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Identifying foundation species in North American forests using long-term data on ant assemblage structure

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Abstract. Foundation species are locally abundant and uniquely control associated biodiversity, whereas dominant species are locally abundant but are thought to be replaceable in ecological systems. It is important to distinguish foundation from dominant species to direct conservation efforts. Long-term studies that remove abundant species while measuring community dynamics have the potential to (1) aid in the identification of foundation vs. dominant species and, (2) once a foundation species is identified, determine how long its effects persist within a community after its loss. Long-term data on ant assemblages within two canopy-manipulation experiments—the Harvard Forest Hemlock Removal Experiment (HF-HeRE) and the Black Rock Future of Oak Forests Experiment (BRF-FOFE)—provide insights into how ant assemblages change and reassemble following the loss of *Tsuga canadensis* or *Quercus* spp. Previous research documented foundation species effects on ants in the HF-HeRE for up to four years after *T. canadensis* loss. Six additional years of data at HF-HeRE presented for the first time here show that removal of *T. canadensis* resulted in taxonomic and some measures of functional shifts in ant assemblages that persisted for ten years, further supporting the hypothesis that *T. canadensis* is a foundation species at Harvard Forest. In contrast, ant assemblages at BRF-FOFE varied little regardless of whether oaks or other tree species were removed from the canopy, suggesting that *Quercus* species do not act as foundation species at Black Rock Forest. Deer and moose exclosures within each experiment also allowed for comparisons between effects on ants of foundation or dominant tree species relative to effects of large herbivores. At HF-HeRE, effects of *T. canadensis* were stronger than effects of large herbivores on taxonomic and functional diversity of ant assemblages. At BRF-FOFE, in contrast, effects of *Quercus* species were weaker than effects of large herbivores on ant taxonomic diversity and some measures of ant functional diversity. These findings illustrate the importance of distinguishing between the roles of irreplaceable foundation species and replaceable dominant ones in forested ecosystems along with other drivers of biodiversity (e.g., herbivory).

Key words: *Adelges tsugae;* dominant species; Formicidae; foundation species; functional diversity; *Quercus; Tsuga canadensis*.

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INTRODUCTION

Ecosystems with high biodiversity are hypothesized to be more resilient to changing environmental conditions than those with lower biodiversity because more species are available in the former to fill functional roles when species are lost (i.e., the insurance hypothesis sensu Yachi and Loreau 1999). However, not all species are functionally equivalent, and the loss of keystone predators

(Paine 1966), dominant species (Whittaker 1965), or foundation species (Ellison et al. 2005*b*) may have unexpectedly large or even irreversible system-wide impacts. In many terrestrial ecosystems, foundation species and dominant species tend to be trees and share the following attributes: large size, local abundance, occupying basal positions in local food webs, and controlling ecosystem processes and dynamics principally through non-trophic interactions (Baiser et al. 2013). In addition, foundation species differ from dominant species in that the former are thought to be irreplaceable in terms of their control on population and community dynamics and ecosystem processes, whereas the latter are considered replaceable (Ellison et al. 2005*b*). Consequently, identifying foundation species should be a key priority for conservation efforts to preserve the processes that they modulate within their communities and ecosystems.

In eastern North American forests, *Tsuga canadensis* (L.) Carrière (eastern hemlock) has been identified as a foundation species (Ellison et al. 2005*b*, 2014); stands dominated by *T. canadensis* are different, both structurally and functionally, from stands dominated by other conifers or mixtures of various deciduous species. Hemlock-dominated stands are dark, cool, and moist; have acidic, nutrient-poor soils with slow rates of nutrient cycling (Orwig et al. 2013); and are populated by generally species-poor assemblages of associated plants and animals (Rohr et al. 2009, Sackett et al. 2011, Orwig et al. 2013).

On the other hand, many eastern North American forests are dominated in terms of numbers or biomass by one or more Quercus (oak) species (Schuster et al. 2008). Unlike *T. canadensis*, however, it is not clear whether oaks determine uniquely the structure and function of the forests they dominate. Although oak masts are important for certain organisms such as small mammals and ticks (Ostfeld et al. 1996, McShea et al. 2007), most core ecosystem processes of oak-dominated forests, including leaf-litter decomposition rates and associated soil nutrient dynamics (Polyakova and Billor 2007), root respiration (Levy-Varon et al. 2012), and net ecosystem exchange (Papale and Valentini 2003), are statistically indistinguishable from forests dominated by other deciduous species or from forests with no clear dominant species.

Many trees, including *T. canadensis* and *Quercus* spp., are threatened with functional loss by a myriad of native and non-native insects and pathogens (Lovett et al. 2016). While we are mourning these impending losses (Foster 2014) and working to control these insects and pathogens, we also have an unparalleled opportunity to study how forests respond to, and reorganize after, the loss of foundation or dominant species by assessing how their loss changes the taxonomic and functional biodiversity of associated species. Furthermore, within these studies we can investigate effects of other drivers of forest dynamics (e.g., ungulate herbivory, earthworms) with additional manipulations.

Here, we used two forest canopy-manipulation experiments to ask how biodiversity within forests changes and reorganizes after the experimental removal of *T. canadensis* or *Quercus* species. Large herbivore exclosures within each experiment also enabled us to test for additive and interactive effects on biodiversity of both the loss of canopy tree species and herbivory by large ungulates. Specifically, we examined the effects of these experimental treatments on the species and trait diversity of ground- and soil-nesting ant assemblages. Ants are a particularly good taxon to use for these studies because they are abundant and widespread omnivores; are known to be responsive to local environmental conditions such as canopy cover, light availability, and soil temperature (Rescaso et al. 2014); modulate and control some soil ecosystem processes (Del Toro et al. 2012), often in concert with the canopy tree species (Kendrick et al. 2015); and are well understood both taxonomically and functionally in northeastern North America (Ellison et al. 2012, Del Toro et al. 2015).

Previous work by the authors reported that the experimental removal of hemlock had large impacts on ant assemblage structure for four years (Sackett et al. 2011). There are now data available for six additional years in experimental plots simulating hemlock loss. Here, we revisit the hypothesis that hemlock is a foundation species for ant assemblages with these six additional years of data (i.e., 10 yr total; Hypothesis 1). It is unknown whether oak species in eastern North American forests act as foundation species. We hypothesize that if oaks are not foundation species, then the loss of oaks will have no detectable impact on the structure of ant assemblages (Hypothesis 2). Alternatively, if oaks are foundation species, then the loss of oaks will have a significant impact on assemblages of ants, analogous to what has been seen for hemlock. Finally, we hypothesize that when a foundation species is present (as established by Hypotheses 1 and 2), the effect of the foundation species on ant assemblages will outweigh the effects of other drivers of biodiversity: here, large herbivores (Hypothesis 3). Large herbivores may influence ant microhabitat by eating understory vegetation. The third hypothesis emphasizes the influence on ant assemblages of foundation species that comprise the canopy, not effects of understory vegetation on ant assemblages.

Materials and Methods

The Harvard Forest Hemlock Removal Experiment

The Harvard Forest Hemlock Removal Experiment (HF-HeRE) is a stand-level manipulation of *Tsuga canadensis*-dominated forests located in the hemlock/hardwood/white pine transition zone of the temperate forest biome of northeastern North America. The experiment is located within the 121-ha Simes Tract at the Harvard Forest in Petersham, Massachusetts, USA (42.47–42.48° N, 72.21° W, 215–300 m a.s.l.). Soils at the Simes Tract are derived from glacial till and composed primarily of coarse-loamy, mixed, mesic Typic Dystrudepts in the Charlton Series (Giasson et al. 2013), and canopy trees within HF-HeRE are 70–150 yr old (Ellison et al. 2014). Harvard Forest Hemlock Removal Experiment is a replicated and blocked before–after-control–impact experiment (see Ellison et al. 2010 for full details on the design and routine statistical analysis of HF-HeRE). Briefly, there are two replicates of each of four treatments, which are grouped into two blocks with equal representation of treatments per block. Each of the eight experimental plots is ≈90 × 90 m in size; *T. canadensis* accounted for >70% of the basal area (BA) of the six plots initially dominated by hemlock. The Valley block is sited in poorly drained rolling terrain bordered on the north by a *Sphagnum*-dominated wetland, whereas the Ridge block is along a forested ridge with well-drained soils. Plots were identified in 2003 and pre-treatment data on plant and ant assemblages were collected for two years prior to any experimental manipulations.

There are two canopy-level manipulations in HF-HeRE. In the first (one hemlock-dominated plot/block), all *T. canadensis* individuals were girdled (as done by Yorks et al. 2003) to simulate physical impact of loss of hemlock caused by the non-native hemlock woolly adelgid (*Adelges tsugae* Annand; Homoptera: Adelgidae). Girdling of all individuals occurred over two days in May 2005 using chainsaws or knives to cut through bark and cambium. Sap flow of girdled trees decreased immediately by 50%, and the trees died within 30 months (Ellison et al. 2010). The rate of hemlock death was comparable to that caused by the adelgid in the southeast United States, but somewhat faster than the 5–10 yr observed routinely in the northeast (McClure 1991). Dead trees were left standing in the girdled plots to slowly disintegrate, as in stands naturally infested by the adelgid. Relative to intact hemlock plots, the girdled plots exhibited significant increases in light, air and soil temperature, and soil moisture as the girdled hemlocks died and forest transpiration decreased (Lustenhouwer et al. 2012). The volume of dead stumps, snags, and coarse woody debris in girdled plots was comparable to the controls in pre-treatment years (Ellison and Barker Plotkin 2009). Two years after girdling, the number of dead stumps and snags increased two- to threefold, but coarse woody debris on the ground did not increase significantly over the first five years of the study (Orwig et al. 2013).

