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Response of macroarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species

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Abstract. In eastern North American forests, eastern hemlock (*Tsuga canadensis*) is a foundation species. As hemlock is lost from forests due to the invasive hemlock woolly adelgid (*Adelges tsugae*) and pre-emptive salvage logging, the structure of assemblages of species associated with hemlock is expected to change. We manipulated hemlock canopy structure at hectare scales to investigate the effects of hemlock death on assemblages of ants, beetles, and spiders in a New England forest. Relative to reference hemlock stands, both in situ death of hemlock and logging and removal of hemlock altered composition and diversity of beetles and spiders, and logging increased the species richness and evenness of ant assemblages. Species composition of ant assemblages in disturbed habitats was non-random relative to the regional species pool, but we found no evidence that interspecific competition shaped the structure of ant, beetle, or spider assemblages, in either manipulated or intact forest stands. Environmental filtering by hemlock appears to maintain low levels of species richness and evenness in forest stands, suggesting that the loss of hemlock due to the hemlock woolly adelgid or human activities will not likely lead to extirpations of ant, beetle, or spider species at local scales.

Key words: *Adelges tsugae*; Araneae; Coleoptera; community assembly; competition; Formicidae; foundation species; invasive species; Massachusetts; nestedness; *Tsuga canadensis*.

Received 26 May 2011; accepted 3 June 2011; **published** 8 July 2011. Corresponding Editor: D. P. C. Peters.
Citation: Sackett, T. E., S. Record, S. Bewick, B. Baiser, N. J. Sanders, and A. M. Ellison. 2011. Response of macroarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species. Ecosphere 2(7):art74. doi:10.1890/ES11-00155.1

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INTRODUCTION

Many ecosystems rely on foundation species that have architectural and functional features that shape communities and modulate ecosystem functions (Dayton 1972, Ellison et al. 2005*a*). In forests, trees are often foundation species; their physical structure, chemistry, and physiology define the environment at scales from sub-millimeter microhabitats to multi-hectare stands. The decline and subsequent loss of any foundation tree species is hypothesized to have strong effects on the organisms and processes that depend upon it, but this hypothesis is challenging to test experimentally because of the long lifespan of foundation tree species and the difficulty of doing stand-level manipulations.

Eastern hemlock (*Tsuga canadensis* (L.) Carrière) is a late-successional, long-lived foundation species in eastern North America (Ellison et al. 2005*a*). The invasive hemlock woolly adelgid (*Adelges tsugae* Annand), which was accidentally introduced to North America in the early 1950s, now ranges from Georgia to central New

England (Fitzpatrick et al. 2010) and causes widespread morbidity and mortality of eastern hemlocks (Orwig et al. 2002). Simultaneously, forest landowners are logging hemlock and realizing economic gain before the adelgid arrives (Orwig et al. 2002, Foster and Orwig 2006). These different types of structural changes to hemlock forests—slow disintegration of boles, coarse woody debris, twigs, and leaves after the trees have died in place versus essentially instantaneous removal of boles and large limbs leaving only small branches, twigs, and leaves atop soil compacted by heavy machinery—should have profound consequences for species dependent on hemlock's different life stages and the environment that it creates.

In this study, we quantified changes in the structure of soil- and litter-dwelling ants, beetles, and spiders in response to two experimental manipulations of structural changes to hemlock stands: slow death and disintegration, and logging. We chose to study these three taxa because of their known utility as indicators of environmental change (e.g., Andersen 1997, Rohr et al. 2007) and their known sensitivity to ecological parameters such as litter structure and depth (Bultman and Uetz 1982, Latty et al. 2006), temperature and moisture (Lessard et al. 2011), and resource supply (Chen and Wise 1999), all of which are affected strongly by the presence or absence of eastern hemlock (e.g., Ellison et al. 2005*a*, 2005*b*, Ford and Vose 2007). The results from this experimental study expand on previous correlative studies of differences in arthropod assemblages among hemlock and hardwood stands (Ellison et al. 2005*b*, Dilling et al. 2007, Rohr et al. 2009) because they allow for stronger inferences regarding the relative importance of three different ecological mechanisms—colonization from the regional species pool, environmental filtering, and interspecific competition—that control the reassembly of arthropod assemblages following loss of hemlock.

Materials and Methods

Experimental design

We manipulated hemlock stand structure in the 121-ha Simes Tract at the Harvard Forest in Petersham, Massachusetts, USA (42.47° to 42.48° N, 72.21° to 72.22° W, 215–300 m a.s.l.). This site lies within the hemlock/hardwood/white pine transition forest region of eastern North America. Stands dominated by hemlock are common in areas that have been intact from the late eighteenth to mid-nineteenth centuries, while hardwood stands dominate in areas that were cleared for agriculture (Foster 1992).

The Harvard Forest Hemlock Removal Experiment (HF-HeRE) includes two canopy-level manipulations that mimic structural changes caused either by the adelgid or by logging, each of which was applied to replicated 90 × 90 m (0.81 ha) forest plots with at least 70% (basal area) hemlock. The complete experimental design is described by Ellison et al. (2010); relevant details are summarized here. In the first treatment, we girdled all hemlocks, from small seedlings to fully mature trees, using knives or chainsaws, as appropriate. The girdled trees died over the course of the next 30 months, about as quickly as they die from adelgid infestations in the southeastern U.S. but more rapidly than they die from adelgid infestations in the northeast (McClure 1991). Since the trees were girdled, the standing dead hemlocks have continued to slowly disintegrate and occasionally topple, resulting in a heterogeneous mixture of tree trunks, large limbs, and small twigs on the forest floor, and structural and environmental (temperature, moisture) changes similar to that from adelgid invasion (Jenkins et al. 1999, Orwig and Foster 1998). In the second treatment, we harvested and removed from the site all hemlocks >20 cm in diameter, along with any merchantable white pine (*Pinus strobus*) and hardwoods (primarily red oak *Quercus rubra*). Both treatments were applied prior to the 2005 growing season: logging between February and April 2005, and girdling in early May 2005.

Plots were identified in 2003 and sampled for two years prior to girdling or logging. Two control plots were established along with each pair of treatment plots—a hemlock control plot in which hemlock accounted for ~70% of the basal area and a hardwood control plot consisting of mixed young (<50 yrs old) hardwoods and small hemlocks. The latter represents the anticipated forest structure following hemlock loss (Orwig and Foster 1998, Ellison et al. 2010). One set of plots of these four treatments (hemlock control, girdled, logged, hardwood control) was estab-

lished in each of two blocks: one on a gently sloping lowland (the "Valley" block) and the other on a north-south ridge (the "Ridge" block). Within each block, the treatments and controls are located within 300 m of each other, have similar topography and aspect, and are on identical soil types. Thus, we are reasonably confident that any differences we observe in arthropod assemblages can be attributed to our manipulations and not to environmental heterogeneity. Finally, we note that when HF-HeRE was established in 2003, the adelgid was not yet present; the treatments were designed to cause changes in forest structure seen in adelgid-infested and logged stands. Additional effects of the adelgid, such as changes in throughfall chemistry caused by run-off of cuticular waxes or honeydew secretions (e.g., Stadler et al. 2006, Templer and McCann 2010) will become apparent only after the adelgid colonizes the hemlock control plots of HF-HeRE (Ellison et al. 2010).

