github.com/janeyl/Evergreen-abundance-drives-ground-beetle-diversity-and-density-in-eastern-temperate-forests

Authors' contributions

All authors contributed to the study conception and design. Data processing and analyses were performed by Janey Lienau with guidance from Robert Buchkowski and Meghan Midgley. The first draft of the manuscript was written by Janey Lienau, and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGEMENTS

We thank Dr. Silvia Alvarez Clare, Andrew Ernat, and Kaylee Rosenberger for feedback on initial project development. We also thank the National Ecological Observatory Network for data provision. This material is based in part upon work supported by the National Science Foundation through the NEON Program. Janey Lienau was supported by the National Science Foundation's Research Experiences for

Undergraduates program, Integrated Tree Science in the Anthropocene (award #1851961), and the Morton Arboretum Center for Tree Science's Research Experiences Extension Fellowship.

References

1. Augusto L, De Schrijver A, Vesterdal L, et al (2015) Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests: Spermatophytes and forest functioning. Biol Rev 90:444–466. https://doi.org/10.1111/brv.12119
2. Averill C, Bhatnagar JM, Dietze MC, et al (2019) Global imprint of mycorrhizal fungi on whole-plant nutrient economics. PNAS 116:23163–23168. https://doi.org/10.1073/pnas.1906655116
3. Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515:505–511. https://doi.org/10.1038/nature13855
4. Brousseau P-M, Gravel D, Handa IT (2019) Traits of litter-dwelling forest arthropod predators and detritivores covary spatially with traits of their resources. Ecology 100:e02815. https://doi.org/10.1002/ecy.2815
5. Büchi L, Vuilleumier S, Leibold AEMA, Bronstein EJL (2014) Coexistence of Specialist and Generalist Species Is Shaped by Dispersal and Environmental Factors. The American Naturalist 183:612–624. https://doi.org/10.1086/675756
6. Cesarz S, Ruess L, Jacob M, et al (2013) Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. Soil Biology and Biochemistry 62:36–45. https://doi.org/10.1016/j.soilbio.2013.02.020
7. Chen L (2019) Tree species identity surpasses richness in affecting soil microbial richness and community composition in subtropical forests. Soil Biology and Biochemistry 9
8. Cornelissen J, Aerts R, Cerabolini B, et al (2001) Carbon cycling traits of plant species are linked with mycorrhizal strategy. Oecologia 129:611–619. https://doi.org/10.1007/s004420100752
9. Eisenhauer N, Migunova VD, Ackermann M, et al (2011) Changes in Plant Species Richness Induce Functional Shifts in Soil Nematode Communities in Experimental Grassland. PLoS ONE 6:9
10. Eissfeller V, Langenbruch C, Jacob A, et al (2013) Tree identity surpasses tree diversity in affecting the community structure of oribatid mites (Oribatida) of deciduous temperate forests. Soil Biology and Biochemistry 63:154–162. https://doi.org/10.1016/j.soilbio.2013.03.024
11. Ganault P, Nahmani J, Hättenschwiler S, et al (2021) Relative importance of tree species richness, tree functional type, and microenvironment for soil macrofauna communities in European forests. Oecologia 196:455–468. https://doi.org/10.1007/s00442-021-04931-w
12. Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and Litter Decomposition in Terrestrial Ecosystems. Annu Rev Ecol Evol Syst 36:191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932
13. Hoekman D, LeVan KE, Gibson C, et al (2017) Design for ground beetle abundance and diversity sampling within the National Ecological Observatory Network. Ecosphere 8:e01744.