In the second canopy manipulation (one hemlock-dominated plot/block), all *T. canadensis* individuals >20 cm diameter (measured at 1.3 m above ground) along with other select merchantable trees (e.g., *Pinus strobus* L., *Quercus rubra* L.) were cut and removed from the site to simulate the pre-emptive salvage logging done by people in anticipation of the arrival of the adelgid (Foster and Orwig 2006). Logging was done between February and April 2005 when the soil was frozen. Logging removed 60–70% of the BA in these plots; slash (i.e., small branches and damaged or rotting boles) were left on site as is typical in local timber-harvesting operations (Ellison et al. 2010).

There also are two control plots in each block at HF-HeRE: intact hemlock (≈70% BA hemlock) and intact stands of mixed hardwoods. When the experiment was sited in 2003, the adelgid was absent from the region. By 2009, however, the adelgid was observed at low densities in the hemlock control plots, and it was widespread in these plots by 2010 (Kendrick et al. 2015). The mixed-hardwood control plots represent the anticipated future of stands in this region following hemlock decline and contain young hardwoods (predominantly *Betula lenta* L. and *Acer rubrum* L. <50 yr old) and small *T. canadensis* and *P. strobus* individuals (Ellison et al. 2010). To ensure that any discernible differences in ant assemblages were caused by the experimental manipulations, not from known environmental heterogeneity, the hemlock removal treatments and control plots within each block were sited within 100 m of one another and occupy similar topography, aspect, and soil type (Ellison et al. 2010). Finally, in 2012, a single 15 × 30 × 2.5 m exclosure fence was erected in the center of each of the eight plots to examine additional effects of large browsers (moose *Alces alces* L. and white-tailed deer *Odocoileus virginianus* Zimmermann) on successional processes (Faison et al. 2016).

Harvard Forest Hemlock Removal Experiment ant sampling.—To document temporal changes in ant assemblages within the eight HF-HeRE plots, ants were sampled annually from 2003 to 2015. Samples were collected in dry weather in June, July, and August (2003–2005); in July and August (2006); and in July only (2007–2015). Ants were collected with pitfall traps, baits, litter samples, and hand collections (the ALL protocol; Agosti and Alonso 2000). Baits (50 mg crumbled Pecan Sandies cookies [Keebler Foods, Elmhurst, Illinois, USA] on white index cards) set out for 1 h and pitfalls (8 cm diameter, 200-mL cups buried flush with the soil surface and containing 10 mL of soapy water) set out for 48 h were placed within a permanent 10 × 10 m grid with 25 evenly spaced sampling points located near the center of each canopy-manipulation plot. Hand-collecting was done across the entire plot for 1 person-hour. Three 3-L litter samples were collected from random locations in the 90 × 90 m plot, but outside of the pitfall and bait sampled grid, and sifted in the field. In 2012, following the installation of the large herbivore exclosures, we added an entire additional 10 × 10 m sampling grid for ants within each exclosure, thus doubling the total sample size.

The Black Rock Forest Future of Oak Forests Experiment

The Black Rock Forest Future of Oak Forests Experiment (BRF-FOFE) is a canopy-level manipulation of oak and non-oak trees. Black Rock Forest is in the Hudson Highlands near Cornwall, New York (Ellison et al. 2007), and BRF-FOFE is located on the north slope of Black Rock Mountain (41.45° N, 74.01° W; 400 m a.s.l) within a "hardwood slope" (Tryon 1930) or "red oak association" (Raup 1938). The glacially derived soils at Black Rock Forest are of the Chatfield and Rockaway series (Denny 1938, Ross 1958). Like HF-HeRE, the BRF-FOFE is a replicated and blocked before–after-control–impact experiment. The experimental plots are 75 × 75 m. There are three replicates of each of four treatments, which are grouped into blocks (lower, middle, and upper slope) with equal representation of treatments per block. Upper slope plots are steeper and have drier soils than the lower slope plots (15–16% and 24% soil water content, respectively; Falxa-Raymond et al. 2012). Plots were sited in 2006 and pre-treatment data on ant assemblages were collected for two years prior to experimental manipulations. *Quercus rubra* and *Quercus prinus* L. make up ≈70% of the canopy; *Acer rubrum* dominates the understory (Schuster et al. 2008). Other non-oak canopy trees in decreasing order of prevalence include *Ac. rubrum* (28%), *Nyssa sylvatica* Marsh. (22%), *B. lenta* (20%), and *Acer saccharum* L. (16%) (Falxa-Raymond et al. 2012). *Tsuga canadensis* is absent from the experimental site.

There are four experimental treatments in BRF-FOFE: all oaks girdled (OG; girdling 74–78% of total plot BA); half of the OG (O50; 15–37% of BA); all non-oaks girdled (NO; 15–37% of BA); and control (no trees girdled; 0% of BA). The intent of the girdling treatment was to simulate effects of pathogens (e.g., sudden oak death: *Phytophthora ramorum* Werres, de Cock & Man in't Veld) or defoliating insects such as gypsy moth (*Lymantria dispar* (L.)). Although sudden oak death is not yet epidemic in the eastern United States (as it is in northern California and southern Oregon), eastern U.S. nurseries have documented infected horticultural stock arriving from western sources and there is concern that it could become established and virulent in eastern North American forests (Grünwald et al. 2012).

Between 27 June and 9 July 2008, chainsaws were used in each plot to girdle trees >2.54 cm diameter by making ≤5-cm incisions that cut through the bark, phloem, and cambium around the entire circumference of each tree at 1.3 m above ground; the <3% of the trees that were <2.54 cm in diameter were not girdled. Unstable girdled trees, typically those stems 2.5–7.5 cm in diameter, were felled for researcher safety. One year after girdling, in the summer of 2009, roughly twice as many oak trees leafed out and re-sprouted in the O50 plots (15% and 46%, respectively) as in the OG plots (8% and 27%, respectively). In the NO plots, over twice as many NO leafed out and re-sprouted after girdling (23% and 69%, respectively) than oaks (10% and 33%, respectively; Levy-Varon et al. 2012). Trees that survived girdling in all OG, O50, and NO plots were re-girdled in subsequent years. In addition to these treatments, each plot contained a 10 × 20 × 3 m exclosure fence to keep out deer and examine effects of browsing on successional trajectories. The many deer at BRF (≈7/km^2 at the start of the experiment) had browsed most of the understory plants prior to the start of the experiment.

Black Rock Future of Oak Forests Experiment ant sampling.—To document temporal changes in ant assemblages within the 12 BRF-FOFE plots, ants were sampled in the first week of July in 2006, 2009, 2011, and 2015. In 2006 (pre-treatment), we used the ALL protocol (pitfalls, baits, litter sifting, hand collection; Agosti and Alonso 2000). All collection methods were the same in the BRF-FOFE as in the HF-HeRE except baits included equal volumes (~1 cm^3) of both oil-packed tuna (Bumble Bee Chunk Light; Bumble Bee Foods, Toronto, Ontario, Canada) and crumbled Pecan Sandies set out in 55 mm long × 15 mm diameter white plastic vials for one hour. Furthermore, pitfalls were placed every 6.5 m along a 75-m transect going through the center of each plot for a total of 10 pitfalls per plot. Three 3-L litter samples were collected from random locations in each plot, but outside of the pitfall and bait sampled transect, and sifted in the field. Post-treatment ant data were made by hand collections from nests for 1 person-hour followed by litter sifting (three 3-L litter samples collected from random locations within the plot) in 2009, 2011, and 2015. Rarefaction analyses of pre-treatment data comparing baits, pitfalls, litter samples, and hand-collecting showed that a combination of hand and litter collections accumulated species more quickly and were sufficient for characterizing diversity (Ellison et al. 2007). Hand-sampling within the deer exclosures was done for 10 person-minutes (time spent sampling within the 200-m^2 exclosures was downscaled from the time spent sampling the rest of the 5625-m^2 plots). Specimens were placed directly into 95% EtOH in the field and subsequently identified at Harvard Forest.