Temporal changes in ant assemblages

In all eight HF-HeRE plots, ants were sampled from 2003–2009 using pitfall traps, baits, sifted litter, and hand collections (the ALL protocol: Agosti and Alonso 2000). Samples were collected in dry weather in June, July, and August (2003–2005); July and August (2006); and in July only (2007–2009). At each sample date, 25 pitfall traps (8-cm diameter, 200-ml cups buried flush with the soil surface and containing 10 ml of soapy water) and 25 baits (50 mg crumbled Pecan Sandies (Keebler Foods, Elmhurst, Illinois) cookies on white index cards) were placed at equally-spaced sample stations within a 10×10-m grid near the center of each plot. Pitfall traps accumulated ants for 48 hrs, baits for 1 hr. Three 3-L litter samples also were collected from random locations within the 90×90-m plot but outside of the pitfall and bait sample grid, and sifted in the field. Hand-collecting was done across the entire plot for 1 person-hour per plot. To avoid confounding individual workers with individual colonies (which possess many workers), thereby inflating estimates of colony abundance, we conservatively estimated abundance as the occurrence (incidence) of each species in a trap or at a bait (Gotelli et al. 2011). Effectiveness of sampling was determined from species accumulation curves and rarefaction plots (Ellison et al. 2007, Gotelli et al. 2011). All ants were identified to species, and voucher specimens were deposited at Harvard's Museum of Comparative Zoology (MCZ) and at the Harvard Forest.

We measured changes in taxonomic and functional similarity (Bray-Curtis index) over time in ant assemblages within each plot relative to the 2003 sample from the same plot. Taxonomic similarity was based on species-level changes. For functional similarity, we first characterized each species using four traits (Appendix: Table A1, data from Coovert 2005, Ellison et al. 2012): total body length (mean, standard deviation); habitat (forest edge, open, forest interior, wet, dry); nest location (under rocks or logs, in litter or soil, or arboreal); and behavior (slavemaker, temporary social parasite, Hemiptera tender/honeydew feeder, seed disperser, predator). These continuous or discrete traits were combined in a trait matrix (Baiser and Lockwood 2011) from which distance (similarity) measures were calculated. Because samples were not correlated across years (autocorrelation plots not shown), plot-level changes in Bray-Curtis similarity (arcsine square-root transformed) from 2003–2009 were tested among treatments using analysis of covariance (ANCOVA; function lm in R version 2.10.0; R Development Core Team 2009) in which block entered as a random effect, treatment as a fixed main effect, and year as a covariate. The treatment $\times$ year interaction was of central interest as it tested whether or not different treatments altered the rate of change of an assemblage's taxonomic or functional similarity.

Spatial variation in assemblages of ants, beetles, and spiders

We assessed post-disturbance, fine-scale spatial variation in assemblages of ants, beetles, and spiders in 2008, three years after the HF-HeRE canopy manipulations. In May, July, and September 2008, we randomly selected five 1-m^2 sub-plots (separated by at least 10 m) within each canopy manipulation plot, sifted all the leaf litter from the sub-plot into Winkler extractors (Krell et al. 2005), and recovered ants, beetles, and spiders over a 10-day period. We also deployed five pitfall traps 3–5 m away from each sub-plot for 10 days. Because spiders and beetles require

more sampling days for adequate species accumulation (Baars 1979; T. Sackett, *personal observation*), these pitfalls remained open longer than those used for our annual ant samples, and were charged with propylene glycol, which does not bloat the spiders. Ellison, Record, and Bewick identified the ant species, and Sackett identified the spider species and assigned beetles to morphospecies within families. Voucher specimens are deposited at the Harvard Forest.

Spatial variation in arthropod assemblages *within* plots was assessed with rarefaction curves and Hurlbert's probability of interspecific encounter (PIE; Hurlbert 1971) as a measure of evenness (calculations done in EcoSim version 7: Gotelli and Entsminger 2001). As with our annual ant samples, we used incidence of ants within a pitfall trap or Winkler extraction as a conservative measure of ant abundance. In contrast, we used the actual number of individuals collected in each pitfall trap or Winkler extraction as a measure of abundance of spiders and beetles. A "sample" consisted of the sum of incidences (of ants) or abundances (of beetles and spiders) from the pitfall traps and associated litter collection.

We used permutational ($n = 1000$ permutations) multivariate analysis of variance (pMANOVA: Anderson 2001, McArdle and Anderson 2001) to test for differences in arthropod assemblage composition (expressed as Bray-Curtis distance matrix) *among* treatments. In the pMANOVA, each sample (the sum of incidences or abundances from the pitfall traps and associated litter collection) was nested within each plot. Plots were assigned to treatments and blocks. Sample date (May, July, September) was entered as a covariate; as successive samples were from different sub-plots, we treated them as independent. F-statistics were estimated from 1000 permutations of the distance matrix using the adonis function in the vegan library of R, version 2.10.0. The overall model tested for differences in species composition among the four treatments, and pair-wise tests were used to contrast between the two control treatments and the two manipulated treatments. Compositional differences among assemblages are illustrated with ordination plots (non-metric multidimensional scaling [NMDS]).

Assembly rules for arthropods in declining hemlock stands

We used null model analysis (Gotelli and Graves 1996) to infer the relative importance of the regional species pool, environmental filtering, and interspecific competition in the reassembly of arthropod assemblages following loss of hemlock. We examined the importance of the regional species pool only for the ants because we have a reliable regional species pool only for that group (Ellison and Record 2009); we do not have quantitative data on a regional species pool or even a regional species list for either beetles or spiders. The species-abundance distribution of ants in the manipulated plots prior to treatment (2003, 2004) or after treatment (2008, 2009) was compared with the species-abundance distribution of ants from the entire Simes Tract (the "region"; Ellison and Record 2009). We tested the null hypothesis that treatment assemblages reflect only random colonization from the regional species pool. Thus the expected distribution in each treatment was derived by sampling each species with a probability proportional to its occurrence in the overall regional species pool. The expected distribution was then compared with the observed distribution in each treatment using an exact multinomial test (1000 iterations of the multinomial.test function from the EMT library of R, version 2.10.0).