https://doi.org/10.1002/ecs2.1744

14. Hooper DU, Chapin FS, Ewel JJ, et al (2005) Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. Ecological Monographs 75:3–35. https://doi.org/10.1890/04-0922
15. Keller AB, Phillips RP (2019) Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. New Phytologist 222:556–564. https://doi.org/10.1111/nph.15524
16. Koivula M (2011) Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. ZK 100:287–317. https://doi.org/10.3897/zookeys.100.1533
17. Lariviere M-C, Larochelle A (2003) Larochelle A, Larivière M-C 2003. A Natural History of the Ground-Beetles (Coleoptera: Carabidae) of America north of Mexico. Faunistica No 27. Pensoft Publishers; Moscow-Sofia. 583 pp.
18. LeVan K NEON USER GUIDE TO GROUND BEETLES SAMPLED FROM PITFALL TRAPS (DP1.10022.001). 18
19. Lister BC, Garcia A (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc Natl Acad Sci USA 115:E10397–E10406. https://doi.org/10.1073/pnas.1722477115
20. MacArthur R, Levins R (1964) Competition, Habitat Selection, and Character Displacement in a Patchy Environment. PNAS 51:1207–1210. https://doi.org/10.1073/pnas.51.6.1207
21. Manhães CMC, Gama-Rodrigues EF, Silva Moço MK, Gama-Rodrigues AC (2013) Meso- and macrofauna in the soil and litter of leguminous trees in a degraded pasture in Brazil. Agroforest Syst 87:993–1004. https://doi.org/10.1007/s10457-013-9614-0
22. Maynard DS, Bradford MA, Lindner DL, et al (2017) Diversity begets diversity in competition for space. Nat Ecol Evol 1:0156. https://doi.org/10.1038/s41559-017-0156
23. McCary MA, Schmitz OJ (2021) Invertebrate functional traits and terrestrial nutrient cycling: Insights from a global meta-analysis. Journal of Animal Ecology 90:1714–1726. https://doi.org/10.1111/1365-2656.13489
24. Meier C, Chesney T, Jones K NEON USER GUIDE TO WOODY PLANT VEGETATION STRUCTURE (DP1.10098.001) AND NON-HERBACEOUS PERENNIAL VEGETATION STRUCTURE (DP1.10045.001). 32
25. Mueller KE, Eisenhauer N, Reich PB, et al (2016) Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. Soil Biology and Biochemistry 92:184–198. https://doi.org/10.1016/j.soilbio.2015.10.010
26. National Ecological Observatory Network (NEON) (2021a) Ground beetles sampled from pitfall traps (DP1.10022.001)
27. National Ecological Observatory Network (NEON) (2021b) Woody plant vegetation structure (DP1.10098.001)

28. Oksanen J, Blanchet FG, Friendly M, et al (2020) vegan: Community Ecology Package. Version 2.5-7URL https://CRAN.R-project.org/package=vegan
29. Potapov AM, Goncharov AA, Semenina EE, et al (2017) Arthropods in the subsoil: Abundance and vertical distribution as related to soil organic matter, microbial biomass and plant roots. European Journal of Soil Biology 82:88–97. https://doi.org/10.1016/j.ejsobi.2017.09.001
30. Schuldt A, Ebeling A, Kunz M, et al (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460. https://doi.org/10.1038/s41467-019-09448-8
31. Scott NA, Binkley D (1997) Foliage litter quality and annual net N mineralization: comparison across North American forest sites. Oecologia 111:151–159. https://doi.org/10.1007/s004420050219
32. Seibold S, Gossner MM, Simons NK, et al (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574:671–674. https://doi.org/10.1038/s41586-019-1684-3
33. Siemann E (1998) Experimental Tests of Effects of Plant Productivity and Diversity on Grassland Arthropod Diversity. Ecology 79:2057–2070. https://doi.org/10.1890/0012-9658(1998)079[2057:ETOEOP]2.0.CO;2
34. Sylvain ZA, Wall DH (2011) Linking soil biodiversity and vegetation: Implications for a changing planet. American Journal of Botany 98:517–527. https://doi.org/10.3732/ajb.1000305
35. Thorpe AS, Barnett DT, Elmendorf SC, et al (2016) Introduction to the sampling designs of the National Ecological Observatory Network Terrestrial Observation System. Ecosphere 7:e01627. https://doi.org/10.1002/ecs2.1627
36. Tilman D (1986) A Consumer-Resource Approach to Community Structure
37. Vician V, Svitok M, Michalková E, et al (2018) Influence of tree species and soil properties on ground beetle (Coleoptera: Carabidae) communities. Acta Oecologica 91:120–126. https://doi.org/10.1016/j.actao.2018.07.005
38. Wardle DA (c2002) Communities and ecosystems : linking the aboveground and belowground components. Princeton University Press, Princeton, N.J. (2017) Insect Biodiversity, 1st edn. John Wiley & Sons, Ltd
39. Ground Beetles | NSF NEON | Open Data to Understand our Ecosystems. https://www.neonscience.org/data-collection/ground-beetles. Accessed 10 Nov 2021