Statistical framework

Here, we describe the basic statistical framework for the two experiments, which forms the basis for permutational multivariate analyses of covariance (PERMANCOVAs) of taxonomic diversity and analyses of covariances (ANCOVAs) as implemented with generalized linear mixed models (GLMMs) of univariate taxonomic and functional diversity. Our goals were to test our three hypotheses related to ant taxonomic and functional diversity: (1) Hemlock is a foundation species whose loss will alter the structure of ant assemblages, (2) oak is a dominant species whose loss will not alter structure of ant assemblages, and (3) when a foundation species is present, its loss will have greater canopy-level impacts on ant assemblages than the loss of understory vegetation by large herbivores. Thus, because *T. canadensis* is a known foundation species, we expected that intact hemlock stands would differ in ant assemblage composition relative to hardwood control, girdled, or logged plots in the HF-HeRE and that deer or moose browsing would have a smaller impact on ant assemblages in intact hemlock stands. In contrast, because *Quercus* spp. are thought not to be foundation species in eastern forests, we expected that in the BRF-FOFE, ant assemblage composition would be similar in stands where oak is present or absent and that deer exclosures would have a stronger effect on ant assemblages than tree canopy manipulations. In both experiments, we anticipated that exclosure effects on ant assemblages would be strongest in plots with canopy disturbance (i.e., logging or girdling) because these disturbances should have led to increased abundance of seedlings and saplings ideal for browse.

Both HF-HeRE and BRF-FOFE are split-plot experiments in which ungulate exclosures are situated within each canopy-manipulation plot. In both experiments, the replicate plots are within blocks (i.e., ridge and valley blocks in the HF-HeRE; low, mid, and upper slope blocks in the BRF-FOFE) sampled through time (covariate).

We therefore used univariate ANCOVAs implemented as GLMMs or PERMANCOVAs to test for effects of canopy treatment, ungulate exclosure, and time on taxonomic and functional diversity (Ellison et al. 2010). For pre-treatment analyses of both HF-HeRE (2003–2005) and BRF-FOFE (2006), block was considered a random effect in the model and canopy treatment was considered a fixed effect. Since large herbivore exclosures in the HF-HeRE were installed in 2012, seven years after the canopy manipulations and three years after the adelgid infested the plots, two post-treatment analyses were done for post-treatment HF-HeRE data. The first analysis included all ant data collected outside the exclosures from 2005 to 2015 with block entering as a random effect, canopy treatment as a fixed effect, a dummy variable for pre (2005–2009)- vs. post-adelgid infestation (2010–2015), and year as a covariate; a canopy treatment × year interaction was used to test for lagged effects of the canopy treatments. We also analyzed the ant data from both within and outside of the exclosures only from 2012 to 2015 (when exclosures were present) using a similar model plus a fixed effect of ungulate exclosure. In contrast, all post-treatment data from BRF-FOFE (2009, 2011, and 2015) were analyzed in a single model because the exclosures were installed concurrently with the canopy manipulations. In the BRF-FOFE models, block entered as a random effect, canopy treatment as a fixed effect, ungulate exclosure as a fixed effect, and year as a covariate; a canopy treatment × year interaction was used to test for lagged effects of the canopy treatments.

Assessing taxonomic composition in ant assemblages over time

Estimates from pitfall traps, litter samples, or baits may overestimate abundance of ants if they happen to occur nearby colonies with actively foraging workers, so we conservatively estimated abundance based on incidences of species from baits, litter samples, or pitfall traps (Gotelli et al. 2011). We believe this is a reasonable approach for three reasons. First, incidence data are well correlated with worker abundance in our region (Ellison 2012). Second, what little actual, published, quantified foraging data we have suggests that the average foraging distances of virtually all our species is <2 m. Certainly, some individuals, especially of large-bodied *Camponotus* and *Formica*, will range further afield. However, field data from North Carolina ant warming chambers substantiate the <2 m claim (Stuble et al. 2013). Third, we have used these data as incidences repeatedly in the past (Sackett et al. 2011). Each hand-collected sample was from a separate nest, and so each was treated as an incidence when estimating abundance. Estimating relative abundances based on incidences enabled the integration of data collected from pitfall traps, litter samples, baits, and hand collections. We plotted species accumulation curves and used rarefaction analyses to assess sampling efficacy across canopy treatments.

We assessed univariate taxonomic composition with estimates of Hill numbers of Shannon diversity (^{1}q) over time (Jost 2007) using GLMMs. We assessed multivariate taxonomic composition for both experiments with PERMANOVA and PERMANCOVA, respectively, to assess variation in ant assemblages prior to manipulation (i.e., pre-treatment) and over time among treatments (i.e., post-treatment). Prior to running multivariate analyses, data were screened for multivariate outliers and to check for non-significant multivariate dispersion of factors using the betadisper function of the R vegan package (Oksanen et al. 2016). The response variable was the Bray-Curtis distance matrix of pairwise distances between species' relative frequencies based on incidences. Estimates of F-statistics were calculated based on 9999 permutations using the PERMANOVA+ package of PRIMER 7.0.13 (Anderson 2001, Clarke and Gorley 2015). For both experiments, pairwise comparisons were used to compare differences between treatments. The GLMMs, PERMANOVAs, and PERMANCOVAs all followed the statistical framework described in *Statistical framework*.

Assessing changes in functional diversity over time

To assess changes in functional diversity over time in ant assemblages, we analyzed functional alpha and beta diversity based on a species × trait matrix that included 12 continuous, binary, and categorical traits. These traits reflect major ant-mediated ecosystem processes: soil movement, decomposition, seed dispersal, and regulation of invertebrate and plant community structure (Del Toro et al. 2015). We used trait definitions and data from Del Toro et al. (2015) and filled in missing data with information from Ellison et al. (2012), AntWeb (http://www.antweb.org), and AntWiki (http://www.antwiki.org). Trait data posted on the Harvard Forest Data Archive indicate the source of trait information for each species.

We calculated a species × species distance matrix from the species × trait matrix using the Gower coefficient (Gower 1971), which can accommodate the trait data we compiled (i.e., ordinal, nominal, and binary data with some missing entries). Two undescribed species (*Leptothorax* sp. and *Myrmica* sp. with species codes AF-can and AF-smi, respectively, in Ellison et al. 2012) that each comprised <0.4% of incidences in each dataset were not included in the analysis as data on their traits were unavailable. Using this distance matrix, we calculated two commonly used measures of functional diversity (Swenson 2014): the abundance-weighted mean pairwise distance (D_{pw}) and abundance-weighted nearest-neighbor distance (D_{nn}). We calculated both alpha (αD_{pw} and αD_{nn}) and beta (βD_{pw} and βD_{nn}) versions of these functional diversity metrics. αD_{pw} and αD_{nn} were calculated using the mpd and mntd functions, respectively, and βD_{pw} and βD_{nn} were calculated with the comdist and comdistnt functions, respectively, from the picante package version 1.6-2 in R version 3.3.3 (Kembel et al. 2010).

To remove the influence of species richness and composition on our functional diversity metrics, we used null models to calculate standardized effect sizes (SES) for each metric (Swenson 2014; Appendix S1). We constructed our null model by shuffling the species names in the species × trait matrix, calculating a distance matrix from the shuffled trait matrix, and then re-calculating the functional diversity metric. We did this randomization 999 times for each metric and then calculated the SES for each metric. Large SES values (>|2|) indicated greater (>2) or less (<−2) functional diversity than expected by chance alone.

For functional beta diversity, we were specifically interested in functional change within each treatment plot through time relative to the pre-treatment condition. Thus, we examined further those pairwise βD_{pw}, βD_{nn}, SES βD_{pw}, and SES βD_{nn} values by comparing each post-treatment sample to the pre-treatment sample. We expect the loss of hemlock (i.e., girdled and logged treatments) to drive changes in functional composition from the pre-treatment assemblages and the control treatment to show relatively less change in functional composition.

Differences among canopy and ungulate exclosure treatments in αD_{pw}, αD_{nn}, SES αD_{pw}, SES αD_{nn}, βD_{pw}, βD_{nn}, SES βD_{pw}, and SES βD_{nn} values were tested using ANCOVAs implemented as GLMMs in which the predictor variables and number of tests for each experiment matched the models outlined in *Statistical framework* above. Given the number of significance tests performed in this study, a Holm correction (Holm 1979) to control for Type I error was performed on all test statistics generated in the analyses with the p.adjust function of the stats package in R version 3.3.3 (R Core Team 2017).

Data and specimen availability

All ant species composition and abundance data, ant-trait data, and R code used for the analyses are available from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data-archive) and datasets HF-118 (HF-HeRE; Ellison 2009) and HF-097 (BRF-FOFE; Ellison and Gotelli 2007). Nomenclature follows Bolton (2016); voucher specimens are stored at the Harvard Forest and at the Museum of Comparative Zoology (MCZ).

RESULTS

At HF-HeRE, we accumulated 47 ant species (2941 incidence records) from 2003 to 2015, but species accumulation did not reach an asymptote (Appendix S2: Fig. S1a). In contrast, we accumulated 48 ant species (1882 incidence records) at BRF-FOFE from 2006 to 2015 and the species accumulation curve reached an asymptote in 2015 (Appendix S2: Fig. S1b). Rarefaction curves for both sites indicated sufficient sampling coverage for estimation of relevant diversity indices (Appendix S2: Fig. S2).

