Community Responses to Eastern Hemlock Loss Across a Latitudinal Gradient

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Abstract - *Tsuga canadensis* (Eastern Hemlock) forests are experiencing widespread mortality due to the invasive insect *Adelges tsugae* (Hemlock Woolly Adelgid). This study sought to document the community response to HWA across latitude. I selected two sensitive response groups—plants and ants— to use as biological indicators of ecosystem change to monitor differences along a natural gradient of Eastern Hemlock mortality among 3 forest types: relatively healthy Eastern Hemlocks, dead or dying Eastern Hemlocks, and hardwood stands. I sampled understory vegetation, ants, and soils at each site and compared sites using a linear mixed-model to discern the best predictors of species density. I also compared analyses of variances across forest types among response variables. There was an average two-fold increase in understory vegetation species density between Eastern Hemlock and hardwood forests; ant species density was not influenced by forest type. Analysis of variance comparisons for understory vegetation showed that forest type affects understory vegetation, a result which was attributable to differences in a few dominant plant species. The linear mixed-model showed that Eastern Hemlock density and latitude were important predictors for both ant and vegetation species densities; soil pH and stand density were predictors for vegetation species density, and litter depth was a predictor for ant species density. My findings show that large structural changes in Eastern Hemlock forest communities (induced by the effects HWA) alter a foundation ecosystem by shifting the composition of understory plant communities, but not ant communities.

Introduction

There is evidence that global changes, such as the spread of invasive species, are leading to large transitions in both structure and function in ecosystems (Chapin et al. 2000, Ribbons 2014). A major question in ecology is how these changes will influence community structure and ecosystem function. Forests serve as important buffers for climate change; however, loss of dominant species can significantly impact their buffering capacity (Whitehead 2011). Ecosystem transitions are increasing under global pressures such as climate change and the spread of non-native invasive pests (Estes et al. 2011), and there is uncertainty about the factors that promote ecosystem resilience to repeated disturbances (Loreau et al. 2001). Studying forests in transition can provide insight into how altered overstory vegetation influences understory arthropod communities, including forest-floor ants, which are known to be ecosystem engineers (Del Toro et al. 2012).

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Foundation species are those that define community structure by creating locally stable conditions exploited by other species; they modulate and stabilize fundamental ecosystem processes (Ellison et al. 2005). In the northern part of its range, *Tsuga canadensis* (L.) Carrière (Eastern Hemlock, hereafter, Hemlock) tends to be a dominant forest species. In the southern portion of its range, Hemlocks occur most frequently in mixed hardwood stands, and are especially important in riparian environments (Krapfl et al. 2011, Nuckolls et al. 2009). Infestation by an introduced invasive pest, *Adelges tsugae* Annand (Hemlock Woolly Adelgid [HWA]), has decimated southern hemlock forests (Kincaid 2007, Kincaid and Parker 2008, Nuckolls et al. 2009) and has reached as far north as Massachusetts (Orwig and Foster 1998, Orwig et al. 2012). Increases in soil temperature, chemistry, and nutrient fluxes have been documented following Hemlock decline (Cobb et al. 2006, Jenkins et al. 1999, Kizlinski et al. 2002, Orwig et al. 2008, Stadler et al. 2006). The loss of Hemlocks has already led to changes in forest hydrology by increasing stream temperature and soil pH (Evans et al. 2011, Ford and Vose 2007, Knoepp et al. 2011, Martin and Goebel 2013), and other functional and structural changes, such as shifts in microbial communities, are likely to follow as forests transition to hardwood-dominated stands. Although the direct effects of dying Hemlock forests are well documented for plant species associated with the forests (Orwig et al. 2012), the cascading effects of Hemlock decline, including changes in ant communities and soil physical properties, have not been explored in a single study; some effects have been explored independently. For example, changes in ant, beetle, and spider community compositions have been documented in Hemlock forests infested with HWA compared with logged Hemlock and reference Hemlock forests (Sackett et al. 2011).

Terrestrial invertebrates, including ants, play important roles in mediating ecosystem processes such as decomposition, and they directly influence soil microbial and plant communities and the nutrient processes they regulate. Ants are seed dispersers and soil bioturbators (Del Toro et al. 2012, Folgarait 1998) and affect terrestrial vegetation structure and arthropod communities (Holldobler and Wilson 1990, Zelikova et al. 2008), but their influence on ecosystem functions has not been well-studied (Sackett et al. 2011). The effects of dying Hemlock forests on invertebrates are well documented at the guild or generic level on a local scale (Dilling et al. 2007, Ingwell et al. 2012, Rohr et al. 2009); however, the cascading effects of Hemlock decline have not been explored across a regional latitudinal gradient.

