

Forest Succession and Tree Identity Shape Species and Functional Group Richness of Ant Communities In New England

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Abstract - Ant communities are an important component of ecosystem functioning, as ant activities often accelerate leaf-litter decomposition and nutrient cycling in forest soils. In Northeastern North America, global climate change is expected to accelerate forest succession, and the effects of this succession on forest ant communities remain relatively unexplored. This work aims to understand the effects of forest succession and productivity on the functional group diversity of New England ant communities by testing a prediction of species–energy theory. Our study took place at the Harvard Forest, MA, where we conducted localized ground surveys for ants and measured the productivity of 4 tree species dominant in New England. We found that both ant species richness and functional group richness were significantly higher in association with deciduous trees compared to coniferous tree types. Species richness and functional group richness were highly correlated. Contrary to the species–energy theory, we found no strong correlations between tree productivity and ant community composition or function. Our findings indicate that local, top-down forest processes may influence the composition and functioning of ant communities as New England forests become dominated by deciduous trees.

Introduction

Ants are often regarded as ecosystem engineers because their activities alter the physical, chemical, and biological properties of soil (Frouz and Jilková 2008). Ant tunnels and galleries increase soil porosity, separating particles according to size and letting additional air and water into the soil (Wardle et al. 2011, Weber et al. 1966). Ants also increase soil nutrient content (nitrogen and phosphorus) by accumulating food and litter in their nests (Frouz and Jilková 2008). For example, the accumulation of extrafloral nectar from the shrub *Acacia constricta* (Benth.) Seigler & Ebinger (Whitethorn Acacia) in the nests of some North American ant species increases most mineral nutrient stocks in soils (Wagner and Fleur Nicklen 2010). Nutrient accumulation in nests along with ant burial of leaf litter (in some species) also increases rates of decomposition, providing an optimal environment for soil microbes (Andersen 1988, Beare et al. 1992, Frouz and Jilková 2008). Increasing soil porosity and soil nutrient content are just 2 examples of the many diverse functional roles that ants play in forest ecosystems. Therefore, changes in the abundances of functional ant groups may fundamentally change forest soil structure and accelerate the movement of nutrients through ecosystems.

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Functional group richness describes the value and variety of species traits, or functional roles, within an ecosystem (Díaz and Cabido 2001). In many terrestrial systems, the functional richness of communities is an essential component of ecosystem functioning (Díaz and Cabido 2001, Mason et al. 2005, Naeem and Wright 2003, Reiss et al. 2009). The amount of available energy in an ecosystem depends largely on the rate at which it is recycled via decomposition (Jacquemin et al. 2012, Kaspari 2004). It has been shown that ant communities with high functional richness help maintain ecosystem functioning by aiding in the decomposition of wood, leaf litter, and soil (Del Toro et al. 2015, Jacquemin et al. 2012, Laakso and Setälä 2000). Ants also facilitate decomposition through nesting, which breaks down large organic particles and aerates the soil (Wardle et al. 2011, Wolters 2000). We expect that forest ecosystems with functionally diverse ant communities—specifically including soil nesters, active litter shredders and wood decomposers—will experience higher rates of organic matter decay and recycling. For example, an ant community performing multiple functional roles such as litter decomposition, soil aeration, and wood decomposition could theoretically decompose and recycle organic matter more effectively than an ant community composed only of wood decomposers (Folgarait 1998). Higher rates of wood and litter decay increase availability of soil nutrients (Prescott et al. 1993). Thus, ant communities that are more functionally diverse may increase the amount of available soil nutrients over time.

Ant functional group richness has often been determined based on ants' taxonomic or morphological similarity, behavioral interactions with other ants, or habitat associations (Andersen 1995, Ellison et al. 2012). For example, Andersen (1995) classified ants into functional groups based on their habitat preference and competitive interactions with other ant species. However, this approach to classification makes it difficult to establish a direct link between ant species traits and the roles they play in ecosystem functioning (Del Toro et al. 2015, Tilman et al. 2001) because their behavioral and morphological traits do not always contribute directly to their functional role in the ecosystem. Del Toro et al. (2015) classified ant species of Northeastern North America into functional groups based on their roles within ecosystems and their subsequent contribution to ecosystem services and processes. Categories within this classification system include “seed dispersers”, “soil movers”, “decomposers”, and other functional groups which impact both forest nutrient cycling and other plant and insect communities (Del Toro et al. 2015). Because functionally diverse ant communities can cycle and modify nutrients more effectively, it is possible that direct and indirect links exist between ant functional richness and ecosystem energy availability.

Species richness has traditionally been used as a unit and metric of assessing community structure and composition (MacArthur and MacArthur 1961, MacArthur et al. 1965, Whittaker 1972). However, considering species richness alone within an ecosystem does not provide insight into the effects of species' traits, morphologies, and behaviors on ecosystem dynamics. The importance of the functional richness of ant communities has gained attention in recent decades, especially considering the variety of roles which ants fulfill in forest ecosystems (Gibb et al. 2015, Parr et al. 2017, Philpott et al. 2010). This work builds on a traditional ecosystems ecology

approach by expanding to consider the functional richness of New England ants and the roles they play in the nutrient cycles of these forest systems.