Compositional and functional changes in ant assemblages over time

The Harvard Forest Hemlock Removal Experiment.—Prior to canopy manipulations at HF-HeRE, there were significant differences between plots for Shannon diversity (^{1}q) of ants (ANCOVA

GLMM $F_{3,11} = 15$, $P = 0.04$): All plots dominated by hemlock (i.e., hemlock control and girdled plots) had lower ant diversity than hardwood control plots (Appendix S2: Table S1). Following canopy manipulations, there were significant differences in Shannon diversity among canopy treatments (ANCOVA GLMM $F_{3,78} = 91$, $P < 0.001$) and pairwise comparisons of all canopy treatments were significantly different from one another, with the exception of the comparison between hardwood control and logged treatments (Appendix S2: Table S2). Shannon diversity was highest for the logged treatment, intermediate for the girdled and hardwood treatments, and lowest for the hemlock control treatment (Fig. 1a). There was also a significant canopy treatment × year interaction (ANCOVA GLMM $F_{3,78} = 20$, $P = 0.006$), but effects of the adelgid infestation (ANCOVA GLMM $F_{1,78} = 0.32$, $P = 1.0$) and year were not significant (ANCOVA GLMM $F_{1,78} = 0.85$, $P = 1.0$).

For multivariate measures of species composition, there were no pre-treatment differences among hemlock-dominated plots (PERMANOVA $F_{3,8} = 0.92$, $P = 1.0$). Post-canopy-manipulation effects on multivariate measures of taxonomic composition were significant for canopy treatment (PERMANCOVA $F_{3,42} = 6.9$, $P = 4.8 \times 10^{-3}$; Fig. 2a) and block (PERMANCOVA $F_{1,42} = 5.5$, $P = 7.0 \times 10^{-3}$), but not year (PERMANCOVA $F_{10,42} = 1.6$, $P = 0.17$), infestation (PERMANCOVA $F_{1,42} = 0.79$, $P = 0.69$) or a year × treatment interaction (PERMANCOVA $F_{30,42} = 0.92$, $P = 1.0$). All pairwise comparisons for the PERMANCOVA between canopy treatments indicated significant differences ($P < 0.05$) in the composition of ant assemblages (Appendix S2: Table S3). The genus *Aphaenogaster* had the highest relative abundances in all canopy treatments (Fig. 3a–d), and this genus was most abundant in the hemlock controls. *Camponotus* also had high relative abundances in all canopy treatments except the hardwood controls. The girdled and logged plots showed greater evenness, especially relative to the *Aphaenogaster*-dominated hemlock controls.

Prior to canopy manipulations at HF-HeRE, there were significant differences between plots for some measures of functional alpha diversity of ants (αD_{pw} ANCOVA GLMM $F_{3,11} = 3.96$,

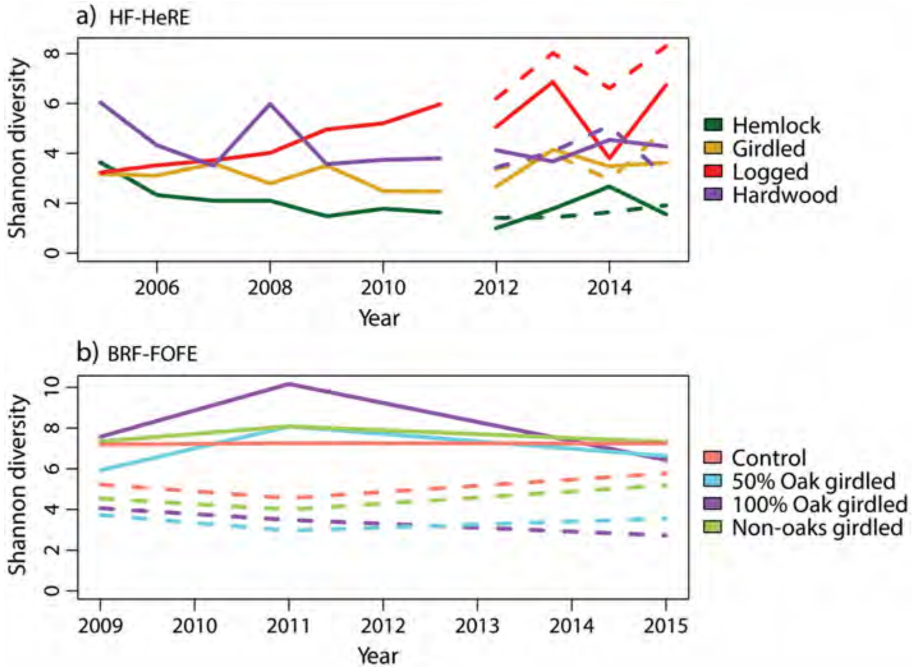

Fig. 1. Shannon diversity (^1q) of ants over time at (a) the Harvard Forest Hemlock Removal Experiment (HF-HeRE) and (b) the Black Rock Forest Future of Oak Forests Experiment (BRF-FOFE). Solid and dashed lines denote diversity values for assemblages outside and inside of large herbivore exclosures, respectively.

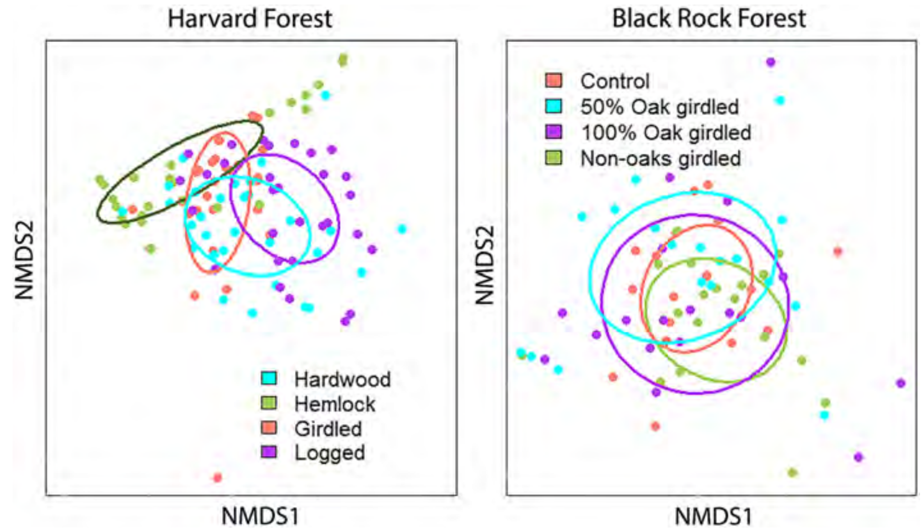

Fig. 2. Non-metric multidimensional scaling (NMDS) ordination plot illustrating differences among sampling plots plotted in species space by canopy treatment at (a) Harvard Forest Hemlock Removal Experiment (HF-HeRE) and (b) Black Rock Future of Oak Forests Experiment (BRF-FOFE). When fitting the NMDS ordinations, scree plots were examined to determine the optimal number of dimensions based on the minimum number of dimensions that resulted in <10.0% stress. Although only the first two axes ($k = 2$) of the NMDS ordinations are shown here, HF-HeRE NMDS was generated with $k = 4$ (linear fit $r^2 = 0.953$; non-metric fit $r^2 = 0.992$) and the BRF-FOFE NMDS with $k = 5$ (linear fit $r^2 = 0.919$; non-metric fit $r^2 = 0.988$). Ovals represent standard deviations of the weighted average of NMDS scores for each treatment.

$P = 0.04$; SES αD_{nn} ANCOVA GLMM $F_{3,11} = 4.48$, $P = 0.03$). Functional alpha diversity of ants in hardwood plots was significantly different than all other pre-treatment plots except for the logged plot according to αD_{pw} (Appendix S2: Table S4). However, some measures of functional alpha diversity did not indicate significant differences between canopy treatments of ants pre-treatment (SES αD_{pw} ANCOVA GLMM $F_{3,11} = 0.02$, $P = 1.0$; αD_{nn} ANCOVA GLMM $F_{3,11} = 0.50$, $P = 1.0$). Following canopy manipulations, there were significant differences in functional alpha diversity among canopy treatments (Fig. 4a–d; SES αD_{pw} ANCOVA GLMM $F_{3,78} = 91$, $P < 0.01$; αD_{pw} ANCOVA GLMM $F_{3,78} = 38$, $P < 0.0001$; SES αD_{nn} ANCOVA GLMM $F_{3,78} = 7.8$, $P < 0.0001$; αD_{nn} ANCOVA GLMM $F_{3,78} = 3.6$, $P = 0.02$). Pairwise comparisons showed hemlock controls were significantly different from all other canopy treatments for both SES αD_{pw} and αD_{pw}, but not for SES αD_{nn} and αD_{nn} (Fig. 4; Appendix S2: Tables S5, S6). There was also a significant canopy treatment × year interaction for αD_{pw} (αD_{pw} ANCOVA GLMM $F_{3,78} = 6.7$, $P < 0.001$), but not for any other measure of functional alpha diversity (αD_{nn} $F_{3,78} = 0.07$, $P = 1.0$; SES αD_{pw} $F_{3,78} = 2.6$, $P = 1.0$; SES αD_{nn} $F_{3,78} = 2.2$, $P = 1.0$). Effects of the adelgid infestation (αD_{pw} $F_{1,78} = 0.12$, $P = 1.0$; αD_{nn} $F_{1,78} = 0.40$, $P = 1.0$; SES αD_{pw} $F_{1,78} = 0.43$, $P = 1.0$; SES αD_{nn} $F_{1,78} = 0.15$, $P = 1.0$) and year were not significant for all measures of alpha diversity (αD_{pw} $F_{1,78} = 2 \times 10^{-4}$, $P = 1.0$; αD_{nn} $F_{1,78} = 0.21$, $P = 1.0$; SES αD_{pw} $F_{1,78} = 1.7$, $P = 1.0$; SES αD_{nn} $F_{1,78} = 0.94$, $P = 1.0$). The majority of standardized measures (SES αD_{nn}, SES$\alpha\beta D_{\mathrm{pw}}$) for pre-treatment and post-treatment plots were <|2|, indicating that functional turnover was no different from expectation associated with taxonomic turnover.