Next, we examined the potential importance of environmental filtering (sensu selective environmental tolerances; Ulrich et al. 2009) in creating species assemblages in the manipulated treatments. We hypothesized that the disturbance and changes in environmental conditions following manipulation of the hemlock canopy would result in extirpation of subsets of species with different environmental tolerances (Ulrich et al. 2009), creating species assemblages in the manipulated treatments that were nested subsets of assemblages in the hemlock controls. Species assemblages in the hardwood controls should then be nested subsets of the assemblages in the manipulated treatments.

Because the analyses testing for environmental filtering did not require knowledge of the regional species pool, we did the analyses for ants, beetles, and spiders. We tested for environmental filtering in two ways—progressive loss of ant species through time, and nested subset

analyses of beetles and spiders in space, taking advantage of the space-for-time substitution in the HF-HeRE design (hemlock control → girdled or logged → hardwood control). In the case of the ants, if environmental filtering had occurred, samples collected later in time should be a nested subset of samples collected earlier in time (Ulrich et al. 2009). For beetles and spiders, if environmental filtering had occurred, samples collected from hardwood plots should be nested subsets of samples collected in hemlock control, girdled, or logged plots. We constructed ant species × year or beetle (or spider) species × plot matrices and tested them for nestedness using the "nestedness based on overlap and decreasing fill" (NODF) metric (Almeida-Neto et al. 2008). NODF measures nestedness by assessing changes in marginal totals and paired overlaps, separately analyzes nestedness among columns and rows, and is invariant to matrix size and shape (Almeida-Neto et al. 2008, Ulrich et al. 2009). To avoid spurious results caused by rare events, species represented by only a single individual were deleted prior to calculations. Computations were done using the nestednodf function in the R vegan library, version 2.10.0 and the significance of the nestedness statistic was evaluated with a null model (oecosimu function in the R vegan library) in which row and column frequencies were retained and a sequential swap method (99 iterations) was used (Gotelli and Entsminger 2001).

Lastly, we evaluated the potential importance of interspecific competition by examining co-occurrence patterns of ants, beetles, or spiders within treatments using the 2008 samples. This analysis assumed that these assemblages had re-attained (at least quasi-) equilibrium conditions in the three years since the treatments had been applied. We tested the null hypothesis that co-occurrence patterns should be the same in control and treated plots; significant decreases in co-occurrence would suggest a change in the influence of competitive interactions in the different treatments. For each plot, we constructed observed species × sample matrices from the data collected for ants, beetles, and spiders in 2008. We then determined the average number of checkerboard units between each pair of species (C-score of Stone and Roberts 1990) and compared this to the C-scores of 5000 randomly created matrices (using EcoSim 7). We used the "fixed-fixed" randomization scheme in which the observed frequencies of occurrences of species and sites in the randomized matrices are retained in the randomized matrices. The fixed-fixed model does not assume that all sites are equally probable for any species; rather, it recognizes (potential) differences among species in site preferences (Gotelli 2000, Ulrich and Gotelli 2007).

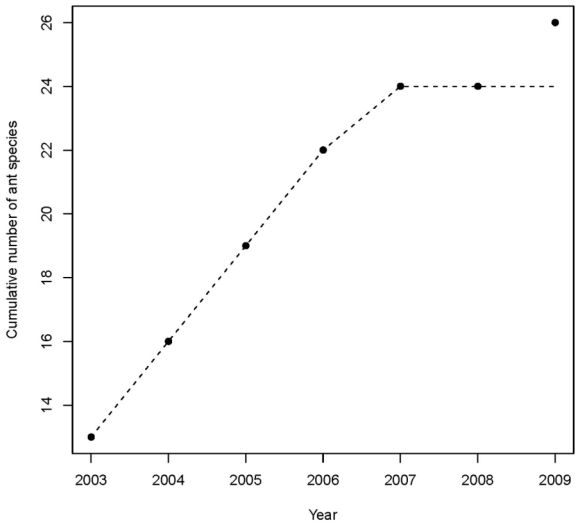

Fig. 1. Accumulation of ant species through time in the Harvard Forest Hemlock Removal Experiment (HF-HeRE), 2003–2009. Points are observations and the dotted line is the best-fit median smoother (function smooth in the R stats library).

Results

Temporal changes in ant assemblages

In seven years of collecting we accumulated a total of 26 ant species in 1295 species occurrences (Fig. 1; raw data available in Ellison 2009). This is greater than 50% of all known species collected from Harvard Forest, which covers a much broader range of habitats than HF-HeRE. Although we continued to find some new species each year, the rate of species accumulation declined (Fig. 1). As expected because of environmental differences between the two experimental blocks, there was a significant block effect on taxonomic diversity ($F_{1,47} = 6.07$, $P = 0.018$). Taxonomic similarity relative to the initial (2003)

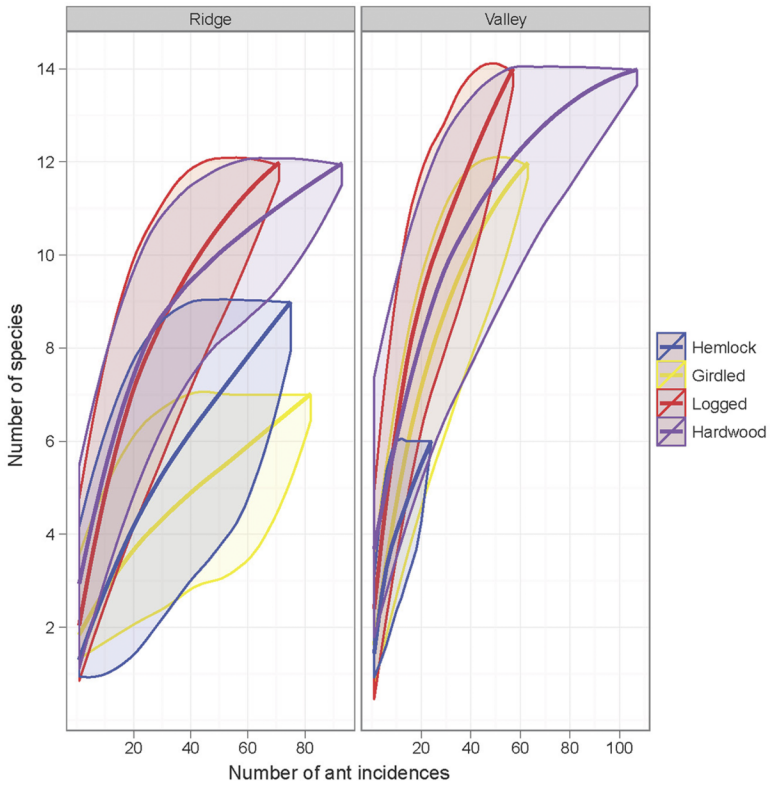

Fig. 2. Rarefaction of ant incidence data from collections made in the Harvard Forest Hemlock Removal Experiment (HF-HeRE), 2003–2009. Different colors indicate different treatments: blue: hemlock control; yellow: all hemlocks girdled; red: hemlocks logged and removed; purple: hardwood control. Dark lines are observed species richness data and shaded areas indicate 95% confidence bounds.

samples declined through time in all treatments ($F_{1,47} = 34.8$, $P = 3.9 \times 10^{-7}$), but it was not affected either by treatment ($F_{3,47} = 1.63$, $P = 0.20$) or by the interaction between treatment and year ($F_{3,47} = 0.243$, $P = 0.87$). The similarities among treatments can be seen clearly in rarefaction curves of the different treatments (Fig. 2). Although logged plots and hardwood plots generally had higher ant species richness, whereas hemlock and girdled plots had lower ant species richness, the 95% confidence intervals all overlapped at comparable sample sizes (i.e., numbers of incidences).