Figures

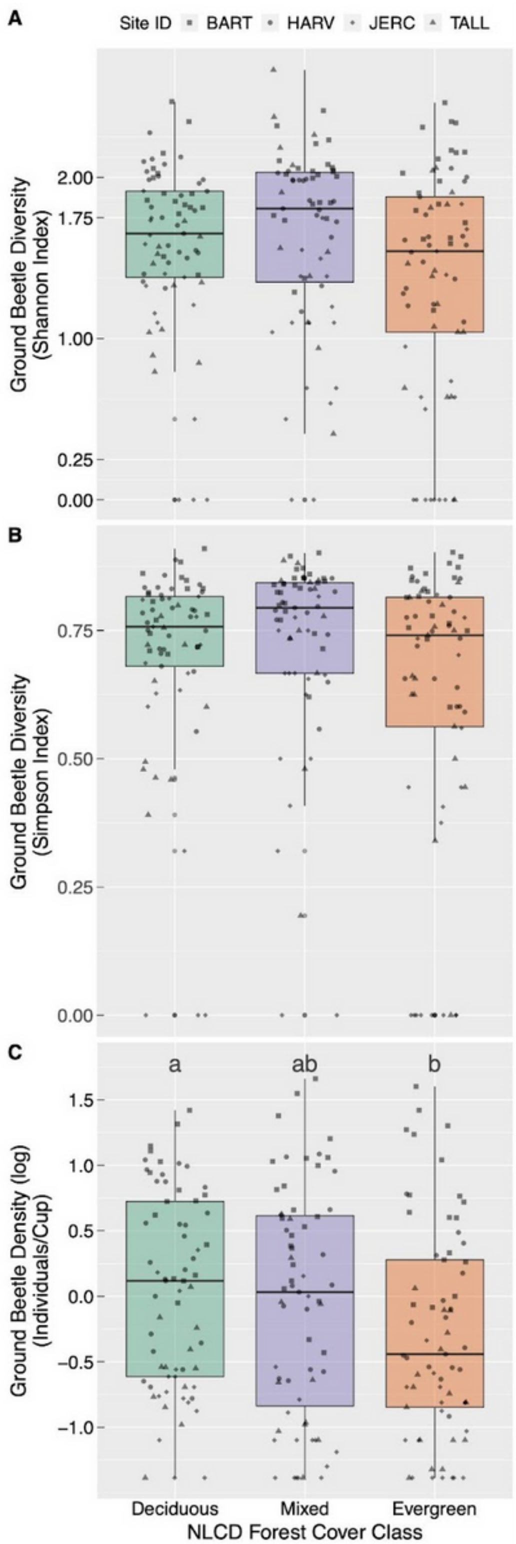

Figure 1

Ground beetle (a) Shannon diversity, (b) Simpson diversity, and (c) density across NLCD forest cover types at BART, HARV, JERC, and TALL