For functional beta diversity, there were significant canopy treatment effects for all measures (i.e., the abundance-weighted mean pairwise distance βD_{pw}, the nearest-neighbor distance βD_{nn}, and their standardized counterparts SES βD_{pw} and SES βD_{nn} ANCOVA; GLMM $P < 0.05$; Appendix S2: Tables S7, S8). The majority of standardized measures (SES βD_{nn}, SES βD_{pw}) for pre-treatment and post-treatment plots were <|2|,

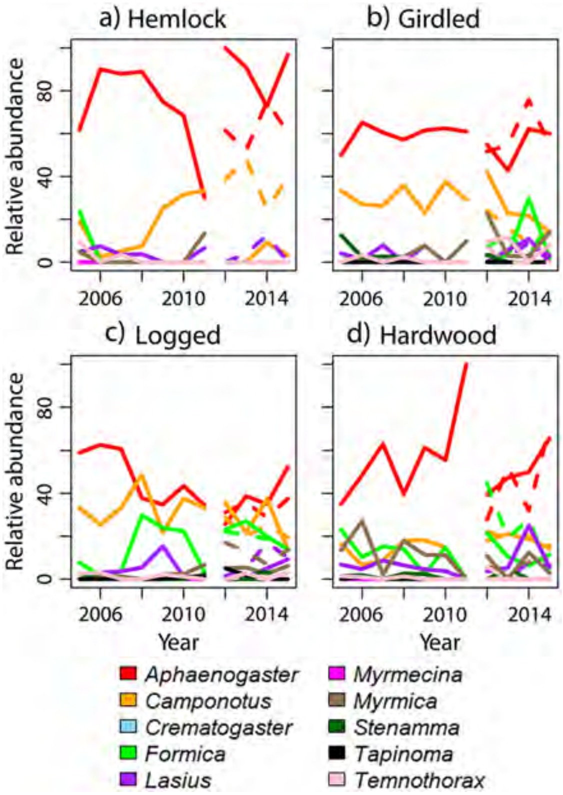

Fig. 3. Relative abundances over time for the top ten most abundant genera in the Harvard Forest Hemlock Removal Experiment. Panels (a–d) represent the hemlock control, hemlock girdled, pre-emptive salvage logged, and hardwood control treatments, respectively. Solid and dashed lines represent ants outside and inside of large herbivore exclosures, respectively.

indicating that functional turnover was no different from expectation associated with taxonomic turnover. Based on SES βD_{pw} and βD_{pw}, the ant assemblage in the hemlock control treatment was functionally more similar to its pre-treatment assemblage than the logged or hardwood treatments were to their pre-treatment assemblages (Appendix S2: Fig. S3a, b). Furthermore, the βD_{pw} measure showed that the hemlock control treatment was functionally more similar to its pre-treatment assemblage than the girdled treatment (Appendix S2: Fig. S3b). However, the nearest-neighbor measures SES βD_{nn} and βD_{nn} indicated that the ant assemblage in the hemlock control treatment was either more functionally different or not functionally different to its pre-treatment assemblage than the other treatments were to their pre-treatment assemblages (Appendix S2: Fig. S3c–d).

There were no effects of herbivore exclosures at HF-HeRE for any taxonomic (Fig. 2a; Appendix S2: Fig. S4a) or functional measures (Fig. 5; Appendix S2: Fig. S5a–d) of diversity (Shannon diversity: ANCOVA GLMM $F_{4,35} = 4.0$, $P = 1.0$; multivariate taxonomic diversity: PERMANCOVA $F_{1,46} = 1.2$, $P = 1.0$; αD_{pw}: $F_{4,35} = 0.17$, $P = 1.0$; αD_{nn}: $F_{4,35} = 0.81$, $P = 1.0$; SES αD_{pw}: $F_{4,35} = 0.60$, $P = 1.0$; SES αD_{nn}: $F_{4,35} = 0.40$, $P = 1.0$; βD_{pw}: $F_{4,35} = 6.2$, $P = 1.0$; βD_{nn}: $F_{4,35} = 5.3$, $P = 1.0$; SES βD_{pw}: $F_{4,35} = 1.4$, $P = 1.0$; SES βD_{nn}: $F_{4,35} = 0.77$, $P = 1.0$).

The Black Rock Forest Future of Oak Forests Experiment.—Prior to canopy manipulations, there were no significant differences in Shannon diversity between plots in the BRF-FOFE (ANCOVA GLMM $F_{3,18} = 0.14$, $P = 1.0$). After canopy manipulations and the erection of exclosures, there were significant effects of herbivore exclosures on Shannon diversity (ANCOVA GLMM $F_{4,58} = 89$, $P < 0.0001$) with ant assemblages within exclosures having lower Shannon diversity for all canopy treatments (Fig. 2b). Shannon diversity was not influenced by canopy treatment itself (ANCOVA GLMM $F_{3,58} = 5.1$, $P = 1.0$), by year (ANCOVA GLMM $F_{1,58} = 0.17$, $P = 1.0$), or by the canopy treatment × year interaction (ANCOVA GLMM $F_{3,58} = 3.3$, $P = 1.0$).

Prior to canopy manipulations at BRF-FOFE, there were no significant differences in multivariate measures of ant composition across plots that were allotted to the canopy manipulations (PERMANOVA $F_{3,18} = 0.29$, $P = 1.0$). Following the canopy manipulations and erection of exclosures, multivariate measures of taxonomic diversity were significantly influenced by herbivore exclosures (PERMANCOVA $F_{4,54} = 1.5 \times 10^{-3}$, $P = 0.04$; Appendix S2: Fig. S4b). Exclosures had a significant effect on multivariate measures of ant assemblage composition in the non-oak girdled and 100% oak girdled plots, but not in the oak control or 50% oak girdled plots (Appendix S2: Table S9). Effects of canopy treatment (PERMANCOVA $F_{3,54} = 1.8$, $P = 0.28$; Fig. 2b), year (PERMANCOVA $F_{2,54} = 2.0$, $P = 0.29$), and canopy treatment × year (PERMANCOVA $F_{6,54} = 2.0$, $P = 1.0$) did not influence ant multivariate composition measures. Genera were evenly distributed in all BRF-FOFE

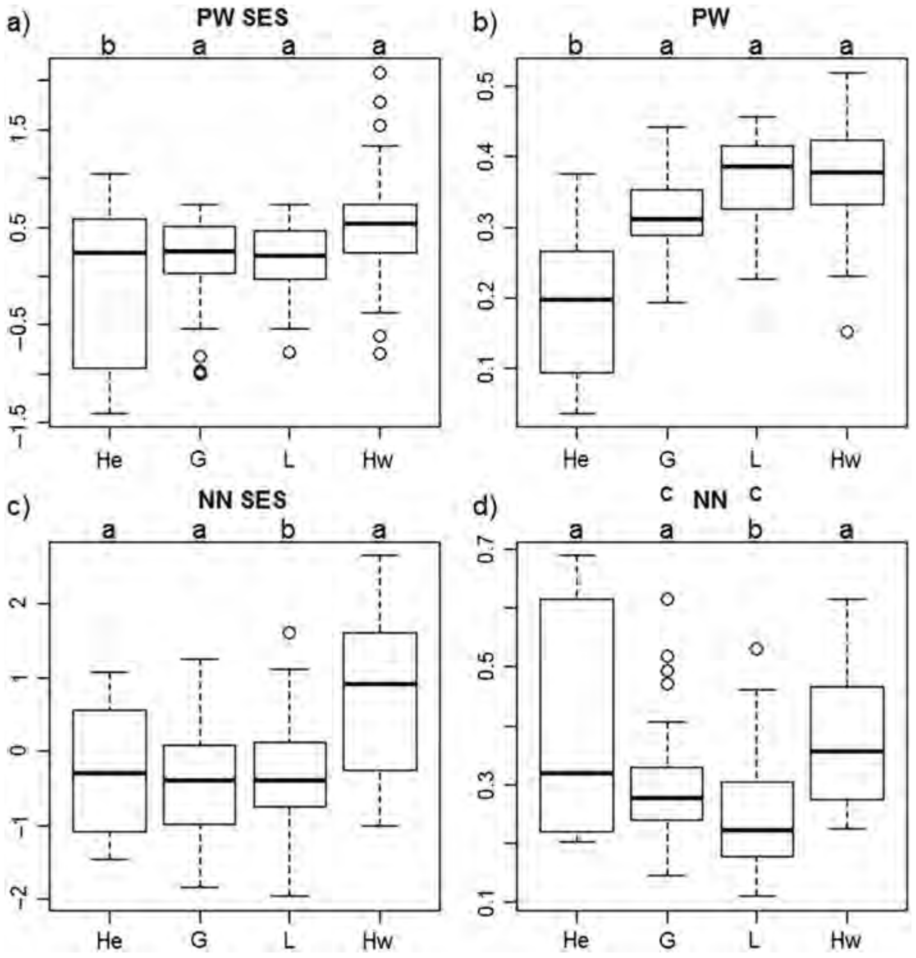

Fig. 4. Boxplots illustrating differences between canopy treatments at the Harvard Forest Hemlock Removal Experiment (HF-HeRE) in terms of functional alpha diversity (i.e., the abundance-weighted mean pairwise distance based on standardized effect size [SES αD_{pw}; a] and raw [αD_{pw}; b] estimates and the abundance-weighted nearest-neighbor distance based on SES [SES αD_{nn}; c] and raw [αD_{nn}; d] estimates). Letters above the boxplots indicate significant differences ($P < 0.05$) for post hoc pairwise comparisons between canopy treatments. Canopy treatments are labeled on the *x*-axis as follows for HF-HeRE (a–d): hemlock control (He), girdled (G), logged (L), and hardwood (Hw).

canopy treatments. *Aphaenogaster*, *Brachymyrmex*, and *Lasius* were dominant in all canopy treatments outside of herbivore exclosures, but *Lasius* was less dominant within exclosures (Figs. 6, 7).