Functional similarity relative to the initial (2003) samples also declined through time in all treatments ($F_{1,47} = 23.1$, $P = 1.6 \times 10^{-5}$). As with species richness, functional similarity was not affected either by treatment ($F_{3,47} = 1.57$, $P = 0.21$) or by the interaction between treatment and year ($F_{3,47} = 0.83$, $P = 0.49$).

Spatial variation in assemblages of ants, beetles, and spiders

In our 2008 post-disturbance sample designed to capture fine-scale spatial variation in assemblages of ants, beetles, and spiders, we collected 19 species of ants (268 occurrences in either a pitfall trap or a 1-m^2 litter sample representing 1039 ant workers; Table 1), 125 morphospecies of beetles (1437 adult individuals in 26 families; Table 2), and 84 species of spiders (6538 individuals in 14 families; Table 3). The rarefied species richness of both spiders and ants was higher in the hardwood and logged plots than in hemlock and girdled plots, and these differences were more pronounced in the plots in the Ridge block than those in the Valley block (Fig. 3). The higher species richness in logged and hardwood plots was mainly due to a higher number of ants in the subfamily Formicinae (Table 1) and spider species across multiple families (Table 3). The

Table 1. Ant species collected in 2008 to quantify post-disturbance, fine-scale spatial variation in assemblage structure.

Species	Canopy treatment			
	Hemlock control	Girdled	Logged	Hardwood control
Aphaenogaster rudis	56	64	49	55
Camponotus novaeboracensis	0	0	10	1
Camponotus pennsylvanicus	3	22	26	18
Formica aserva	0	0	1	3
Formica neogagates	0	0	2	4
Formica subaenescens	0	1	3	5
Formica subsericea	0	1	7	5
Lasius alienus	2	0	2	0
Lasius nearcticus	0	0	0	1
Lasius umbratus	0	0	0	6
Myrmecina americana	2	0	0	3
Myrmica punctiventris	0	1	2	30
Myrmica sp. 1 ("AF-scu")	0	0	1	0
Ponera pennsylvanica	0	0	0	1
Stenamma brevicorne	0	1	0	0
Stenamma impar	14	16	7	7
Stenamma schmittii	0	1	0	0
Temnothorax longispinosus	0	2	5	5
Total	77	109	115	144

Notes: Values shown are the sums of occurrences in pitfall traps and 1-m^2 litter samples of each species. Voucher specimens are stored at the Harvard Forest.

Table 2. Families and number of morphospecies of beetles collected in 2008 to quantify post-disturbance, fine-scale spatial variation in assemblage structure.

Family	No. morphospecies	Canopy treatment			
		Hemlock control	Girdled	Logged	Hardwood control
Bostrichidae	1	0	0	0	12
Carabidae	20	140	134	110	120
Cerambycidae	1	0	1	0	0
Chrysomelidae	5	2	3	0	5
Coccinellidae	1	0	0	1	0
Curculionidae	9	21	17	5	88
Derodontidae	1	0	0	1	0
Elateridae	12	5	7	3	12
Endomychidae	1	0	0	1	0
Lampyridae	1	0	4	1	4
Latridiidae	1	0	0	1	2
Leiodidae	4	10	5	4	4
Lucanidae	1	0	0	0	2
Lycidae	1	0	0	1	0
Melandryidae	1	0	0	0	1
Mordellidae	2	0	0	4	0
Mycetophagidae	1	0	0	1	0
Nitidulidae	5	23	5	3	82
Ptilidae	1	2	0	6	0
Scaphidiidae	3	5	6	2	1
Scarabaeidae	7	16	3	16	21
Scydmaenidae	1	50	13	14	31
Silphidae	2	0	0	4	0
Staphylinidae	40	89	85	41	176
Tenebrionidae	2	1	0	1	0
Throscidae	1	4	2	3	0
Total	125	368	285	223	564

Notes: Values shown are the total numbers of individuals of all morphospecies within a family collected in pitfall traps and 1-m^2 litter samples. Voucher specimens are stored at the Harvard Forest.

Table 3. Spider species collected in 2008 to quantify post-disturbance, fine-scale spatial variation in assemblage structure.