Linking the large-scale disturbances of Hemlock mortality with understory plant and ant communities may provide vital information on the future trajectory of these forests, with insights into forest-floor regeneration and ecosystem health. One group of forest ants, the *Aphaenogaster rudis* complex (thread-waisted ants), are common in Hemlock forests, and are known to disperse up to 77% of all forest plant seeds (Sackett et al. 2011); as such, they directly influence plant community dynamics and are organisms worthy of study. This study sought to quantify the abundance and distribution of understory plants and leaf-litter ants in low-mortality Hemlock, high-mortality Hemlock, and hardwood forests. I used a space-for-time

substitution of Hemlock loss by comparing the three forest types, as designed by El-lison et al. (2010) for the Hemlock Removal Experiment. I also aimed to determine compositional differences across a latitudinal and mortality gradient.

Field Site Description

To examine patterns in community responses to the loss of Hemlocks, I sampled 9 sites throughout the species' range, and across the HWA invasion range (Fig. 1; Supplemental Table 1 in Supplemental File 1, aavailable online at http://www. eaglehill.us/SENAonline/suppl-files/s13-sp6-2001m-Ribbons-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/HA2001M.s1). The nine sites were (in order from south to north): Smoky Mountains (SM), Frozen Head (FH), Fall Creek (FC), Gauley River (GR), Rothrock (RR), Willington Hill (WH), MacLeish (ML), Black Rock (BR), and Finger Lakes (FL). At each of these 9 sites, I estab-lished three 100-m^2 (0.01-ha) plots, 1 in each of 3 forest-cover types: uninfested or low-mortality Hemlock, heavily HWA-infested or dead Hemlock, and mixed-hardwoods, henceforth referred to as Hemlock, dead Hemlock, and hardwood, respectively; no stands had a completely open canopy. I identified to species all overstory trees within the plots, recorded diameter at breast height (DBH) (trees with DBH > 8 cm) for each, and counted and identified to species all tree saplings
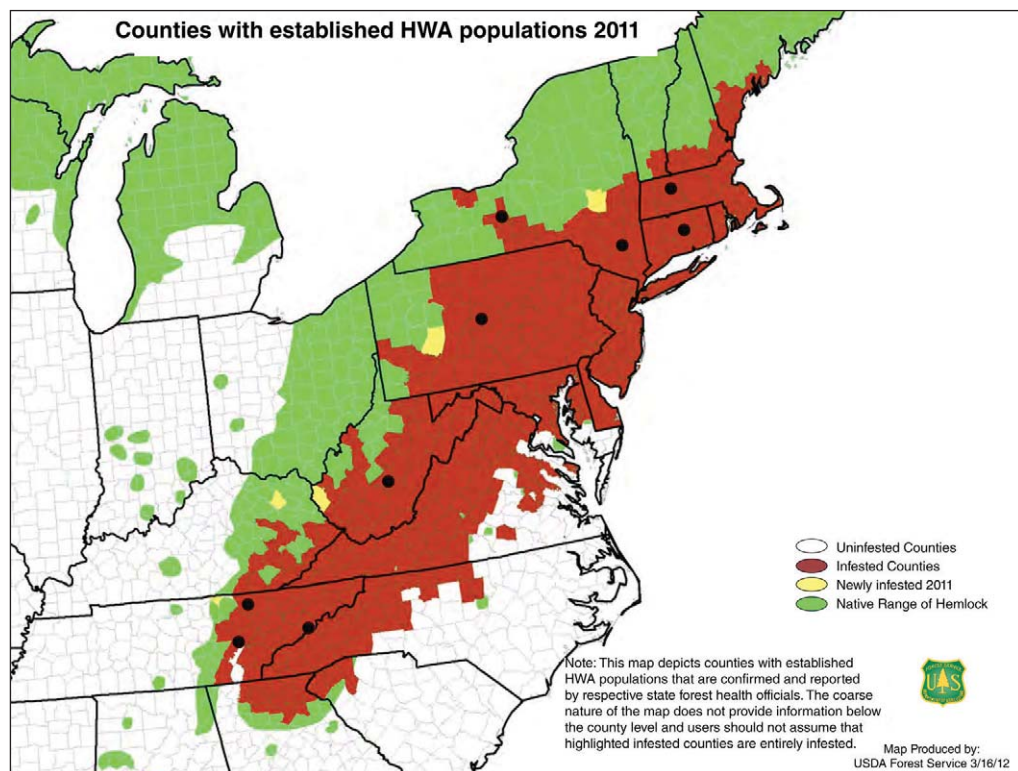

Figure 1. Map of the distribution of counties with HWA as of 2011, with study locations overlaid in black circles (courtesy of the US Forest Service).

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(tree height < 1 m, DBH < 8 cm) within the plot. I compared basal area, density, and relative importance values among forest types and across latitude using two-way analysis of variance (ANOVA). Within each plot, I collected 9 soil samples for pH analysis and recorded soil moisture and temperature. To examine understory diversity across gradient, I collected data on plant and ant communities using 9 randomly stratified 1-m^2 subplots (n = 27 subplots/site; 243 subplots in total) evenly spaced in checkerboard patter within a grid .