Although previous research has established clear links between species richness and productivity, the link between the functional richness of ecological communities and ecosystem energy availability is not yet well established (Gou and Berry 1998, Kaspari et al. 2000a, Tilman et al. 1996). Energy availability has long been considered a limiting factor of species richness for many groups of individuals, or species (Hutchinson 1959). Species–energy theory suggests that taxon density (i.e., the number of individuals within a species in a standardized area) is the single largest predictor of species richness and that density will correlate positively with habitat productivity (Kaspari et al. 2000b, Srivastava and Lawton 1998). Species richness is a strong predictor of functional richness, and we expect that for ants increased species density and species richness will induce high ant functional group richness (Del Toro et al. 2015). In short, the rate at which energy enters an ecosystem limits species richness—or number of species found in an area—by limiting the density of individuals. In the case of woodland ants, density refers to the number of active colonies. Although the relationship between species richness and functional richness is still largely undocumented in most ecosystems (Bihn et al. 2010), the two have been found to be correlated in several studies (Hooper et al. 2006, Tilman et al. 1997). This study examines the correlation between energy availability, or productivity, in trees and the functional richness of ant communities in New England forests.

The forests of northern New England are characterized by mixed deciduous and coniferous trees with patches of *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) thickly dominating some stands (Ellison et al. 2005). Woodland ants are both abundant and diverse in these forests, with over 140 species found in the New England region (Gotelli and Ellison 2002), making them an ideal taxon to study in relation to the productivity of their forest habitats. Tree productivity contributes greatly to ecosystem functionality, and changes in biomass can be used to estimate rates of net primary productivity (NPP) in trees (Clark et al. 2001, Ellison et al. 2005). It is well established that rates of NPP are lower in forests dominated by coniferous species compared with deciduous species, particularly in hemlock stands (Catovsky et al. 2002). This study tested species–energy theory by exploring how ant diversity and community functioning differ between deciduous and coniferous tree types with differing productivity. We expected that deciduous trees would exhibit (1) higher rates of NPP, (2) increased ant colony abundances and (3) increased species richness and functional group richness of forest ant communities.

Materials and Methods

Study system and significance

Forest succession could have lasting impacts on New England ant communities in the future (Niemelä et al. 1996, Punttila 1996). It is already well established that New England forests are currently experiencing gradual succession from coniferous- to deciduous-dominated forests (Hibbs 1983, Richardson and Friedland

2016) as a function of regional climate change. In the future, global climate change is expected to accelerate forest succession by prolonging warmer and wetter conditions which favor both deciduous tree types and insect pests of coniferous trees (Foster and Aber 2006, Orwig and Foster 1998). Relatively little is currently known about how forest ant communities will be impacted by climate-driven forest succession, particularly their functional richness and role in ecosystem nutrient cycling.

Study design

Our study took place at the Harvard Forest in Petersham, MA, from June to August 2018. Specifically, we collected our data in the Harvard Forest MegaPlot, a 35-ha, long-term research site containing >100,000 woody stems of eastern mixed hardwoods (Orwig et al. 2015). We mined tree data including basal area, species, and location from the Harvard Forest database from surveys conducted in 2013. We used R (Version 3.5.0; R Core Team 2013) to subset and select a random stratified sample of all living trees in the MegaPlot larger than 10 cm in diameter (according to mined data) and representative of the 4 dominant New England species: Eastern Hemlock, *Pinus strobus* L. (White Pine), *Acer rubrum* L. (Red Maple), and *Quercus rubra* L. (Northern Red Oak) (Fig. 1). We then sampled ant assemblages around the bases of all selected trees ($n = 208$) within the southern 250 m x 700 m section of the MegaPlot (Fig. 1; Orwig et al. 2015).

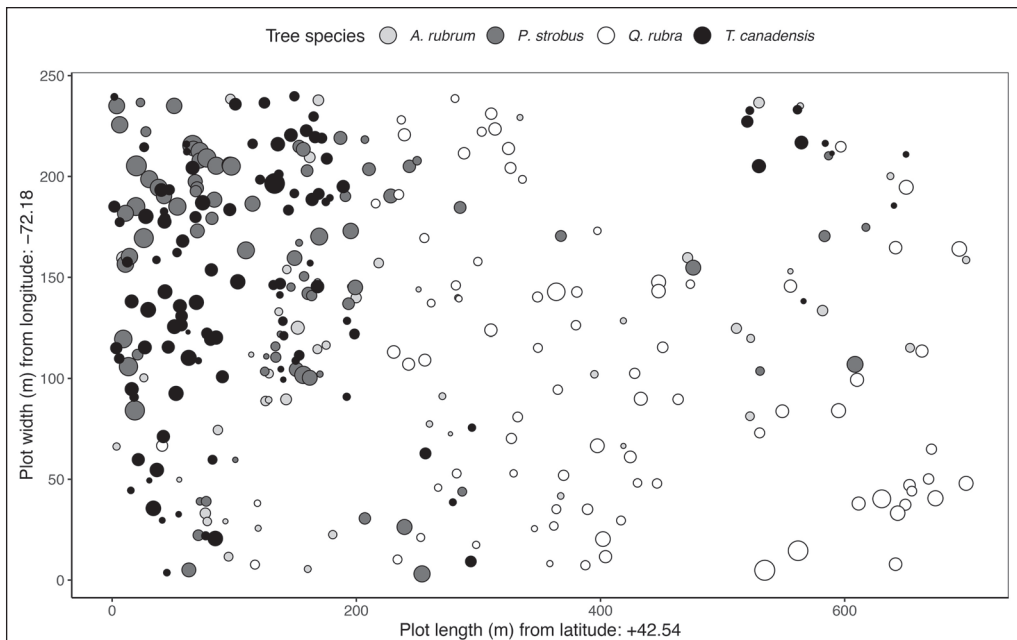


Figure 1. Map of all trees sampled. Trees are located within the southern 250 m x 700 m portion of the Harvard Forest MegaPlot (latitude: 42.54°N, longitude: 72.18°W, elevation: 340–368 m). Point shade denotes tree species (black = *Acer rubrum* [Red Maple], dark grey = *Pinus strobus* [White Pine], light grey = *Quercus rubra* [Northern Red Oak], white = *Tsuga canadensis* [Eastern Hemlock]) and point size denotes tree basal area which varied from 80 cm² to nearly 4000 cm².