Family	Species	Canopy treatment			
		Hemlock control	Girdled	Logged	Hardwood control
Agelenidae	*Agelenopsis utahana*	1	0	1	0
Amaurobiidae	*Amaurobius borealis*	70	73	28	130
Amaurobiidae	*Callobius bennetti*	5	2	3	4
Amaurobiidae	*Coras juvenilis*	1	0	0	0
Amaurobiidae	*Wadotes calcaratus*	5	1	0	1
Amaurobiidae	*Wadotes hybridus*	12	8	7	10
Araneidae	*Araniella displicata*	0	1	0	0
Clubionidae	*Clubiona spiralis*	0	0	0	1
Corinnidae	*Castianeira cingulata*	0	0	9	0
Corinnidae	*Castianeira longipalpa*	0	0	3	0
Corinnidae	*Phrurotimpus alarius*	0	5	19	41
Corinnidae	*Phrurotimpus borealis*	0	8	16	4
Dictynidae	*Cicurina arcuata*	2	6	1	8
Dictynidae	*Cicurina brevis*	2	2	0	9
Dictynidae	*Cicurina itasca*	0	0	0	1
Dictynidae	*Cicurina pallida*	0	0	0	1
Dictynidae	*Cicurina robusta*	0	1	1	1
Dictynidae	*Dictyna minuta*	0	0	0	1
Dictynidae	*Emblyna sublata*	0	0	1	2
Dictynidae	*Lathys foxi*	0	0	0	4
Gnaphosidae	*Zelotes duplex*	0	0	9	2
Gnaphosidae	*Zelotes fratris*	0	1	7	0
Gnaphosidae	*Zelotes hentzi*	0	0	1	0
Hahniidae	*Cryphoeca montana*	3	1	2	1
Hahniidae	*Hahnia cinerea*	0	4	1	1
Hahniidae	*Neoantistea magna*	36	27	23	50
Linyphiidae	*Centromerus cornupalpis*	0	0	0	4
Linyphiidae	*Centromerus persolutus*	32	0	0	5
Linyphiidae	*Ceraticelus fissiceps*	0	4	0	2
Linyphiidae	*Ceraticelus laetabilis*	25	29	8	33
Linyphiidae	*Ceraticelus minutus*	7	38	36	48
Linyphiidae	*Ceratinella brunnea*	95	113	43	8
Linyphiidae	*Ceratinella buna*	1	0	0	0
Linyphiidae	*Ceratinops annulipes*	0	1	4	4
Linyphiidae	*Ceratinopsidis formosa*	0	0	0	1
Linyphiidae	*Ceratinopsis interpres*	0	0	1	0
Linyphiidae	*Collinsia oxypaederotipus*	85	69	10	82
Linyphiidae	*Eperigone brevidentata*	11	8	1	10
Linyphiidae	*Eperigone maculata*	8	3	1	13
Linyphiidae	*Eperigone serrata*	0	0	0	1
Linyphiidae	*Helophora insignis*	1	0	0	4
Linyphiidae	*Macrargus multesimus*	1	1	0	6
Linyphiidae	*Meioneta simplex*	6	19	8	0
Linyphiidae	*Microneta viaria*	11	9	2	0
Linyphiidae	*Pocadicnemis americana*	0	2	0	2
Linyphiidae	*Scylaceus pallidus*	0	0	7	14
Linyphiidae	*Sisicottus montanus*	0	1	0	0
Linyphiidae	*Sisicus penifusifer*	1	4	1	3
Linyphiidae	*Tapinocyba minuta*	42	65	12	10
Linyphiidae	*Tapinocyba simplex*	3	2	3	7
Linyphiidae	*Tenuiphantes sabulosus*	1	1	1	18
Linyphiidae	*Tenuiphantes zebra*	22	29	5	10
Linyphiidae	*Walckenaeria atrotibialis*	1	0	0	1
Linyphiidae	*Walckenaeria brevicornis*	0	1	0	0
Linyphiidae	*Walckenaeria castanea*	0	0	0	1
Linyphiidae	*Walckenaeria digitata*	0	1	0	0
Linyphiidae	*Walckenaeria directa*	7	2	3	1
Linyphiidae	*Walckenaeria minuta*	1	6	3	13
Linyphiidae	*Walckenaeria pallida*	4	3	1	3
Liocranidae	*Agroeca ornata*	2	19	12	27
Lycosidae	*Hogna frondicola*	0	0	2	0
Lycosidae	*Pardosa distincta*	0	0	1	0
Lycosidae	*Pardosa moesta*	0	0	13	0
Lycosidae	*Pardosa xerampelina*	0	9	88	0

Table 3. Continued.

Family	Species	Canopy treatment			
		Hemlock control	Girdled	Logged	Hardwood control
Lycosidae	*Pirata montanus*	29	26	16	110
Lycosidae	*Trochosa terricola*	0	0	4	3
Salticidae	*Eris militaris*	0	0	0	2
Salticidae	*Habronattus viridipes*	0	0	4	0
Salticidae	*Naphrys pulex*	0	0	1	0
Salticidae	*Neon nelli*	7	8	5	9
Salticidae	*Pelegrina proterva*	0	0	1	0
Salticidae	*Phidippus whitmani*	0	0	1	0
Theridiidae	*Pholcomma hirsutum*	0	1	3	28
Theridiidae	*Robertus pumilus*	1	0	0	1
Theridiidae	*Robertus riparius*	13	0	1	30
Thomisidae	*Ozyptila distans*	4	1	0	4
Thomisidae	*Xysticus elegans*	0	0	0	1
Thomisidae	*Xysticus fraternus*	0	0	0	1
Total		558	615	434	792

Notes: Values shown are the total numbers of mature individuals identifiable to species (37% of the total) collected in pitfall traps and 1-m^2 litter samples. Voucher specimens are stored at the Harvard Forest.

rarefied species richness of beetles did not differ among the four treatments (Fig. 3).

Assemblages of both beetles and spiders had high evenness, with PIE values >90% in all treatments (Table 4). Ants had lower evenness than either beetles or spiders in every treatment. Ant assemblages in logged and hardwood treatments were more even than those in hemlock and girdled treatments, mainly due to the dominance of *Aphaenogaster rudis* in the latter two treatments.

For all macroarthropod taxa, there were significant differences in species composition among the four treatments (pMANOVA for ants: $F_{3, 106} = 4.8$, $P = 0.004$; beetles: $F_{3, 114} = 4.0$, $P = 0.009$; spiders: $F_{3, 115} = 6.2$, $P = 0.0006$; Fig. 4). Pair-wise treatment comparisons for beetle and spider assemblages indicated all treatments were significantly different from one another ($P < 0.001$). For ants, hemlock assemblages were not different from those found in the manipulated treatments, although hardwood treatments had a significantly different assemblage composition than girdled ($F_{1,53} = 10.5$, $P = 0.002$), logged ($F_{1,53} = 4.1$, $P = 0.047$), or hemlock ($F_{1,53} = 6.1$, $P = 0.016$) plots. Ant assemblages in girdled plots were similar to those in logged plots ($F_{1,53} = 2.6$, $P = 0.11$).

Assembly rules for arthropods in declining hemlock stands

Null model analysis of the ants indicated that the relative proportions of ant species in the logged and girdled treatments, both pre- (2003–2004) and post- (2008–2009) manipulation, did not represent a random selection from the regional species pool ($P < 0.001$; Fig. 5). Rather, formicines (species in the genera *Formica, Lasius, Camponotus*) were over-represented in the hardwood control plots prior to treatments and colonized the logged plots after treatments (Fig. 5).

Further analysis of the shifts in composition of ant species assemblages over time within each treatment indicated that there were no significant nested patterns of ant species loss in any treatments from 2003 to 2009 ($P > 0.05$). Similarly, analysis of nestedness of spiders and beetles using the space-for-time substitution revealed that assemblages of these groups in manipulated treatments (logged or girdled) were not nested within either of the control treatments (hemlock or hardwood), nor were assemblages in hardwood stands nested within assemblages of either of the hemlock canopy manipulation plots ($P > 0.05$, all cases; Fig. 6).

Co-occurrence patterns of assemblages of ants, beetles, and spiders in all collection periods in 2008 were not lower than those expected by chance ($P > 0.05$, all cases). In one case—ant assemblages in the hardwood plots—we found *more* co-occurrence than expected by chance, indicating the aggregation of species within a treatment ($P = 0.01$).