Methods

I tried to establish plots within a site at similar topographic position, elevation, and aspect to reduce potential confounding effects between microhabitat features and forest types (see Supplemental Table 1 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s13-sp6-2001m-Ribbons-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/HA2001M.s1). All field sampling occurred during daylight hours (8:00 AM until 6:00 PM). I sampled each site once between May and July in 2012, starting in the south and traveling northward to track phenology over the season.

To determine soil physical properties, I extracted 9 soil cores using a checkerboard pattern of sampling locations within each plot using an AMS soil corer (15-cm depth, 5-cm diameter; AMS Soil, Inc., American Falls, ID). I sifted soils using a 2-mm-mesh sieve to homogenize the soil for pH analysis, following the soil sampling protocol of Carter and Gregorich (2008). Within each of these plots, I collected 2 soil-moisture measurements using a HydroSense monitor, and 2 temperature-point measurements using a standard thermometer.

For canopy tree species, I calculated basal area and density of the overstory and understory (saplings and seedlings) for each plot. I then calculated relative importance values for each species at each site, as the sum of relative basal area and relative density for each species. All herbaceous and woody vegetation within the subplots was identified to species and assigned a percent groundcover using a modified Braun-Blanquet scale ranging from 1–100% in 5% increment classes. Nomenclature follows Gleason and Cronquist (1991). In addition to assigning a percent-cover estimate, I identified and counted all tree seedlings located within each subplot. I listed all species encountered within the 100-m^2 plot to account for species not contained within the understory vegetation subplots (see Supplemental Table 2 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s13-sp6-2001m-Ribbons-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/HA2001M.s1).

I selected 9 stratified 1-m^2 subplots at random and collected leaf-litter from them for Winkler extraction following the protocol of Agosti and Alonso (2000). After collection, I took the samples to the lab and left them to extract for 72 h until the litter was dry (Ivanov and Keiper 2009, Ivanov et al. 2010). After emptying litter from the Winkler, I added any remaining ants to the extracted ant samples, placed the ants into 70% ethanol, and sorted them to species-level. I deposited ant voucher specimens at the Harvard Forest Long-Term Ecological Research Site (Petersham, MA).

Data analyses

I determined species density, richness, percent groundcover for vegetation, and the incidence of occurrence (presence/absence) for ants across the latitudinal gradient. To test for differences among forest types and across latitude, I compared richness estimates and species density for understory vegetation and ants using two-way ANOVAs of forest type, latitude, and richness. Not all plant or ant species ranges extended throughout the entire gradient, and I expected a decline in species richness as latitude increased. To account for this potential effect, I compared intra-site species density among forest types, and constructed a linear mixed model to test which variables were the best predictors of vegetation and ant species density. I tested for interactions between ants and vegetation, local site factors, soil properties, and temperature to determine the best predictors of species density.

To test for differences in community composition and dissimilarity among forest types across the latitudinal gradient, I used non-metric multidimensional scaling (NMDS). The EstimateS program (Colwell 1997) was used to estimate ant abundance across the sites; this program also showed that although ants were under-sampled at all sites, they were similarly under-sampled across all sites. Raw abundance data for both vegetation and ants were fourth-root transformed prior to multivariate analyses, and all distance-based metrics used a Bray-Curtis dissimilarity matrix. I visually analyzed vegetation and ant communities at each site using NMDS plots to determine initial clustering and dispersal among forest types at a site ($n = 9$ sites), with 95% confidence intervals around clouds of points to determine differences among forest types. For clarity of results I used binary-transformed data (presence/absence) for final NMDS graphs. NMDS were constructed in Primer 6 version 6.1.13 (Primer-E, Ltd.; see Anderson 2001, McArdle and Andersen 2001).

To test which variables were the best predictors of vegetation richness and ant species density, I used a linear mixed model approach in the lme4 package (Bates et al. 2012) in R statistical program (version 2.15.0; R Core Team 2013).

Results

Total basal area and stand density did not differ significantly across latitude or among forest types (Table 1); results of ANOVAs showed mean Hemlock basal area and density differed significantly among forest types but not across latitude (Table 2). Mean soil temperature, soil volumetric water content (VWC), litter depth, and soil pH did not differ among forest types (Table 3). Vegetation percent

Table 1. Stand structure mean (standard deviation) values for basal area (m^2/ha, BA), density (stems/ha, Density) of all overstory tree species for each forest type, and Hemlock basal area (BA), relative importance value (IV), and density (Density) for each forest type.