Ant sampling

We sampled ant colonies from the ground and leaf litter in the area within 1 m of the base of each tree. Trees differed in diameter at breast height (DBH), and larger trees thus had larger sampling areas, reflecting the amount of area equally affected by the trees' productivity. Individual trees have a direct influence on the biogeochemistry of soils at scales of 5–15 m away from their bases (Binkley and Giardina 1998), and thus we determined our sampling areas to be representative of direct tree influence on the forest floor. We cleared all leaf litter from the area prior to sampling before checking it for ant colonies. We also checked sticks and acorns for ant nests. We standardized the amount of time per unit area; sampling time at each tree varied between 5 and 15 minutes in proportion to the sampled ground area, with more time spent at larger trees. During sampling, we collected representative individual ants from each ground nest (i.e., only full colonies with queens) and later identified them to species in the lab using Ellison et al. (2012). We did not collect individual foraging ants, as ant colonies were the main focus of this study. Ant colony size was not measured in this study, as it would have been very difficult to estimate the size of so many ground nests.

Tree productivity

To calculate tree NPP, we took DBH measurements for each tree at the time of ant sampling in 2018. We then inferred aboveground biomass (AGB) for each tree using a series of allometric equations developed by the USDA Forest Service (Jenkins et al. 2004, Smith and Brand 1983). These equations are species-specific, as tree species mature at different rates and some carry a larger proportion of their biomass in their branches and foliage than others. They were developed based on recorded tree biomass measurements and regression models that assume carbon forms 50% of dry AGB (Munger and Wofsy 1993). We estimated NPP ($\text{gC m}^{-2} \text{yr}^{-1}$) by calculating the difference between 2018 AGB based on our own data taken at the time of sampling and 2013 AGB measurements taken from the same trees during the Harvard Forest MegaPlot census 5 years previously (see Orwig et al. 2015 for tree census details). This difference represented the net result of both productivity and loss of AGB (Clark et al. 2001).

Analyses

We calculated ant species and functional richness for individual trees using Hill numbers. Hill numbers, or effective numbers of species, are used increasingly in ecology as they represent taxonomic species richness and functional richness expressed in units of equally abundant species (Chao et al. 2014). We determined ant functional richness based on functional categories previously established for New England ant species by Del Toro et al. 2015 (see Appendix 1). In addition to species and functional richness, we determined ant nest abundances by summing the total number of ant colonies found at each tree. Because the size of our sampling areas differed based on tree size, species richness, functional richness, and colony abundance were all calculated per unit area. We compared nest abundance, species

richness, and functional richness to NPP and tree type (deciduous or coniferous) using an analysis of variance (ANOVA). We also generated a generalized linear model (GLM) to assess the effects of our continuous variables on both species richness and functional richness. We assumed a gamma distribution for both species and functional richness datasets in this GLM (Appendix 2). Gamma distributions are commonly used within GLMs to analyze zero-inflated data (Zuur and Ieno 2016). We used stepwise variable selection to identify the variables that best informed the diversity patterns. Finally, an Akaike information criterion (AIC) was used to estimate the influence of each predictor in our GLMs.

Results

Ant species

We collected a total of 473 ants from individual nests representing 11 species and 5 functional groups (Table 1). The majority (80%) of ant nests were from 2 congeneric species: *Aphaenogaster picea* and *A. fulva*. Ant species richness and functional group richness were strongly correlated across both coniferous (ANOVA: $F = 10.12$, $P < 2.2e^{-16}$), and deciduous (ANOVA: $F = 11.22$, $P < 2.2e^{-16}$) tree types, suggesting that species richness is predictive of functional richness in New England ant communities (Fig. 2).

Tree productivity and ant colony abundance

Tree NPP varied over 3 orders of magnitude across all sampled trees, with deciduous tree types exhibiting significantly higher rates of NPP than coniferous tree types (ANOVA: $F = 385.91$, $P < 2.2e^{-16}$; Fig. 3A). NPP also varied significantly between tree species (ANOVA: $F = 35.36$, $P < 2.2e^{-16}$; Fig. 3B). At the species level, NPP was highest in *Q. rubra* and *A. rubrum* and lowest in *T. canadensis* and *P. strobus*. Nest abundance varied widely across all species, with an average of 2.3 nests per tree (min–max = 0–9). Nest density (nests per m²) varied from 0 to 2.2 nests (mean = 0.6 nests) and had a weak but significant positive relationship with tree NPP (ANOVA: $F = 0.65$, $P = 0.42$; Fig. 4A). Deciduous trees had, on average, higher nest density (ANOVA: $F = 4.24$, $P = 4.08e^{-2}$; Fig. 4B).

Species richness and functional group richness

Both ant species richness and functional richness were explained by tree type, although not by tree NPP. Deciduous trees had both higher species richness (ANOVA: $F = 9.75$, $P = 2.07e^{-3}$) and higher functional richness (ANOVA: $F = 11.69$, $P = 7.66e^{-4}$) (Fig. 5). In general, deciduous trees were associated with more individual ant species and had higher abundances of soil-moving and wood-decomposing ant functional groups (see Appendix 3). However, coniferous and deciduous trees did not differ in their relationships between NPP and species richness (ANOVA: $F = 0.27$, $P = 0.61$) or functional richness (ANOVA: $F = 0.24$, $P = 0.62$) (Fig. 6). The GLM confirmed these results, indicating that species richness and functional richness were explained by tree type alone (Table 2).