Prior to canopy manipulations, there were no significant differences in functional alpha diversity between plots in the BRF-FOFE (ANCOVA GLMMs αD_{pw} $F_{3,18} = 0.02$, $P = 1.0$; SES αD_{pw} $F_{3,18} = 0.05$, $P = 1.0$; SES αD_{nn} $F_{3,18} = 1.2$, $P = 1.0$; αD_{nn} $F_{3,18} = 1.8$, $P = 1.0$). After canopy manipulations and the erection of exclosures, there were no significant effects of herbivore exclosures on functional alpha diversity according to SES measures (Fig. 8a, c; ANCOVA GLMM SES αD_{pw}: $F_{4,58} = 2.6$, $P = 0.1$; SES αD_{nn}: $F_{4,58} = 0.26$, $P = 1.0$), but there were significant differences according to raw measures (Fig. 8b, d; ANCOVA GLMM αD_{pw} $F_{4,58} = 6.2$, $P < 0.001$; αD_{nn} $F_{4,58} = 8.0$, $P < 0.0001$). Functional alpha diversity was not influenced by canopy treatment itself (Fig. 9; ANCOVA GLMMs αD_{pw} $F_{3,58} = 1.4$, $P = 1.0$; SES αD_{pw} $F_{3,58} = 0.18$, $P = 1.0$; SES αD_{nn} $F_{3,58} = 0.08$, $P = 1.0$; αD_{nn} $F_{3,58} = 1.8$, $P = 1.0$), by year (ANCOVA GLMMs

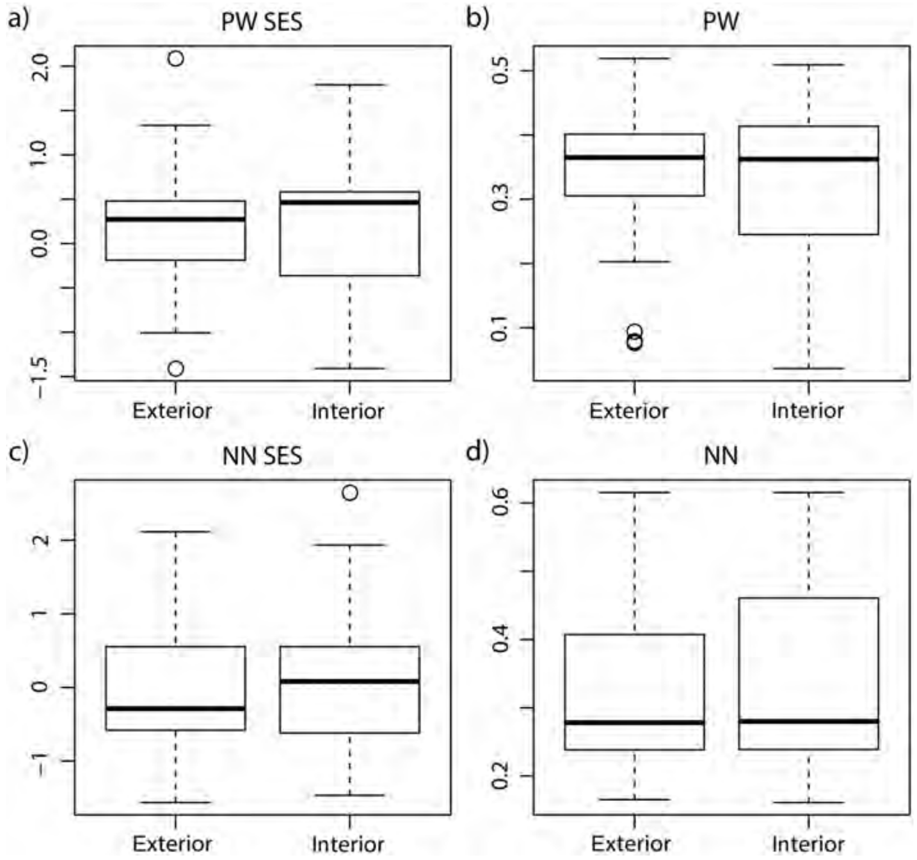

Fig. 5. Boxplots illustrating differences between exclosure treatments at the Harvard Forest Hemlock Removal Experiment in terms of functional alpha diversity (i.e., the abundance-weighted mean pairwise distance based on standardized effect size [SES αD_{pw}; a] and raw [αD_{pw}; b] estimates and the abundance-weighted nearest-neighbor distance based on SES [SES αD_{nn}; c] and raw [αD_{nn}; d] estimates). Asterisks on the x-axis label indicate significant effects of exclosure treatments.

αD_{pw} $F_{1,58} = 0.62$, $P = 1.0$; SES αD_{pw} $F_{1,58} = 0.39$, $P = 1.0$; SES αD_{nn} $F_{1,58} = 0.59$, $P = 1.0$; αD_{nn} $F_{1,58} = 0.57$, $P = 1.0$), or by the canopy treatment × year interaction (ANCOVA GLMMs αD_{pw} $F_{3,58} = 0.40$, $P = 1.0$; SES αD_{pw} $F_{3,58} = 0.53$, $P = 1.0$; SES αD_{nn} $F_{3,58} = 0.50$, $P = 1.0$; αD_{nn} $F_{3,58} = 0.64$, $P = 1.0$).

The functional beta diversity of ant assemblages in the pre- and post-treatment plots within each canopy treatment did not differ across treatments regardless of the measure used (Appendix S2: Fig. S5e–h). Furthermore, there were no significant effects of year or its interaction with canopy treatment (ANCOVA GLMMs $P > 0.05$). Ant assemblages outside the herbivore exclosures were functionally more like their pre-exclosure assemblages than those within the exclosure were to their pre-exclosure assemblages (ANCOVA GLMM D_{nn} $F_{1,58} = 50$, $P < 0.0001$; Appendix S2: Fig. S5h). However, all other functional beta diversity measures indicated no significant effects of the exclosure treatment (ANCOVA GLMMs $P > 0.05$; Appendix S2: Fig. S5e–g). For both functional alpha and beta diversity at BRF-FOFE, the majority of standardized measures (SES αD_{nn}, SES$\alpha\beta D_{pw}$) for pre-treatment and post-treatment plots were $<|2|$, indicating that functional turnover was no different from expectation associated with taxonomic turnover.

DISCUSSION

Foundation species, by definition, are unique in terms of the processes that they control (Ellison

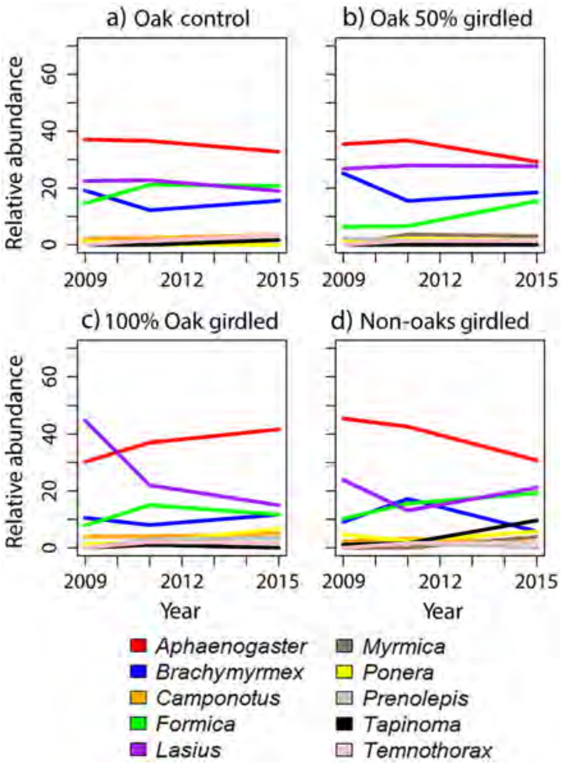

Fig. 6. Relative abundances over time for the top ten most abundant genera in the Black Rock Forest Future of Oak Forests Experiment outside of the herbivore exclosures. Panels (a–d) represent the oak control, 50% oak girdled, 100% oak girdled, and non-oaks girdled treatments, respectively.

et al. 2005*b*), and it is important to distinguish them from replaceable dominant species and from other factors determining ecosystem structure and function (Baiser et al. 2013). The results reported here are the first that can be used to reveal differing effects of dominant and foundational tree species on the taxonomic and functional diversity of an associated assemblage: that of ants. Simultaneously, the large herbivore exclosure treatments in both experiments enable us to begin to disentangle effects of foundation species from other important drivers of biodiversity in temperate forests.