Canopy	Overstory		Hemlock		
	BA	Density	BA	IV	Density
Dead hemlock	205.33 (98.08)	244.44 (48.76)	120.56 (68.83)	61.22 (24.60)	142.67 (36.40)
Hardwood	188.22 (80.27)	296.67 (109.10)	8.33 (16.99)	5.78 (12.22)	16.44 (27.54)
Hemlock	211.22 (86.82)	271.89 (94.18)	177.67 (91.42)	83.22 (13.80)	192.22 (66.10)

groundcover (similar to abundance) generally decreased as latitude increased along the gradient, with the exception of hardwood sites, which showed increases in groundcover (Fig. 2). Ant abundance remained fairly consistent along the gradient except for the northernmost site which had lower ant abundance, with no significant differences observed between forest types (Fig. 2). Vegetation and ant species richness trends were similar to percent groundcover and abundance trends (Fig. 3).

A total of 87 plant species and 29 ant species were collected across the gradient (see Supplemental Tables 2, 3 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s13-sp6-2001m-Ribbons-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/HA2001M.s1). Species density of the plant communities differed significantly across latitudes ($F = 7.87$, $P = 0.009$) and among forest types ($F = 3.97$, $P = 0.03$) (Table 2), and a post-hoc Tukey's honest significant differences test showed the greatest difference of all pairs between Hemlock and hardwood plots ($M = 7.33$, $P = 0.02$). Vegetation species density

Table 2. Analysis of variances table including degrees of freedom (df), *F*-values, and associated *P*-values ($\alpha = 0.05$, with * indicating a significant *P*-value) for forest community stand dynamics including total basal area, stand density, Hemlock basal area, Hemlock density, vegetation species density, and ant species density across latitude and among forest types.

Source	DF	F	P
Total basal area			
Latitude	1	0.350	0.56
Forest types	2	0.159	0.85
Hemlock basal area			
Latitude	1	0.022	0.82
Forest types	2	15.110	0.001*
Total stand density			
Latitude	1	0.890	0.35
Forest types	2	0.790	0.46
Hemlock density			
Latitude	1	0.744	0.39
Forest types	2	34.000	0.001*
Vegetation species density			
Latitude	1	7.870	0.009*
Forest types	2	3.970	0.03*
Ant species density			
Latitude	1	12.862	0.001*
Forest types	2	0.853	0.44

Table 3. Mean soil physical and chemical properties for each forest type, volumetric water content (VWC), temperature, litter depth, and soil pH.

Canopy	Soil VWC	Soil temp (C)	Litter depth (cm)	Soil pH
Dead hemlock	15.81 (9.37)	16.43 (9.37)	1.77 (0.63)	4.41 (0.56)
Hardwood	13.11 (8.14)	16.73 (8.14)	1.79 (0.50)	4.52 (0.59)
Hemlock	10.15 (2.56)	15.86 (2.56)	1.89 (0.69)	4.45 (0.68)

generally was highest in hardwood forests in the far northern sites (WH, ML and BR) and far southern sites (SM, FH, and FC), followed by dead Hemlock and Hemlock forests; however the response was more mixed at the intermediate sites (GR, RR and FL). A total of 3648 ants were collected using Winkler extractors. Ant species density differed significantly across latitude ($F = 12.862$, $P = 0.001$), but not among forest types ($F = 0.853$, $P = 0.44$) (Table 2).

The following predictor variables from each plot were put into the linear mixed model: temperature (mean annual temperature as recorded by the closest weather station), canopy (forest type), total basal area, total stand density, Hemlock density, soil VWC, soil temperature, litter depth, and soil pH. Additional variables including elevation, latitude, longitude, Hemlock basal area, and importance values were measured at the sites, but not included in the model due to a high correlation with at least one of the variables already in the model. To determine the best model for predicting richness, I used AIC stepwise model selection in the MASS package (Venables and Ripley 2002). For vegetation richness, the best model was predicted by stand density + Hemlock density + soil temperature + soil pH + canopy type. For ant richness, the best model was predicted by Hemlock density + temperature + litter + canopy type.
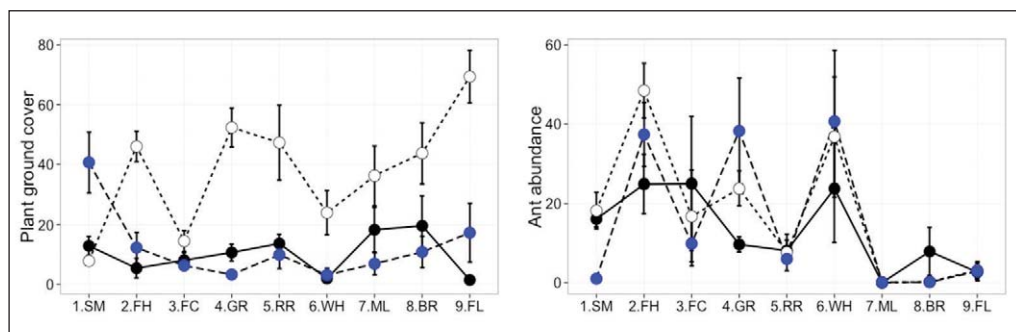