Table 1. Census of total ants collected in this study, including taxa information, number of ant nests sampled, and ant functional groups as specified by Del Toro et al. 2015 (see Appendix 1 for further descriptions). Note that only one individual was sampled per ant nest. Supporting information includes colony size, feeding preference, primary habitat, and biogeographic affinity, also adapted from Del Toro et al. 2015.

Ant subfamily	Ant species	# of nests sampled	Ant functional group (Del Toro et al. 2015)	Colony size	Feeding preference	Nest substrate	Primary habitat	Biogeographic affinity
Formicinae	<i>Lasius alienus</i> (Foerster)	19	Soil movers	Medium	Omnivore	Soil	Open	Warm climate
Formicinae	<i>Formica neogagates</i> Viereck	2	Soil movers	Medium	Predatory	Soil	Forests	Widespread
Formicinae	<i>Camponotus nearcticus</i> Emery	6	Wood decomposers	Medium	Omnivore	Wood	Forests	Widespread
Formicinae	<i>Camponotus novaeboracensis</i> (Fitch)	3	Wood decomposers	Medium	Omnivore	Wood	Forests	Widespread
Formicinae	<i>Camponotus pennsylvanicus</i> (De Geer)	8	Wood decomposers	Very Large	Omnivore	Wood	Forests	Widespread
Myrmicinae	<i>Aphaenogaster fulva</i> Roger	107	Seed dispersers	Medium	Granivore	Wood	Open	Widespread
Myrmicinae	<i>Aphaenogaster picea</i> (Wheeler, W.M.)	274	Seed dispersers	Medium	Granivore	Wood	Conifer forests	Cold climate
Myrmicinae	<i>Tennothorax longispinosus</i> (Roger)	28	Decomposers	Small	Omnivore	Acorns	Forests	Widespread
Myrmicinae	<i>Myrmica punctiventris</i> Roger	17	Decomposers	Small	Omnivore	Soil	Forests	Widespread
Myrmicinae	<i>Myrmica americana</i> Weber	4	Invertebrate community regulators	Small	Predatory	Soil	Subterranean	Widespread
Myrmicinae	<i>Stenamma impar</i> Forel	5	Invertebrate community regulators	Medium	Predatory	Soil	Forests	Widespread

Discussion

As New England forests shift over time to become dominated by deciduous trees, our data suggest that a subsequent shift in ant communities may also occur. An important caveat here is that our study is conducted at the scale of individual trees and thus our results cannot be fully extrapolated up to a forest-wide scale. Tree type, but not productivity, was significantly correlated with both the species

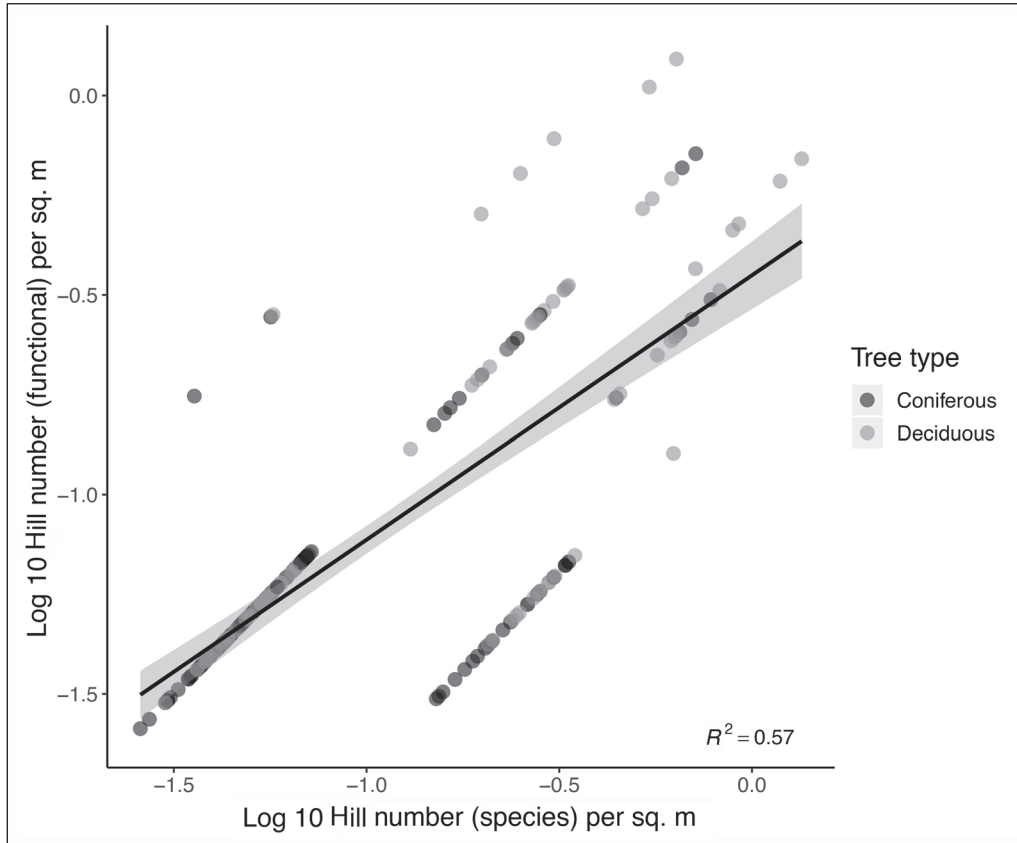


Figure 2. Linear regression showing the relationship between ant species richness and ant functional group richness. Both species and functional richness were strongly correlated in association with both coniferous trees (ANOVA: $F = 10.12$, $P < 2.2e^{-16}$), and deciduous trees (ANOVA: $F = 11.22$, $P < 2.2e^{-16}$). Both species and functional richness were calculated using Hill numbers and are transformed on a log 10 scale.