Hypothesis I

Previous work using four years of post-treatment data from HF-HeRE showed that the loss of *Tsuga canadensis* had a large and significant impact on ant assemblages (Sackett et al. 2011). Here, we used an additional six years of data to test the prediction that intact hemlock stands would differ in ant assemblage composition relative to hardwood control, girdled, or logged plots at HF-HeRE due to the effects of *T. canadensis*, the foundation species in this forest. Our findings for taxonomic diversity were in line with this prediction: We found significant differences in taxonomic diversity in hemlock control plots relative to all the canopy manipulations for both univariate Shannon diversity (^1q) and multivariate taxonomic composition (Figs. 1a, 2a). Hemlock control plots had lower Shannon diversity than all other treatments, primarily because of the dominance of *Aphaenogaster* species. Like previous research on ants within HF-HeRE (Sackett et al. 2011, Kendrick et al. 2015), we found that hemlock control plots were largely dominated by *Aphaenogaster picea* and *Aphaenogaster fulva*, but lacked the *Formica* spp. that eventually colonized

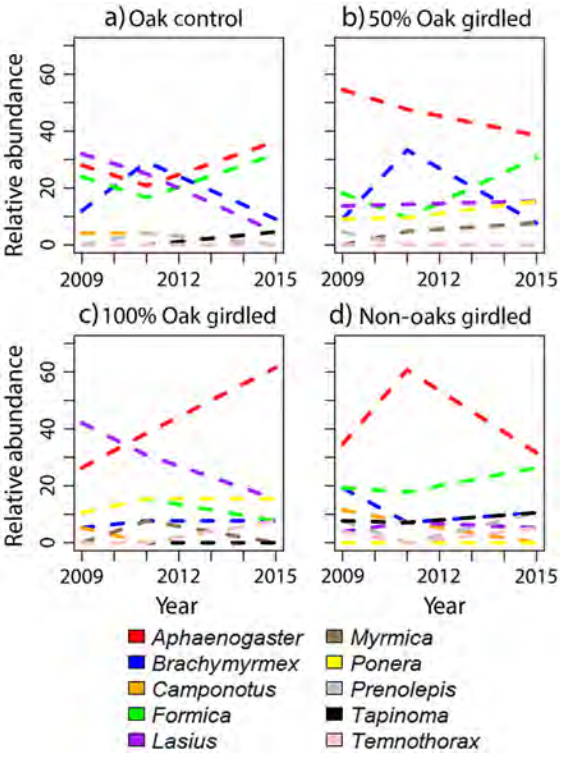

Fig. 7. Relative abundances over time for the top ten most abundant genera in the Black Rock Forest Future of Oak Forests Experiment within the herbivore exclosures. Panels (a–d) represent the oak control, 50% oak girdled, 100% oak girdled, and non-oaks girdled treatments, respectively.

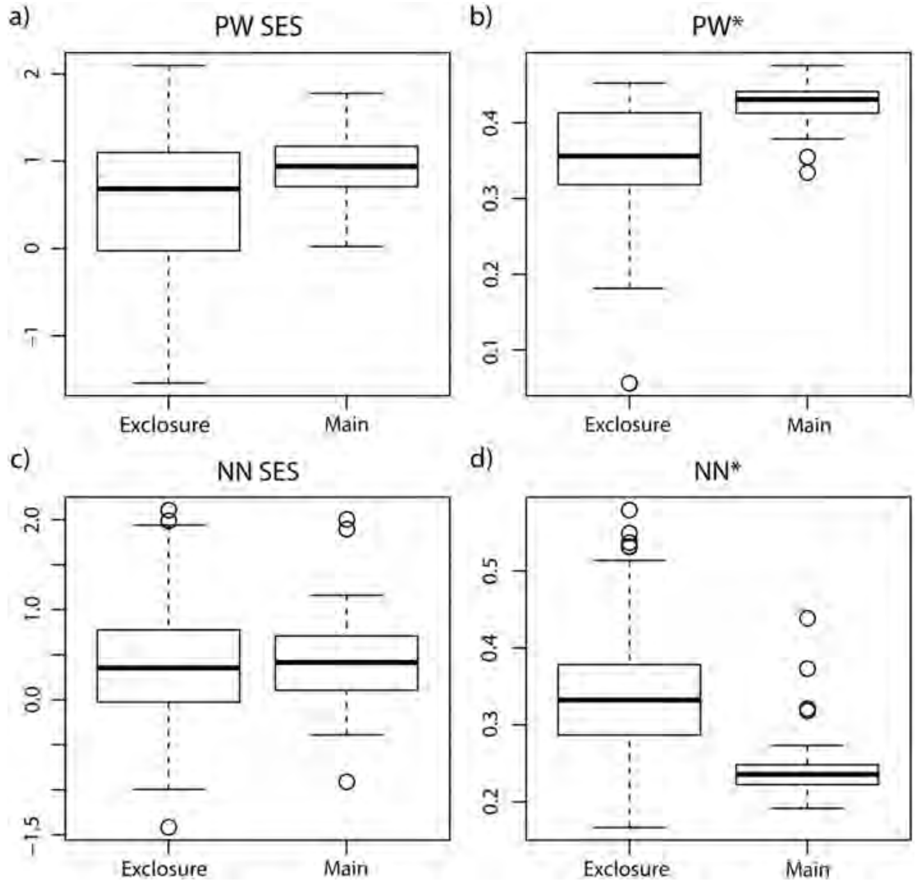

Fig. 8. Boxplots illustrating differences between exclosure treatments at the Black Rock Forest Future of Oak Forests Experiment in terms of functional alpha diversity (i.e., the abundance-weighted mean pairwise distance based on standardized effect size [SES αD_{pw}; a] and raw [αD_{pw}; b] estimates and the abundance-weighted nearest-neighbor distance based on SES [SES αD_{nn}; c] and raw [αD_{nn}; d] estimates). Asterisks on the *x*-axis label indicate significant effects of exclosure treatments.

all the plots in which the canopy was manipulated (Fig. 3). The logged and girdled plots with their greater amounts of coarse woody debris (Orwig et al. 2013) had the greatest number (incidences) of larger-bodied carpenter ants (*Camponotus* spp.). Previous work with ants in declining hemlock stands illustrated the common association in New England *T. canadensis* stands of *Aphaenogaster* spp., *Camponotus pennsylvanicus,* and *Temnothorax longispinosus*, and the lack of *Formica* spp. and rarity of *Lasius* spp. in the same stands (Ellison et al. 2005*a*). The low temperature and insolation within hemlock stands (Lustenhouwer et al. 2012), and their lack of dense understory vegetation (Orwig et al. 2013) that otherwise would provide high habitat complexity and aphids for tending by *Formica* and *Lasius* spp., are key direct and indirect effects of *T. canadensis* on ant species composition in northeast U.S. forests (Ellison et al. 2005*a*).

Our analysis of functional diversity at HF-HeRE provided weaker support for this first hypothesis. Functional alpha diversity as measured by both pairwise metrics followed our hypothesis that the hemlock control treatment would be significantly different than all other treatments, but this was not so for the nearest-neighbor metrics (Fig. 4). For functional beta diversity, ant assemblages in intact hemlock plots were functionally more like their pre-canopy treatment assemblages than were those in the hardwood control and logged plots for pairwise