Figure 2. Percent groundcover of understory vegetation (a) and Mean abundance of ants (b) across the 3 forest-cover types (black = dead hemlock, white = hardwood, and blue = healthy Hemlock), with sites arranged from south to north (left to right) along the x-axis.
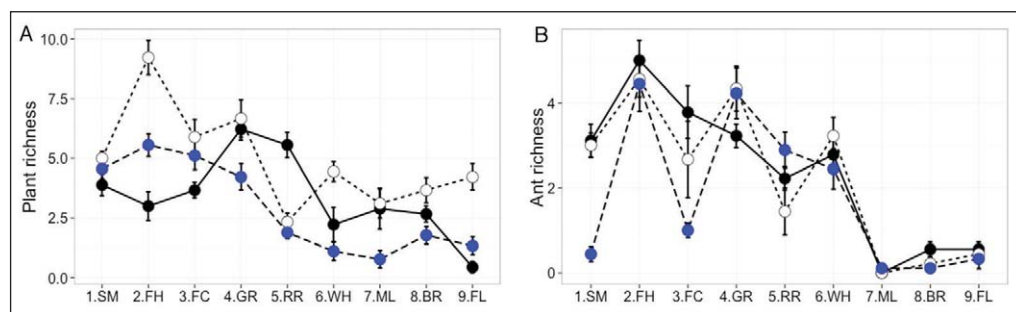

Figure 3. Mean richness of understory vegetation (a) and ants (b) across the 3 forest-cover types (black = dead hemlock, white = hardwood, and blue = healthy Hemlock), with sites arranged from south to north (left to right) along the x-axis.

Discussion

Differences in forest community structure due to hemlock loss

The loss of Hemlock in forests leads to changes in vegetation and some ant communities (Figs. 4, 5); however, the effects are reflected associated with Hemlock loss differ among forest types representing a gradient of Hemlock mortality. I documented an overall decline in basal area, density and relative importance of Hemlock across the latitudinal gradient, with highest losses at the southern sites, consistent with previous studies (Kincaid 2007, Kincaid and Parker 2008). At many sites, Hemlock remained within the understory; however, similar to the findings of Orwig et al. (2008), regeneration was low at my sites, as represented by seedlings
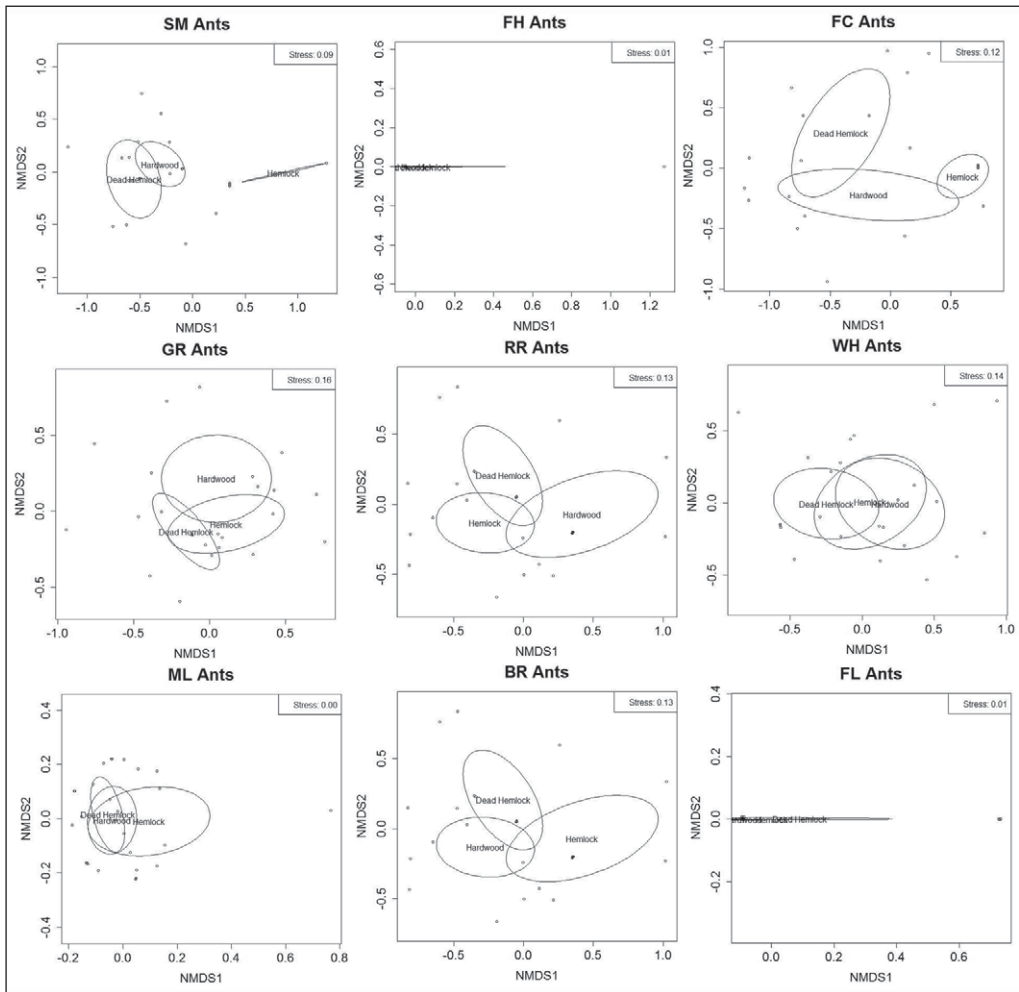