Table 2. Summary of best fit GLMs for detailed variable selection output (see supplementary data and code referenced in Appendix 3). * indicates significance at $P < 0.05$.

Model	Variables	Estimate	P-value	AIC
Ant species richness	NPP	-0.002	0.986	-153.33
	Tree type	-0.733	0.008 **	-151.33
Ant functional richness	NPP	-0.047	0.716	-250.09
	Tree type	-0.793	0.008 **	-243.00

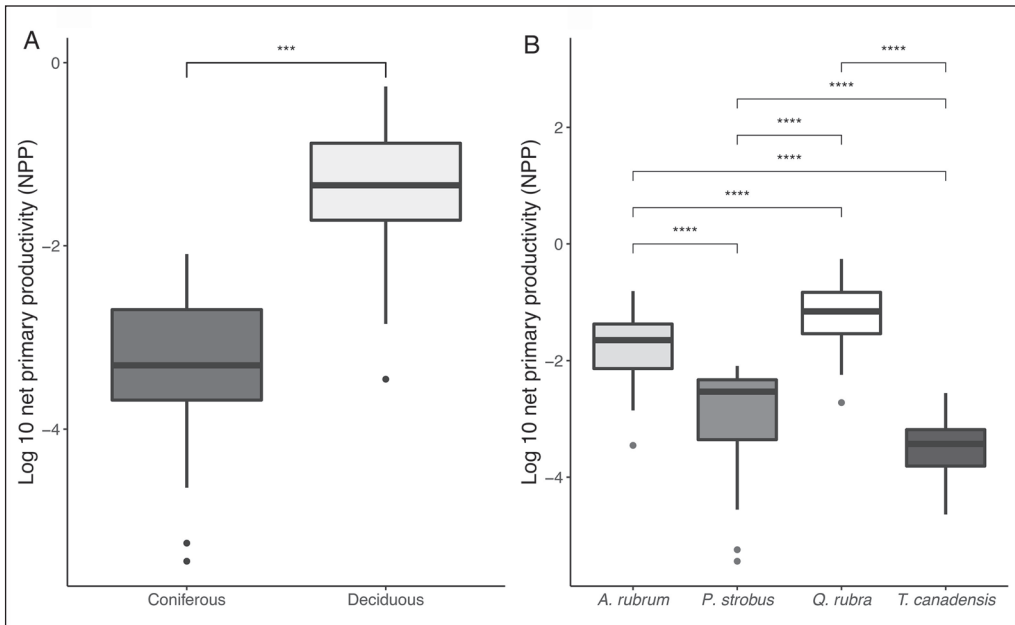


Figure 3. Boxplots showing the difference in NPP ($\text{gC m}^{-2} \text{yr}^{-1}$) (A) between deciduous and coniferous tree types and (B) between all tree species sampled in this study. Note: NPP data is transformed on a log 10 scale. Significance codes are as follows: **** $P < 0.001$, *** $P < 0.005$, ** $P < 0.01$, and * $P < 0.05$.

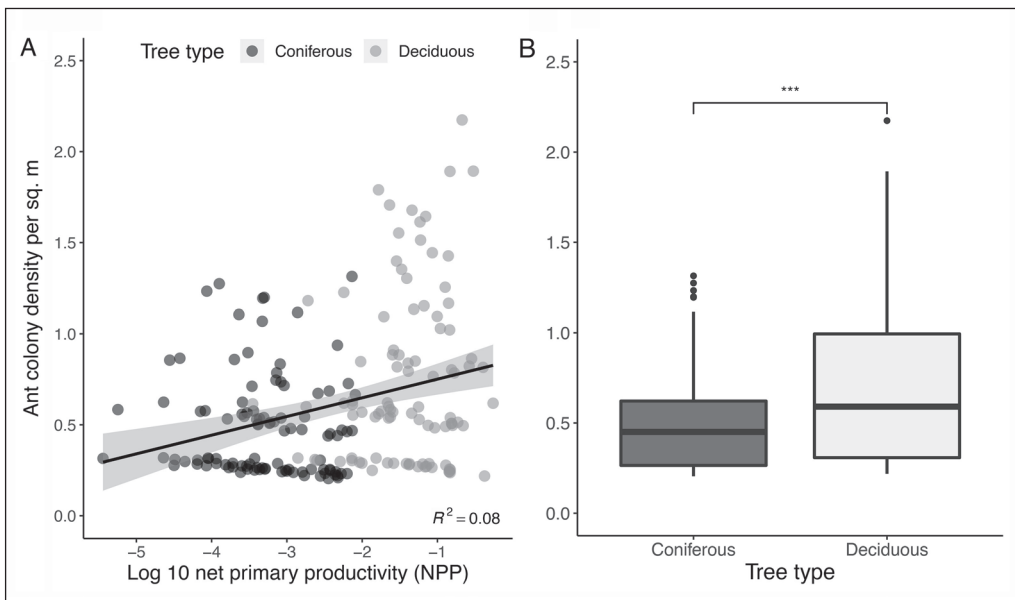


Figure 4. (A) linear regression showing the relationship between ant colony density per tree and tree NPP ($\text{gC m}^{-2} \text{yr}^{-1}$) and (B) boxplot showing how ant colony density differs between tree types. The low R^2 in A suggests a significant but weak relationship. Significance codes for B are as follows: **** $P < 0.001$, *** $P < 0.005$, ** $P < 0.01$, and * $P < 0.05$.