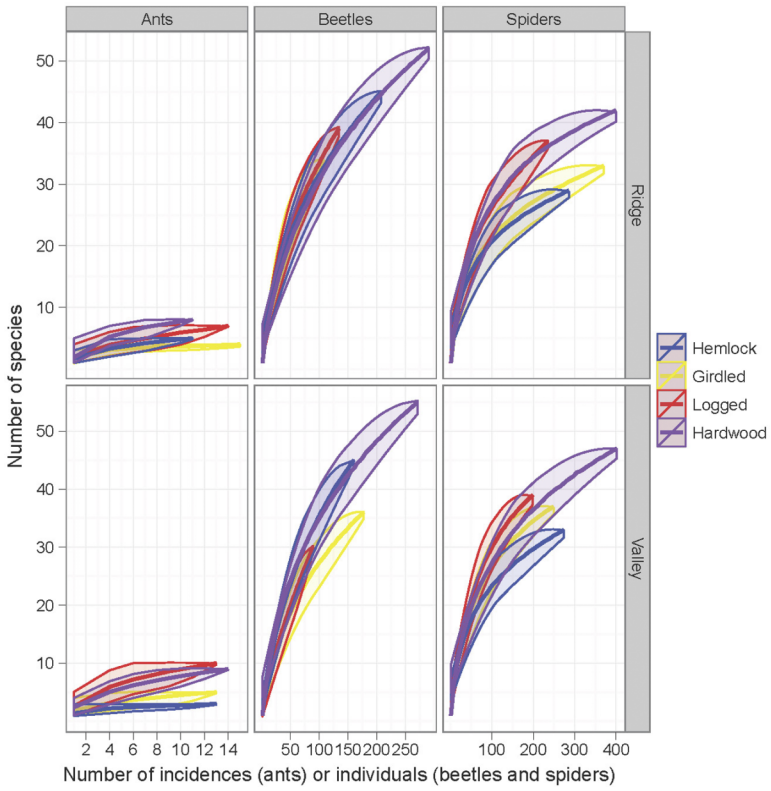

Fig. 3. Rarefaction of ant incidence data, and beetle and spider individual data from collections made in the Harvard Forest Hemlock Removal Experiment (HF-HeRE) in 2008. Colors are as in Fig. 1. Dark lines are observed species richness data and shaded areas indicate 95% confidence bounds.

Discussion

In many temperate forest ecosystems, specific foundation tree species define the nature and structure of the forest and its associated biota (Ellison et al. 2005*a*). Eastern hemlock, which deeply shades and cools the forest floor and which sheds needles that form a slowly decomposing, thick, organic layer, provides unique habitats for some insects but is inhospitable to others (Ellison et al. 2005*a*, Dilling et al. 2007, Rohr et al. 2009). Although our long-term experimental results generally support the conclusions of these previous correlative studies—that arthropod diversity will change as hemlock declines—we are able to provide new evidence that the type of hemlock removal affects arthro-

Table 4. Evenness (expressed as the probability of interspecific encounter [PIE]) of ants, beetles, and spiders collected in 2008 to quantify post-disturbance, fine-scale spatial variation in assemblage structure.

	Ants		Beetles		Spiders	
Canopy treatment	Species/sample	PIE	Adults/sample	PIE	Adults/sample	PIE
Hemlock control	53	0.53^{A} (0.46–0.58)	368	0.94^{AB} (0.92–0.95)	560	0.91^{A} (0.91–0.92)
Girdled	68	0.61^{A} (0.56–0.62)	285	0.92^{AB} (0.90–0.93)	619	0.92^{AB} (0.91–0.92)
Logged	79	0.75^{B} (0.72–0.77)	223	0.91^{A} (0.91–0.92)	434	0.93^{B} (0.93–0.93)
Hardwood control	68	0.79^{B} (0.78–0.80)	561	0.94^{B} (0.93–0.95)	801	0.93^{B} (0.92–0.93)

Notes: Values (and 95% confidence intervals in parentheses) in a column with different superscripted letters indicate significant differences among treatments ($P < 0.05$) based on non-overlap of 95% confidence intervals from an independent sampling algorithm with 1000 iterations.

pod assemblages in different ways. Logging of hemlock and removing the boles from the site led to greater changes to macroarthropod assemblage diversity (cf. Niemela et al. 1993, Palladini et al. 2007, Buddle 2008) than did our simulation of adelgid damage: girdling the trees and leaving the boles standing. And perhaps most importantly, our experimental study allows for strong inferences regarding potential mechanisms underlying these observed changes.

We have the most data, in both time and space, for ant assemblages (Table 1; Ellison 2009). Ants responded rapidly to hemlock removal (Fig. 3) by increasing their species richness, overall abundance, and evenness (Figs. 2, 3; Tables 1, 4). One subfamily of ants, the Formicinae, which includes large-bodied carpenter ants (*Camponotus*) and *Formica* species, as well as smaller, soil-dwelling *Lasius* species, initially were common only in hardwood plots, but rapidly increased in abundance in logged plots (Fig. 5). Assemblages of ants differed among treatments (Fig. 4), but nestedness analysis did not suggest a temporal environmental filter in ant assemblages (cf. Gotelli and Ellison 2002, Palladini et al. 2007) and null model analysis did not support the hypothesis that the ant assemblages were competitively structured. Rather, ant assemblages in the later-successional hemlock stands tend to be nested within hardwood stands, suggesting a progressive loss of ant species through succession (Fig. 6). Prior surveys of ants in southern New England showed an inverse relationship between hemlock cover (expressed as percent of total basal area) and the number of ant species present, and a similar appearance of Formicinae once hemlock declined to less than 50% of the total basal area (Ellison et al. 2005*b*). Thus, we suggest that the Formicinae are reliable responders to loss of hemlock. In contrast, Rohr et al. (2009) identified *Aphaenogaster* (but not a particular species) as an indicator of hardwood stands in Shenandoah National Park. In southern New England, *Aphaenogaster rudis* (*sensu lato*) is abundant in hemlock stands, but it is numerically dominant in both hardwood and hemlock stands (Table 1) and would not be suitable as an indicator of disturbance. The numerical dominance of *A. rudis* in all treatments is most likely responsible for our failure to detect significant differences in taxonomic or functional diversity