Figure 4. Non-metric multidimensional scaling plots (NMDS) for ants across all 9 sites, with clusters of points from the same forest type indicating distinct communities compared with dispersal of points across all forest types (which indicate no relationship between ants and forest types). Data were binary transformed, and ellipses around forest treatments indicate a 95% confidence interval.

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within hardwood and dead Hemlock stands. Across the gradient, most sites contained abundant *Acer rubrum* L. (Red Maple) seedlings, which were especially prominent in dead Hemlock stands, suggesting that this species will largely replace Hemlocks. This finding is consistent with reports for other mixed hardwood forests across the eastern US (Abrams 1998). Typically, structural changes in overstory vegetation and a shift to hardwood-dominated forests is first reflected in the understory (Mahan et al. 2004, Orwig et al. 2002).

Individual species responses vary by forest type for vegetation, but not ants

Similar to other studies between forest types (Hill et al. 2008), species density and plant-community composition varied among forest types across the gradient, but I observed less variation in ant communities, which suggests that ants may
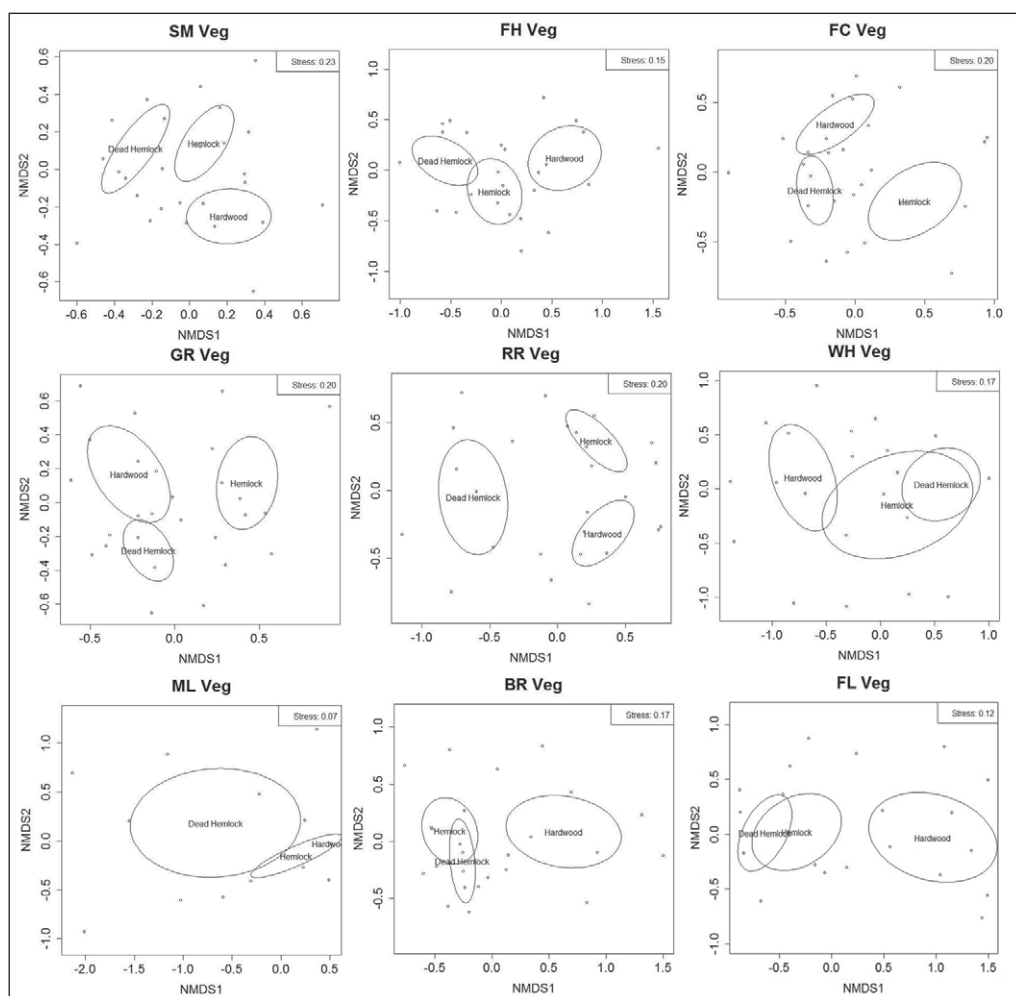

Figure 5. Non-metric multidimensional scaling analysis for understory vegetation across all 9 sites, with clusters of points from the same forest type indicating distinct communities compared with dispersal of points across all forest types. Data were binary transformed, and ellipses around forest treatments indicate a 95% confidence interval.