richness and functional group richness of ant communities. Although deciduous trees had significantly higher NPP compared to coniferous trees, we found no strong associations between tree productivity and ant community dynamics. In short, while our findings do not support species–energy theory in this instance, they do suggest that as New England forests become dominated by deciduous trees, local ant species richness and functional richness will also increase, especially with the arrival of new deciduous tree species. These changes may lead to higher abundances of ants which function as soil movers and wood decomposers. Such increases in ant nest abundances and functional group richness will likely lead to more rapid and widespread decomposition of forest leaf litter or shifting patterns of understory vegetation community composition. Thus, increased functional richness of ant communities may subsequently influence local ecosystem processes such as nutrient cycling (Kendrick et al. 2015) and other key ant-mediated ecosystem processes like seed dispersal (Handel et al. 1981).

Impact of ant activities on soil nutrients

Ants are known to alter soil nutrient dynamics through the building of their nests by foraging for and accumulating nutrient-rich food, transferring mineral and organic particles between soil layers, and increasing the porosity of soil through the building of galleries (Petal 1980). Over time, these changes can drastically accelerate rates of nutrient cycling in forests soils. It is already well established that ant nests entrap organic matter, significantly increasing the local nitrogen and phosphorus content of the soil over time (Boulton et al. 2003, Eldridge and Meyers 1998). Our study indicates that as forests become dominated by deciduous trees

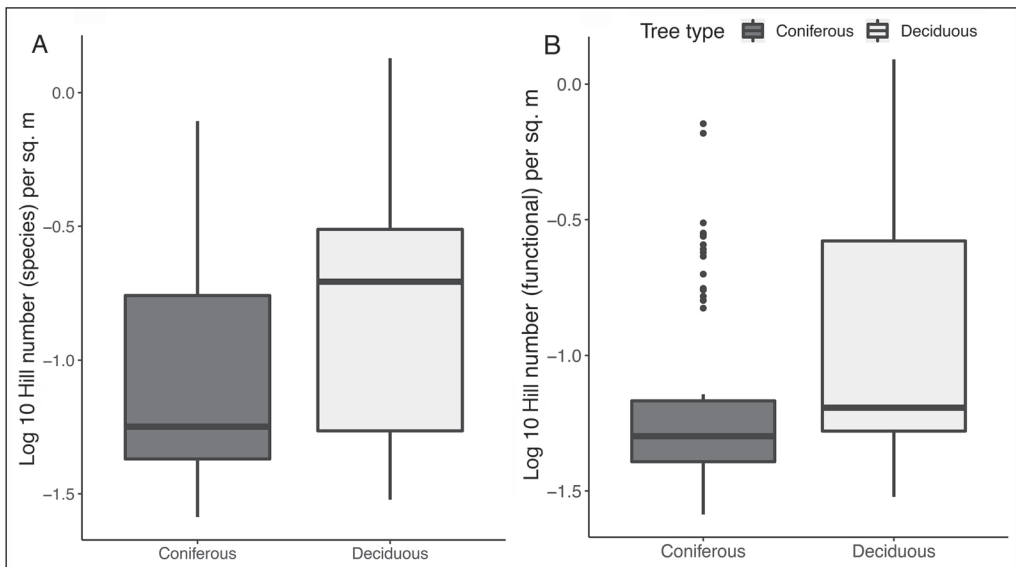


Figure 5. Boxplots showing differences in (A) ant species richness and (B) ant functional richness between deciduous and coniferous tree types. Both species and functional richness were calculated using Hill numbers. Significance codes are as follows**** $P < 0.001$, *** $P < 0.005$, ** $P < 0.01$, and * $P < 0.05$.

and leaf litter accumulates, the number of ant functional groups will likely increase (especially decomposers and soil movers), accelerating both the incorporation of leaf nutrients into the soil. Additionally, many nutrient-limited plants would benefit from a greater availability of soil nutrients resulting from increased ant activities. Accelerated decomposition rates would make more nutrients available to be taken up and used by plants, potentially resulting in long-term increases in forest understory productivity.

Functioning of *Aphaenogaster* ant species

It should be noted that the majority of ants identified in this study were species of *Aphaenogaster* (*picea* and *fulva*) which are only recognized functionally as a seed disperser in this study. We found that these already-dominant ant species increased in abundance in association with deciduous trees (see Appendix 3). Ant-dispersed (myrmecochorous) plants make up roughly half of the herbaceous understory in most New England forests—including the Harvard Forest—and a third of their biomass (Handel et al. 1981). Thus, our results imply that as forests become increasingly dominated by deciduous trees, increased prevalence of seed-dispersing *Aphaenogaster* species could cause myrmecochorous plants such as *Trillium* species to become more widespread (Higashi et al. 1989). In addition to