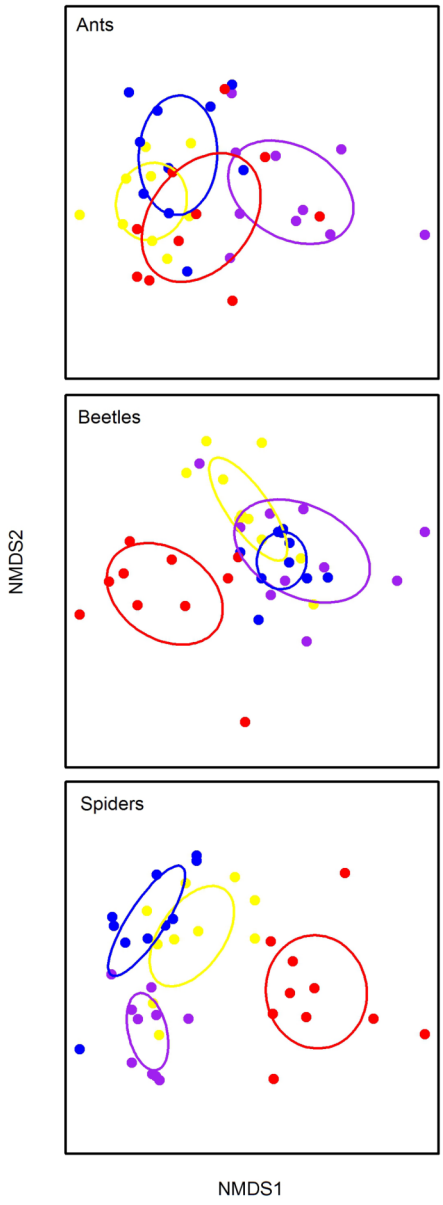

Fig. 4. Ordination (NMDS) plots of ants, beetles, and spiders sampled in the Harvard Forest Hemlock Removal Experiment (HF-HeRE) in 2008. For spiders and beetles, collection month significantly affected assemblage composition according to the npMANOVA. Thus, we present the NMDS plots for the collections showing the greatest differences among treatments: May for spiders and July for beetles. For ants, month did not significantly affect assemblage composition, so the NMDS plot includes all ant data. Points are individual observations and ellipses enclose 1 SD of the data. Colors are as in Fig. 1.

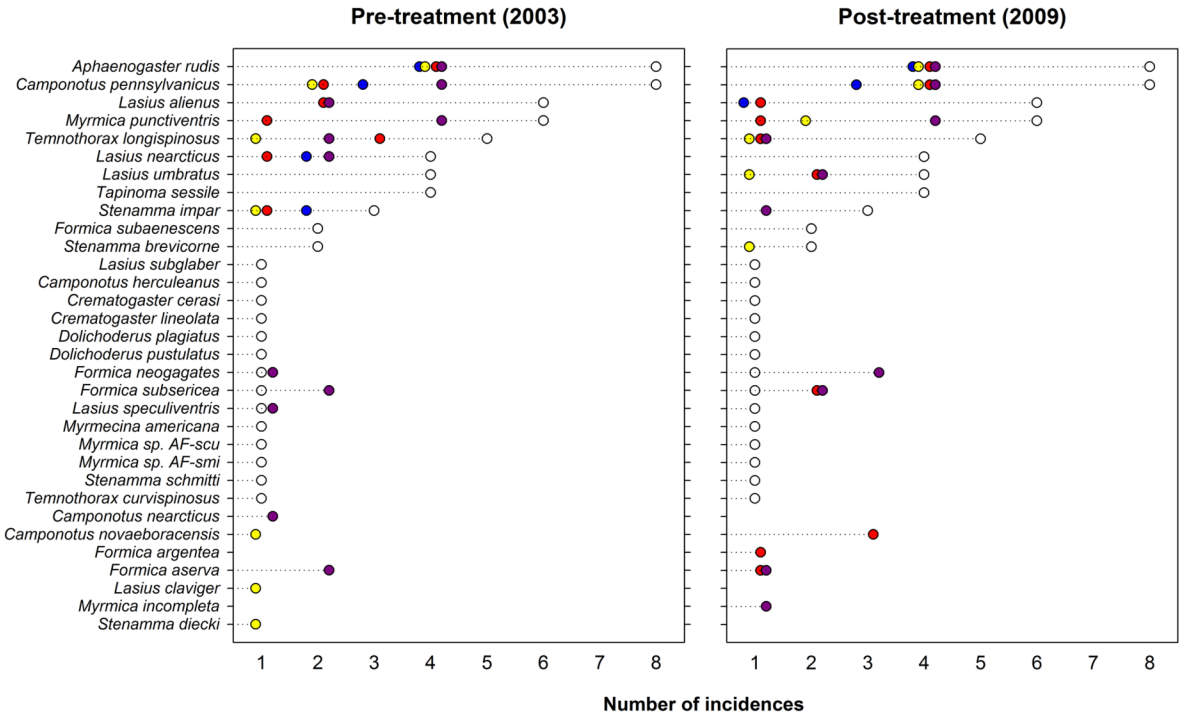

Fig. 5. Distribution of ants in the regional species pool (open circles) and in the manipulated plots of the Harvard Forest Hemlock Removal Experiment (HF-HeRE) prior to treatment (left) and after treatment (right). Values are number of incidences. Colors are as in Fig. 1.

among the four treatments. Our observation that both taxonomic and functional similarity declined through time in all treatments is most parsimoniously explained as a sampling effect: as we accumulated more ant species in all plots in the seven years of sampling (Fig. 1), we increased

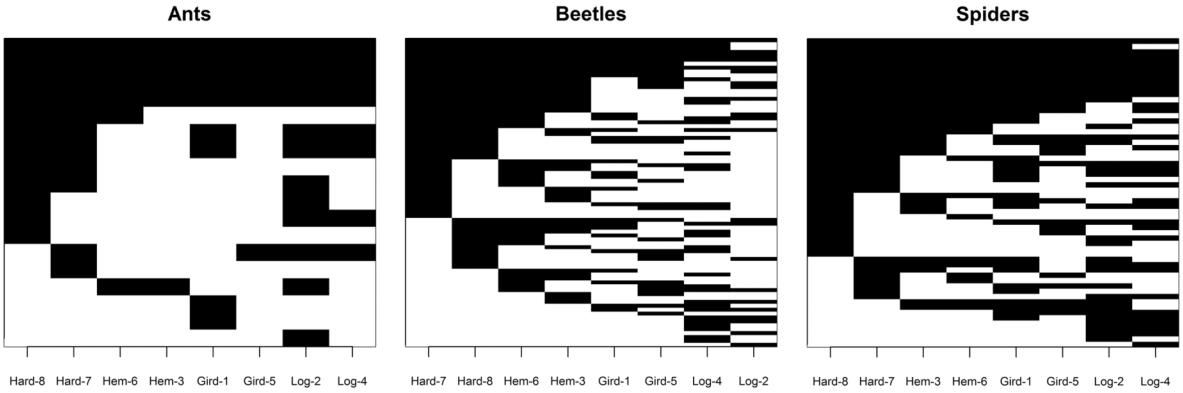

Fig. 6. Nestedness of ants, beetles, and spiders in 2008 in the manipulated plots of the Harvard Forest Hemlock Removal Experiment (HF-HeRE). Each column represents the species composition of one of the 90 × 90 m plots (Hem: hemlock control; Gird: all hemlocks girdled; Log: hemlocks logged and removed; Hard: hardwood control); plots 1, 2, 3, and 8 are in the Valley block, and plots 4–7 are in the Ridge block. Black squares indicate instances where species occurred in a given treatment plot.

our representation of rare species and functionally different ones.