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respond less to forest type and are more sensitive to open versus closed habitats (Del Toro 2013). Red Maple was present at all sites, but I found the greatest number of Red Maple seedlings and the highest percent groundcover in the dead Hemlock plots. A few plant species including *Aralia nudicaulis* L. (Wild Sarsaparilla), *Hammamelis virginiana* L. (Witch Hazel), and *Lindera benzoin* L. (Blume) (Spicebush) were only detected in the Hemlock and dead Hemlock forests, suggesting that these plants will decrease in abundance in the future. Some sites had vegetation species gains or losses characterized by forest types. For example, at site SM, *Mitchella repens* L. (Partridgeberry) was absent in hardwoods, but was present with high abundance in Hemlocks. Conversely, at site FH, *Hexastylis arifolia* (Michx.) (Little Brown Jug; an ant-dispersed plant) was absent in Hemlocks, and highest in abundance in hardwood stands. Witch Hazel and Partridgeberry were fairly widespread across numerous habitats in eastern North American forests, including those not sampled in this study, and as such, are not species of concern (NRCS 2014).

Disturbed environments are ideal settings for new invasions of non-native plant species (Wardle et al. 2011), and increased species richness following Hemlock mortality does not necessarily indicate increased native species diversity or serve as an indicator of increased ecosystem health. This pattern of change has implications for the long-term resilience and stability for forests with declining Hemlock because the replacing stand may contain more non-native or invasive plant species. I observed 4 non-native invasive species across the gradient of sites, including *Berberis thunbergii* DC (Japanese Barberry), *Microstegium vimineum* (Trin.) A. Camus (Japanese Stiltgrass), *Lonicera morrowii* A. Gray (Morrow's Honeysuckle), and *Euonymus alata* (Thun.) Siebold (Burning Bush). Studies in the Delaware Water Gap National Recreation Area (Eschtruth et al. 2006) have documented the influx of invasive non-native plant species that were not found in initial 1993 plot surveys, but which occured in 35% of permanent plots 10 years later, including *Ailanthus altissima* (Mill.) Swingle (Tree-of-Heaven), *Alliaria petiolata* (M. Bieb.) Cavara & Grande (Garlic Mustard), Japanese Barberry, Japanese Stiltgrass, and *Rosa multiflora* Thunb. (Multiflora Rose). As the spread of invasive plant species continues, highly disturbed sites such as declining Hemlock stands appear to provide ideal habitat for new populations to establish. Long-term studies and repeated sampling efforts are needed to determine if invasive plant species colonize sites with high Hemlock mortality. It has been shown that invasive pests that co-occur with HWA, such as *Fiorinia externa* Ferris (Elongate Hemlock Scale) pose a threat to Hemlocks (Preisser et al. 2008) by altering regeneration (Preisser et al. 2011), growth, and foliar chemistry (Miller-Pierce et al. 2010).

Examination of ants provides insight into how structural changes in forest vegetation influence insects which mediate important ecosystem services such as nutrient cycling, seed dispersal, and decomposition (Del Toro et al. 2012, Folgarait 1998). Similar to vegetation, ant community composition and species density respond strongly to hemlock loss, with some species increasing in frequency and species density in declining hemlock forests; however, this correlation was not consistent across the gradient of sites. This result suggests the relationship between

changes in vegetation and ants is not a direct linear relationship, but a more complicated interaction. For example, some ants are either favored by or prefer the conditions of disturbed hemlock forests, such as *Prenolepis imparis* (Say), *Stigmatomma pallipes* (Haldeman), and *Temnothorax longispinosus* (Roger); however, with a more thorough ant sampling, this trend may not hold true as some of these species typically nest in trees (*T. longispinosus*). Some ant species, such as *Aphaenogaster picea* (Wheeler) and *Stenamma schmittii* (Wheeler) are resilient to changes in forest ground cover or overstory and persist in similar abundance in both healthy and declining hemlock forests. Several species preferred the hardwood forests, including *Lasius claviger* (Roger), *L. umbratus* (Nylander), *L. nearcticus* (Wheeler), and *Ponera pennsylvanica* (Buckley) (although *P. pennsylvanica* is found in a wide variety of habitats throughout the region). One species was equally common across hardwood and hemlock forest types but much less abundant in the dead hemlock forests, *Myrmica punctiventris* (Roger), which I suggest is due to either a difference in environmental conditions or competitive exclusion by more-dominant ant species once the forest habitat is disturbed (see Del Toro et al. 2013). Although I observed marked declines in the abundance of *Aphaenogaster rudis*, as hemlocks are removed from the overstory, this trend was not significant; however, more sampling might have yielded a stronger trend. I postulate this phenomenon might be caused by competitive exclusion of behaviorally sub-dominant ants in the *A. rudis* complex when large-scale disturbances occur (Del Toro et al. 2013), since their abundance decreases in the disturbed (dead hemlock) sites.