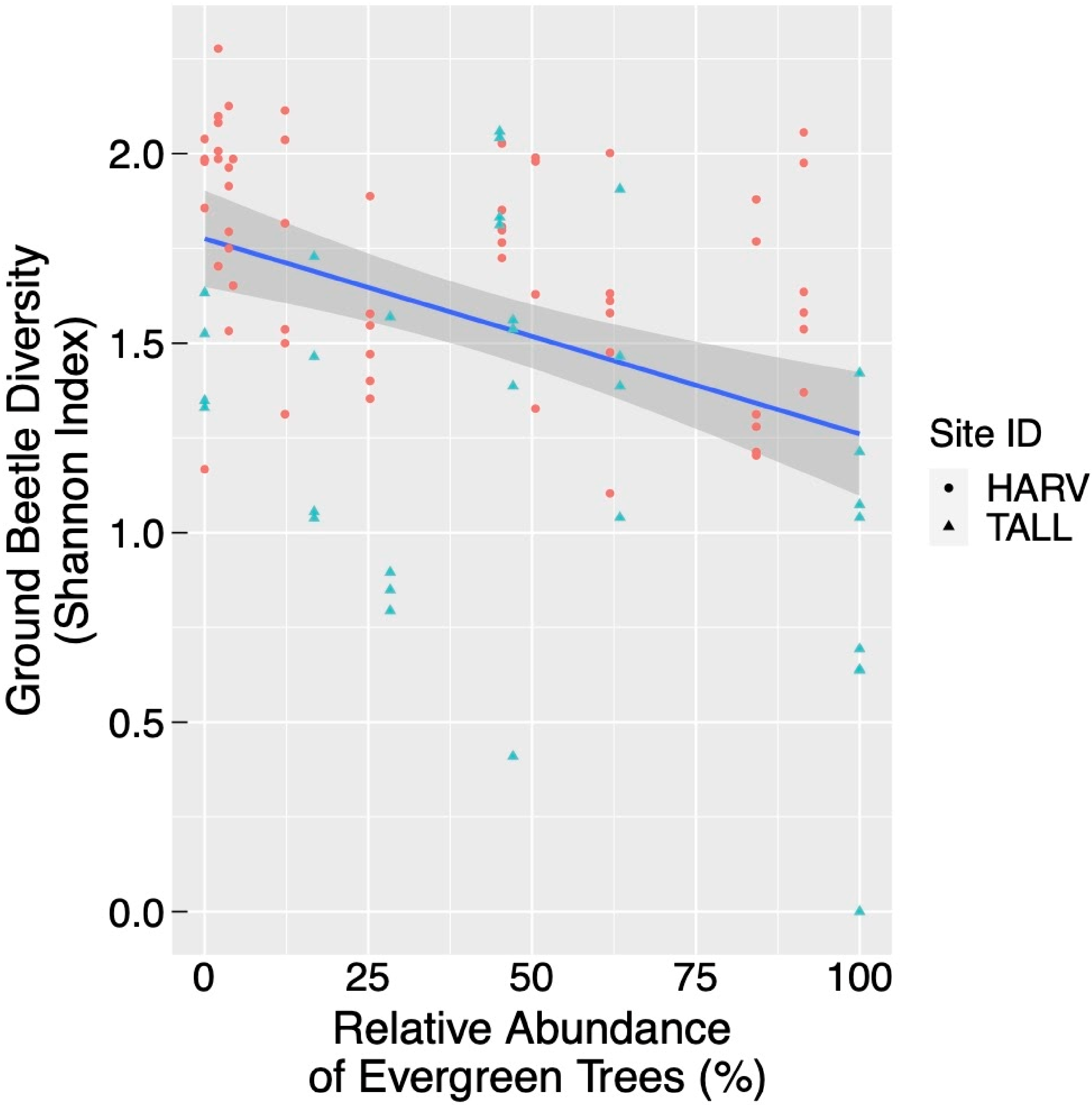

Figure 2

Ground beetle density at HARV and TALL predicted by the relative abundance of evergreen trees (based on basal area) in a plot