In our post-treatment snapshot (2008) the spider assemblages across all treatments were dominated by litter-dwelling Linyphiidae, Lycosidae, and the Amaurobiidae species *Amaurobius borealis* (Table 3). There were many more species of spiders in the logged plots and the hardwood control plots than in either the girdled or hemlock control plots (Fig. 3), but spider abundance in the girdled plots was nearly as high as that found in the hardwood control plots (Fig. 3, Table 3). Evenness of spiders was uniformly high; ordination revealed differences among spider assemblages across treatments (Fig. 4), while nestedness analysis (Fig. 6), and co-occurrence analysis suggests that changes in spider species composition as hemlock is removed from the system is more influenced by immigration of species not normally found in hemlock plots than by disappearance of species found in hemlock stands.

Taken together, these results suggest that environmental filtering determines species composition in these forest stands, but not in the direction that we had expected. Rather, environmental filtering is apparently more intense in the unmanipulated hemlock stands than in the girdled or logged stands. Most interpretations of data on changes in nestedness after disturbance are based on the assumption that the disturbance will increase the intensity of environmental filtering, with consequent losses of species from an area (Ulrich et al. 2009, Louzada et al. 2010). In this hemlock removal experiment, however, the disturbance appeared to release local species from environmental filtering and led to an increase in species influx into the manipulated plots. An increased species richness of arthropods in our manipulated plots and other disturbed forest plots, such as those created by logging, can be due to the influx of open habitat specialists (Niemela et al. 1993), although this does not always offset species losses (Pearce et al. 2004).

Similar to that of spiders, beetle species richness was highest in hardwood stands (Fig. 3), and the beetles exhibited high evenness in species composition in all treatments (Table 4). Carabid and staphylinid morphospecies were common in all plots; nitidulid beetles were common only in the undisturbed hemlock and hardwood control plots, and curculionids were most common in the hardwood control plots (Table 2). Although beetle assemblages differed among the four treatments (Fig. 4), these assemblages showed no patterns of spatial nestedness (Fig. 6), nor any evidence for competitive structuring. Our relatively coarse temporal scale of sampling, however, is likely to have missed beetles with short adult lifespans or very early emergence. For example, the tiger beetle *Cicindela sexguttata* established breeding populations in the logged plots in 2006 (A. M. Ellison, *personal observation*), but the adults are only active in late April and early May and so were not captured in our samples.

Overall, our data provide experimental support for earlier correlative observations (Ellison et al. 2005*b*, Dilling et al. 2007, Rohr et al. 2009) that species richness and evenness of macroarthropods increases when hemlocks disappear. Our experimental data provide little evidence that competitive interactions structure assemblages of the ants, spiders, or beetles in these northern forests, but they do provide evidence for environmental filtering—far fewer species are present in late-successional hemlock stands than in disturbed forest stands or in early-successional hardwood stands. Thus, the loss of hemlock could actually increase arthropod "biodiversity" at local scales in northeastern North America. However, as hemlock forests are replaced by deciduous forests (Orwig and Foster 1998), macroarthropod assemblages will become more homogeneous across the landscape (Ellison et al. 2005*b*, Rohr et al. 2009).

Acknowledgments

Portions of this work were supported by NSF grants 00-80592, 04-52254, and 06-20443. Tara Sackett was supported by a FQRNT (Le Fonds québécois de la recherche sur la nature et les technologies) postdoctoral fellowship. Alex Arguello, Katie Bennett, Jonathan Chen, Israel Del Toro, David Díaz, Alyssa Hernandez, Samantha Hilerio, Chelsea Kammerer-Burnham, Matthew Lau, Ernesto Rodriguez, and Grace Wu assisted with field sampling and arthropod sorting. Stefan Cover (MCZ) confirmed our identifications of ant specimens. E. Marks and two anonymous reviewers provided helpful comments on the manuscript. This work is a publication of the Harvard Forest Long Term Ecological Research (LTER) Site.

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Appendix

Table A1. Functional trait matrix for the ant species collected in the Harvard Forest Hemlock Removal Experiment (HF-HeRE), 2003–2009.

Species	Habitat	Nests	Body length (mm)	Slave–maker	Temporary social parasite	Tender or honeydew feeder	Seed disperser	Carni–vore
Aphaenogaster rudis (species complex)	second-growth forests and deep woods	under rocks, in rotten logs, and in litter	5.2	No	No	No	Yes	Yes
Camponotus herculeanus	conifer forests	in rotten logs	9.1	No	No	Yes	No	No
C. nearcticus	second-growth forests and deep woods	under bark and in rotten wood	5.3	No	No	No	No	No
C. novaeboracensis	second-growth forests and deep woods	in rotten logs	8.2	No	No	Yes	No	No
C. pennsylvanicus	second-growth forests and deep woods	in rotten logs	10.1	No	No	Yes	No	No
Formica argentea	open woodlands and forest edges	under rocks and in soil	6.6	No	No	Yes	No	Yes
F. aserva	open woodlands and forest edges	under logs	6.4	Yes	Yes	Yes	No	Yes
F. neogagates	mesic woods	in soil and in rotten wood	4.3	No	No	Yes	No	No
F. subsericea	open woodlands and forest edges	atop soil in a low mound	6.4	No	No	Yes	No	No
Lasius alienus	second-growth forests and deep woods	under rocks, in rotten logs, and in litter	3.2	No	No	Yes	Yes	Yes
L. latipes	open woodlands and forest edges	under rocks	4.4	No	Yes	Yes	No	No
L. nearcticus	second-growth forests and deep woods	under rocks and in rotten logs	3.3	No	No	Yes	No	No
L. neoniger	open fields, lawns	in soil	3.2	No	No	Yes	No	Yes
L. speculiventris	deep woods	under rocks and in rotten logs	4.9	No	Yes	Yes	No	No
L. umbratus	second-growth forests	in soil	4.4	No	Yes	Yes	No	No
Myrmica incompleta	moist woods and wetlands	in soil or Sphagnum	4.9	No	No	Yes	No	No
M. punctiventris	second-growth forests	under bark and rocks, in rotten logs, and in leaf litter	5.0	No	No	No	Yes	No
Ponera pennsylvanica	moist woods and wetlands	under bark and in rotten wood	3.4	No	No	No	No	Yes
Stenamma brevicorne	open woodlands and forest edges	under rocks and in rotten logs	3.5	No	No	Yes	No	Yes
S. impar	moist woods and wetlands	in soil and in rotten wood	2.8	No	No	No	No	No
S. schmitti	moist woods and wetlands	in soil and in rotten wood	3.3	No	No	No	No	Yes
Tapinoma sessile	open woodlands, forest edges and wetlands	under bark and rocks, in rotten logs, and in leaf litter	2.8	No	No	Yes	Yes	Yes