In this study, neither plant community composition nor species density can be used as surrogates to consistently predict ant community composition or species density, which is in agreement with Hill et al.'s conclusions (2008). This finding contrasts with a study documenting vegetation as the best indicator for non-ant ar-thropod richness (Schaffers et al. 2008), suggesting the vegetation–ant relationship is decoupled by large-scale, stand-replacing Hemlock decline. Thus, the observed differences between ant and plant species richness patterns among forest types across the latitudinal gradient may be due to the disturbed nature of the forest as Hemlocks declined, rather than by underlying differences in forest types. It is possible that as canopy closure increases over time, that vegetation may become a better predictor of arthropod richness.

Community composition differences vary among forest type and across latitude

Research has documented community and ecosystem responses to HWA at local and regional scales (Cobb et al. 2006, Evans et al. 2011, Nuckolls et al. 2009, Orwig and Foster 1998, Orwig et al. 2013, Stadler et al. 2005); however, a regional-scale examination of the interactions between community responses to Hemlock loss has been lacking. Although species diversity changes in vegetation communities across the gradient I studied, I observed no statistical differences in ant communities composition across the gradient. This finding suggests that ants are more resilient to the physical changes in forest structure as Hemlock declines, and that Hemlock species do not explicitly control ant fauna. Based on the ANOVA results, latitude,

a surrogate for the effects of climate, was the strongest predictor of differences for ant species density. Forest type was important at local scales at some sites, but not others. Both forest type and latitude were strong predictors for differences in vegetation species density. In both models for ant and vegetation species density, latitude, canopy type, and hemlock density were important parameters. For plants, total stand density and soil pH were also important predictors of species density, whereas litter depth was an important additional predictor for ants. These results suggest that the loss of acidic needle inputs into the litter layer and increased stand-stocking levels by newly recruited tree saplings as overstory Hemlocks die, are both important factors that influence understory plant communities.

While patterns in species density were consistent with my predictions and those observed in other studies (D'Amato et al. 2009), these trends varied across latitude suggesting a non-uniform response to the loss of Hemlocks on a regional scale. Contrary to my predictions, ants demonstrated variable responses in species density, with no consistent trend among forest type, but a direct relationship with latitude. My results suggest that plant species are more sensitive to changes in overstory vegetation than ant communities, which may require more extreme habitat alterations before a response is observed, e.g., a shift from a closed-canopy forest to an open-canopy habitat. There are several caveats when considering this result in the larger context of community and invasion ecology: 1) dispersal limitation could be an important factor (Caspersen and Saprunoff 2005, Clark et al. 1999); 2) Hemlock forests are species-poor with strong top-down controls over soil-chemical properties such as pH, compared with other temperate forest ecosystems; and 3) the invasive HWA is a host-specific pest, so although response patterns were similar among Hemlock stands across the gradient, more generalist invasive pests may elicit different responses in forest communities.

Conclusions

The loss of Hemlocks will alter the forest landscape in the eastern US and change the trajectory of these forests in the future. Many forested ecosystems maintain a legacy effect of Hemlocks, as noted by sharp contrasts between highly acidic soil and greater litter depth at formerly Hemlock-dominated sites and the higher pH soils and shallower litter layer in hardwood stands without previous hemlock composition. In this study, I found that vegetation within the Hemlock community was immediately influenced by changes in canopy light and the influx of novel organisms at sites with Hemlock mortality. Ants appeared to be resilient to changes in overstory and understory vegetation, a finding consistent with previous studies (Del Toro 2013); however there were marked declines in important seed-dispersing species (*A. rudis* complex) in hardwood and transitioning Hemlock forests compared with intact Hemlock forests. While these changes may not have immediate effects on ecosystem health, the long-term trajectory of these forest communities may be significantly altered by the loss of ecosystem engineers such as the seed-dispersing ant species. I suggest that managers consider local site factors and land-use history at specific forests, and the results of regional and local research to inform their

management decisions. In this study, I demonstrated that invasive HWA-induced structural changes in Hemlock forest communities led to consistent compositional shifts in understory plant communities but not in ant communities, suggesting that ants are not good bio-indicators in these highly disturbed Hemlock forests.

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