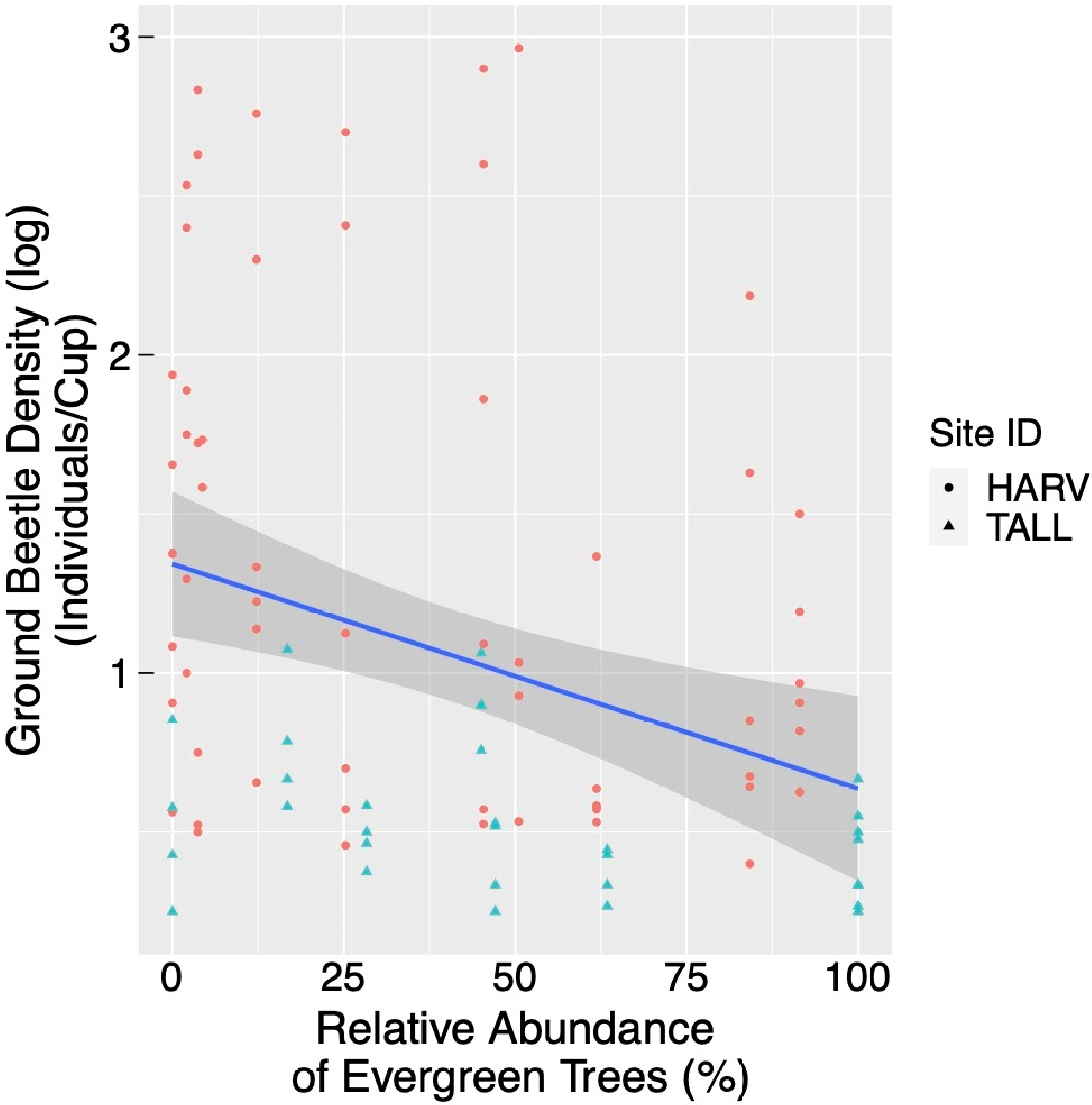

Figure 3

Ground beetle density at HARV and TALL predicted by the relative abundance of evergreen trees (based on basal area) in a plot