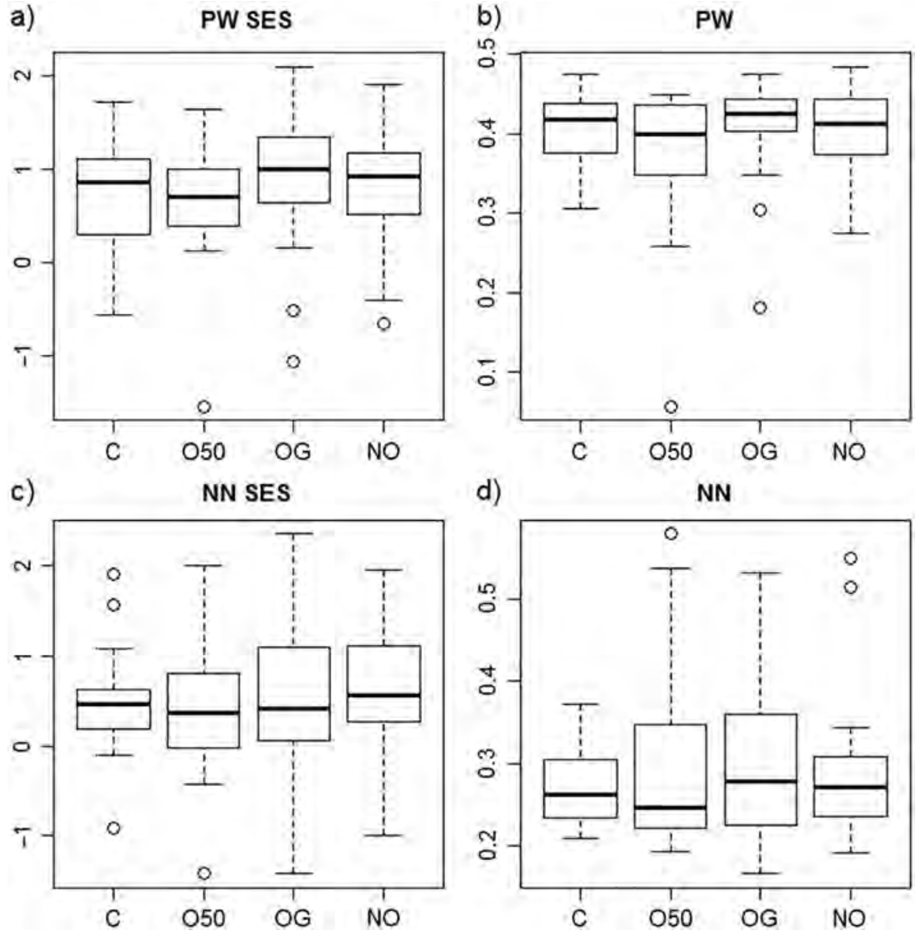

Fig. 9. Boxplots illustrating differences between canopy treatments at the Black Rock Forest Future of Oak Forests Experiment (BRF-FOFE) in terms of functional alpha diversity (i.e., the abundance-weighted mean pairwise distance based on standardized effect size [SES αD_{pw}; a] and raw [αD_{pw}; b] estimates and the abundance-weighted nearest-neighbor distance based on SES [SES αD_{nn}; c] and raw [αD_{nn}; d] estimates). The lack of letters above the boxplots indicates no significant differences ($P < 0.05$) for post hoc pairwise comparisons between canopy treatments. Canopy treatments are labeled on the *x*-axis as follows for BRF-FOFE (a–d): control, no trees girdled (C); 50% oaks girdled (O50); 100% oaks girdled (OG); and non-oaks girdled (NO).

metrics, but not nearest-neighbor metrics (Appendix S2: Fig. S3a–d). Differences between these functional diversity measures are not uncommon (Liu et al. 2016). Rohr et al. (2009) also compared arthropod communities in intact hemlock and hardwood stands within Shenandoah National Park in the mid-Atlantic Appalachian Mountains of the eastern United States and found that arthropod abundance and richness was lower in hemlock than hardwood stands, but that functionally the ant assemblages were similar in the two forest types.

The insurance hypothesis (Yachi and Loreau 1999) predicts that higher biodiversity will maintain ecosystem function in the face of unstable environments because more species are available to fill functional roles when species are lost. In our comparison of foundation and dominant tree species, we found that functionality of ant assemblages with or without the foundation species was in some instances similar depending on the metric calculated, but taxonomic diversity was lower, in the presence of *T. canadensis*. At the local scale (i.e., alpha diversity), functional similarity may change through time for all treatments. Such temporal dynamics may be generated by the regional-scale structure (i.e., beta diversity) provided by hemlock stands interspersed with hardwood stands that creates spatial asynchrony in a metacommunity context (Loreau et al. 2003). This asynchrony across local communities provides neighboring trait pools that can readily disperse across habitat patches leading to stability at a regional spatial scale through a spatial insurance effect (Wang and Loreau 2016).

Hypothesis 2

At BRF-FOFE, our data supported the hypothesis that ant assemblages would be compositionally and functionally similar whether or not oaks were removed because oaks are dominant species, but not foundation species in this forest (Figs. 1b, 2b, 8). Even acorn-nesting *Temnothorax* spp. did not show lower relative abundances in oak-girdled plots relative to other treatments, most likely because they also nest in twigs and other small cavities (Ellison et al. 2012). A study on the effects of different forest management practices of oaks on ant communities in Bavaria found that there were significantly higher numbers of *Temnothorax affinis, Temnothorax corticalis*, and *Dolichoderus quadripunctatus* in stands with coppiced oaks than in stands with intact oaks (Dolek et al. 2009). Furthermore, other species and ecosystem functions may respond differently to oak loss. For example, Bray (2015) suggested that oaks function as a foundation species for mites, collembola, and some arachnids at BRF-FOFE. Levy-Varon et al. (2014) found that soil respiration in 100% oak girdled plots declined much more rapidly than in the control, non-oak girdled, or 50% oak girdled plots; these differences persisted from two weeks to two years post-treatment. One caveat of all studies performed at the BRF-FOFE on foundation species effects is that multiple species of oaks are assumed to have very similar functional roles. Potential loss of specific species of oaks and concomitant increases in other hardwood species could have broader effects on forest dynamics that will depend on newly established species, their interactions with pests and pathogens (Spaulding and Rieske 2011), and functional characteristics (Falxa-Raymond et al. 2012).

Hypothesis 3

We hypothesized that the effect of the foundation species on ant community structure would outweigh the effect of large herbivores, which alter microhabitats by eating understory vegetation. This third hypothesis emphasizes the influence of foundation species that comprise the canopy on ant communities, as opposed to the effects of understory vegetation on ant communities. Our results of taxonomic and functional diversity at HF-HeRE supported this hypothesis: We saw stronger effects of canopy treatments than of large herbivore exclosures on ant assemblages. At BRF-FOFE, large herbivores influenced taxonomic diversity of ant assemblages. Deer and moose indirectly influence ground-dwelling insects by altering habitat structure through soil disturbance and by browsing understory vegetation, both of which may decrease soil moisture and humidity and increase temperature and light (Rooney and Waller 2003, Foster et al. 2014). At BRF-FOFE, Shannon diversity was lower within exclosures, a finding that is opposite to that found in a meta-analysis (Foster et al. 2014). This meta-analysis suggested that herbivory by large mammals generally had a negative effect on Hymenoptera richness and abundance through changes in vegetation quantity and structure. However, other species or genera of insects can be affected positively by ungulate browsing (e.g., taxa that benefit from bare soil exposure resulting from decreased vegetation cover; Stewart 2001). At BRF-FOFE, soil-nesting *Lasius* spp. were more abundant outside of exclosures where grazing pressure was higher. The greater Shannon diversity outside of exclosures can be linked to the higher abundance of *Lasius* spp. outside of the exclosures, as *Lasius* is one of the most species-rich genera at the site.

Large herbivores did not influence functional diversity of ants at BRF-FOFE (except for with the αD_{nn}, αD_{pw}, and βD_{nn} measures), providing mixed support for Hypothesis 3. We expected herbivores to have a greater impact on ant communities through their manipulation of the forest understory when a dominant, but not foundation species (i.e., oak) is lost. The large browsers in New York and Massachusetts are moose and white-tailed deer. At the start of BRF-FOFE, deer densities were nearly twice as high as at Harvard Forest (7.3 vs. 4.2–5.7/km^2), but over the course of the study, increased culling of the deer population at BRF brought deer densities down to levels comparable to those seen in New England (W. S. F. Schuster, *personal communication*). The relatively low densities of herbivores in New England and the fluctuating populations of deer in Black Rock Forest over the course of the study somewhat complicate our ability to disentangle effects of foundation species and effects of browsers on local ant assemblages.

CONCLUSION

In sum, data from two long-term hectare-scale experiments in eastern North America illustrate how ant assemblages reassemble after the loss of a canopy tree species. The loss of a foundation species at HF-HeRE resulted in clear taxonomic, but less clear functional, changes in ant assemblages attributable to effects of the foundation species. The loss of dominant *Quercus* species at BRF-FOFE did not result in significant taxonomic or functional changes in ant assemblages, and large herbivore effects outweighed effects of loss of canopy tree species irrespective of species identity.

There is a possibility that differences in ant assemblages between *Tsuga* and *Quercus* stands are influenced by more general differences between deciduous and coniferous tree stands. However, Southwood (1961) found that differences in taxonomic species richness in insect species co-occurring with different tree genera were not highly correlated, whether trees were evergreen or deciduous. Rather, species richness of co-occurring insects correlated more with geographic location, abundance, and the presence (or absence) of a tree genus over long timescales in an area based on Quaternary records. Thus, the effects of foundation species on co-occurring assemblages of organisms may depend in part on historic differences that lead to species dominance in an area. Determining what historic and biogeographic differences may lead to a species taking on foundational roles over time (Ellison et al. 2014) will further aid in identifying foundation species for conservation.

Our results also illustrate the importance of distinguishing between the roles of irreplaceable foundation species and replaceable dominant species at local vs. regional scales. Future coordinated research efforts across forested ecosystems will provide additional invaluable insights into the role of dominant or foundation species. Indeed, there already are several large-scale forest experiments in place that could provide future insights into foundation vs. dominant species effects on communities and ecosystems at local to regional spatial scales (see Adams et al. 2004 for a list of experimental forests maintained by the U.S. Department of Agriculture Forest Service; and see also Kalb and Mycroft 2013).

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