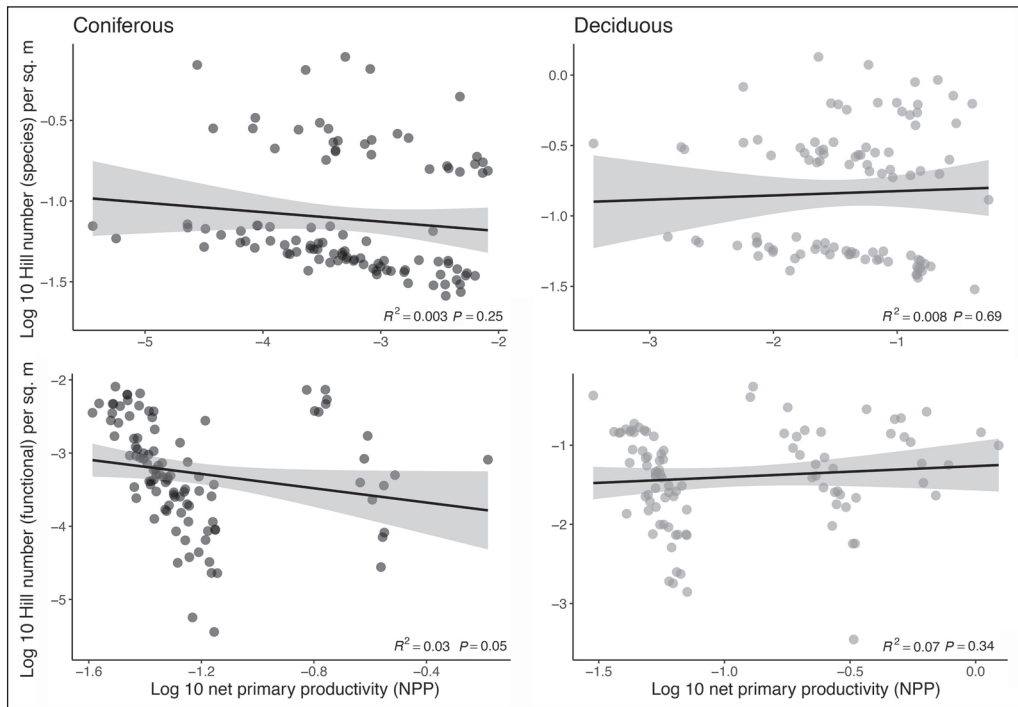


Figure 6. Linear regressions showing the relationship between ant species richness and ant functional richness and tree net primary productivity. Relationships are shown for both coniferous (dark grey) and deciduous (light grey) tree types. Both species richness (top) and functional richness (bottom) were calculated using Hill numbers. All values are transformed on a log 10 scale.

their functional role as seed dispersers, the presence of *Aphaenogaster* species also has substantial impacts on decomposition and soil nutrients (Warren and Bradford 2012). It is therefore likely that in such high abundances as observed in this study, the multiple functional impacts of *Aphaenogaster* species may be further amplified. Previous studies show that *Aphaenogaster* foraging and nesting behavior likely contributes to the structure, spatial distribution, and diversity of herbaceous forest-plant communities (Handel et al. 1981, Lengyel et al. 2009). It is also likely that high ant colony density of *Aphaenogaster* species will increase soil nutrient content over time as food accumulates in nests (Frouz and Jilková 2008). Considering the multiple effects of these ants on ecosystems, *Aphaenogaster* species may be more realistically classified into multiple functional categories: both seed dispersers and decomposers. This insight warrants further consideration of the possibility that some ant species may occupy more than 1 functional role within an ecosystem. We recommend that such considerations should be taken moving forward.

Local tree-mediated effects on ant communities

Our study has demonstrated that local ant community composition and function is likely influenced by whether a tree is deciduous or coniferous, with deciduous species supporting a wider variety of ant species and functions. The reason for these differences likely lies in the ability of deciduous oaks and maples to annually shed their large, nutrient-rich leaves to the forest floor. Accumulating leaf litter under trees provides a dry and sheltered nesting habitat for many ants, especially leaf-litter specialists. These include *Temnothorax* species, which are known to build their nests inside of fallen acorns, a characteristic that we observed in the field while collecting individuals of *Temnothorax longispinosus*. As more leaf litter accumulates in increasingly deciduous-dominated forests, we expect subsequent increases in those ant species that are better adapted to litter nesting. It is worth noting that all effects in this context are highly localized, as leaf litterfall is largely confined to the area directly beneath the tree. In short, our results suggest that both leaf litter and tree type (conifer or hardwood) are influential in shaping ant communities.

Trees as facilitators of microclimates

We have shown that tree identity plays a crucial role in determining local ant community richness and functioning. We were able to determine this relationship directly because our sampling was limited to established ant colonies at the bases of trees. Because our results are highly local and specific to individual trees, we are not able to make any definitive conclusions about the effects of forest-wide succession on large-scale patterns of ant species and functional richness. However, we expect that local tree-mediated microclimates play a major role in the composition and functioning of local ant communities. If we envision a forest as a series of microclimates moderated from the top-down by litterfall from different types of trees, then it is evident that increased prevalence of deciduous trees in New England mixed forests could have wide-ranging impacts across multiple ecosystem levels.

Implications of forest succession

We expect to see a change in those ant species and functional groups which are better-adapted to forest soil habitats derived from deciduous leaf litter as forest succession in New England progresses from coniferous-dominated to deciduous-dominated mixed forest types. Coniferous-dominated stands were more closely associated with wood-decomposer ants such as *Camponotus* species and invertebrate community regulators, including species of *Myrmica* (see Appendix 3). Both genera are omnivorous and predatory (Table 1), suggesting that they may be better adapted to survive in less-productive habitats by functioning as secondary consumers. Thus, the persistence of many ant species may depend upon both their functional redundancy within an ecosystem and their ability to adapt quickly to changing environments.