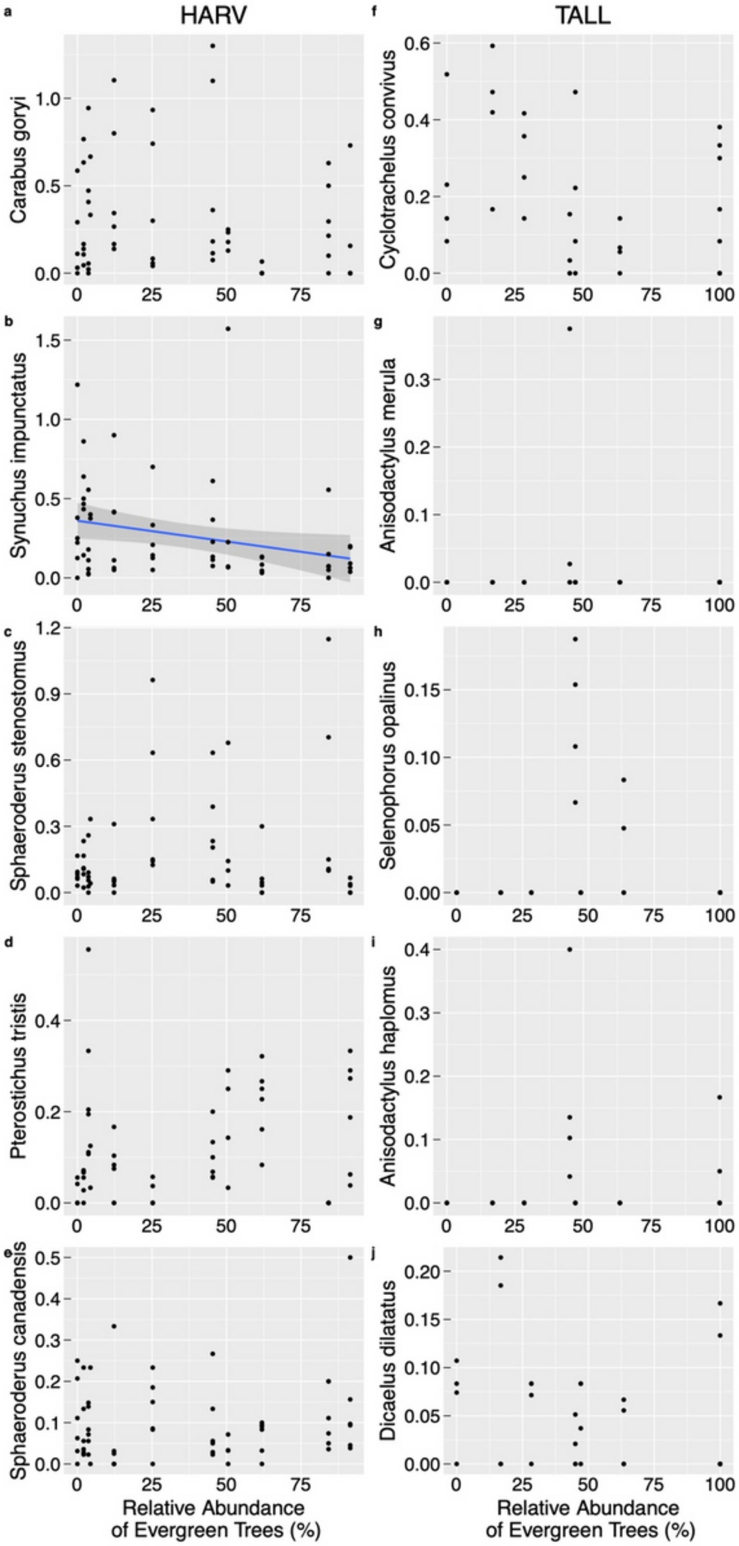

Figure 4

The densities of the top five most abundant species of ground beetles at both HARV and TALL, predicted by the relative abundance of evergreen trees in a plot

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- JLienauSupplemental.docx