Conclusions

Although our study does not provide direct support for species–energy theory, it does establish a strong link between tree types and the richness and functioning of local ant communities, indicating that tree effects other than productivity are positively correlated with the richness and function of ant communities in Harvard Forest and giving insight into how these relationships may change in the future. Previous research indicates that global climate change will have drastic and lasting effects on the geographic distributions of ant communities (Del Toro 2015, Roura-Pascual et al. 2004), just as it has during prehistoric changes in global climate (Elias 1991). In New England mixed forests, climate change will likely promote warmer and wetter conditions, facilitating forest succession to a deciduous-dominated ecosystem. Already, research at the Harvard Forest has shown regional declines in the conifer Eastern Hemlock (Orwig and Foster 1998) and increases in densities of fast-growing deciduous species such as Red Maple (Ellison et al. 2010). In addition to accelerating forest range shifts, warmer and wetter conditions alone will likely increase rates of leaf-litter decomposition (Butenschoen et al. 2011). Although we have yet to observe the exact impacts of climate change on forest succession, the indirect effects of these changes on forest ant communities—particularly in terms of their functional group richness—can now be better anticipated.

Understanding the relationship between ant functional richness and forest succession is also necessary from a conservation perspective. The vast majority of conservation work to date is species-centered, focusing on the establishment of protected areas or protective regulations. While much work has been done to conserve the biodiversity of ecosystems or to save particular charismatic species from extinction, it is only relatively recently that conservation efforts have implemented an ecosystem-wide approach. When we assess the relationship between species or communities and their environment from a conservation standpoint, we must consider the way that they interact with each other, namely the various roles that species play to maintain dynamic equilibrium or otherwise benefit the ecosystems in which they live. Thus, considering the functional group richness of species or entire communities has the potential to greatly inform and benefit conservation efforts in the future.

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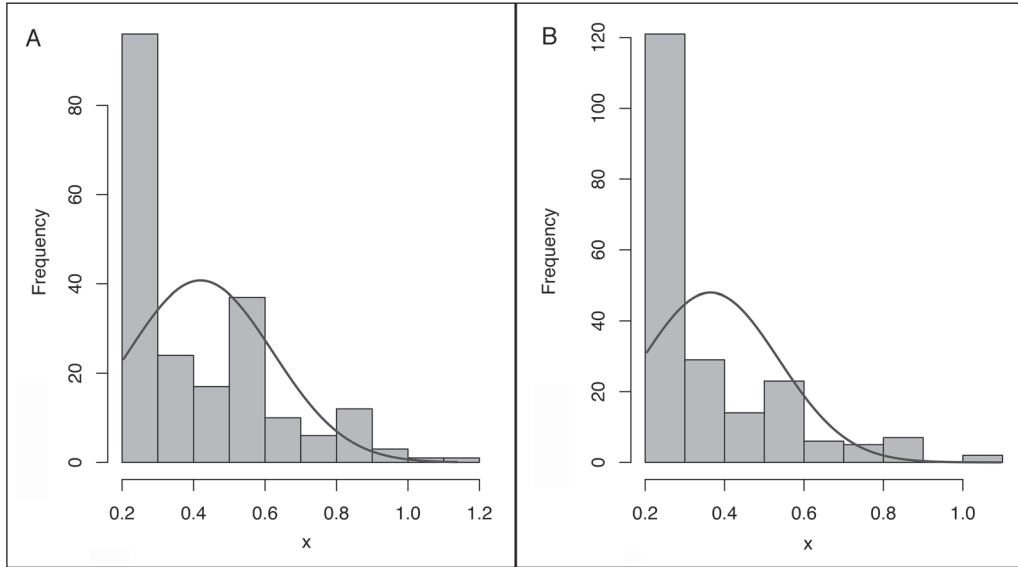
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Appendix 1. We clustered 70 common ant species of the northeastern US into functional groups based on morphometric, taxonomic, behavioral, and natural history traits. The second column (Description) specifies the traits which clustered species into their respective functional groups. Adapted from I. Del Toro et al. (2015:Table 1).

Group #	Description	Primary functional role
1	Medium-bodied, soil-dwelling, omnivorous, and widespread Formicinae species occupying open and sandy habitat in warm climates	Soil movers
2	Large-bodied, omnivorous, wood-dwelling <i>Camponotus</i> species occupying forest and edge habitat	Wood decomposers
3	Medium body sized, omnivorous, grass- and soil-dwelling, widespread Dolichoderinae species occupying forest and edge habitat	Invertebrate community regulators
4	Large-bodied, omnivorous, soil-dwelling, social parasitic, dominant <i>Formica</i> species occupying forest and edge habitat	Ant community regulators
5	Large-bodied, omnivorous, submissive <i>Formica</i> species with medium-sized colonies and occupying forest and edge habitat	Soil movers
6	Large-bodied, omnivorous, soil-dwelling, non-parasitic, dominant <i>Formica</i> species	Soil movers
7	Medium- to large-bodied, omnivorous, seed-dispersing Myrmicinae (some are behaviorally dominant) occupying forest and edge habitat	Seed dispersers
8	Medium-bodied, omnivorous, soil-dwelling, widespread Myrmicinae species occupying forest habitat in warm climates	Decomposers
9	Small-bodied, small colonies, omnivorous, soil-dwelling, widespread Myrmicinae species occupying open habitat in warm climates	Decomposers
10	Small bodied, predatory, widespread species with small colonies often found in litter in warm climates	Invertebrate community regulators

Appendix 2. Frequency distributions of ant community data showing (A) species richness and (B) functional richness.



Appendix 3. Bar graph showing distributions of (A) ant species and (B) ant functional groups between coniferous and deciduous tree types. For full ant genus names see Table 1. Project data and code: https://github.com/AND04570/Anderson-DelToro_NENA2020. git. Repository: AND04570/Anderson-DelToro_NENA2020.

