Changes in Ant Community Structure and Composition Associated with Hemlock Decline in New England

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ABSTRACT

Impacts of invasive species on the structure of the invaded communities is an active area of ecological research, but the effects of the hemlock woolly adelgid (HWA) on forest organisms other than economically important timber trees rarely have been examined. To date, studies of HWA impacts principally have assessed mortality rates of hemlock and their subsequent replacement by early-successional hardwoods, and changes in core ecosystem properties. However, if certain taxa are restricted to hemlock forests, or if dominance by hemlock precludes the colonization or occurrence of particular species, then removal of hemlock could result in changes in overall species diversity and composition within HWA-infested stands and across the landscape. We examined this hypothesis for forest ant communities in southern New England. Specifically, we asked how ant species richness and composition differed among intact hemlock stands, HWA-infested and damaged stands, and mid-successional hardwood "controls." In total, 22 species of ants were collected from 16 sites spread across Connecticut and Massachusetts. Average species richness among sites ranged from three to 12 (mean = 7), and was inversely related to the percent of hemlock basal area in the stand. Average dissimilarity among sites was 73%; notably, *Formica* spp. were virtually absent from intact, uninfested hemlock stands. At the stand level, loss of hemlock due to HWA results in an increase in ant species diversity, but this local increase in diversity is offset by homogenization of diversity across the landscape. The rate and impacts of colonization by *Formica* spp. into HWA-infested stands may alter ecosystem structure and dynamics in these forests and merits further study.

KEYWORDS

Ants, diversity, hemlock woolly adelgid, New England, species richness.

INTRODUCTION

Quantifying and predicting the impacts of invasive species on the structure and function of communities is a major focus of ecological research (*e.g.,* Vitousek 1986, Levine 2000, Crooks 2002, Gurevitch and Padilla 2004). To date, studies of the impacts of the hemlock woolly adelgid (HWA) on eastern U.S. forests principally have assessed mortality rates of hemlock and their subsequent replacement by early-successional hardwoods (*e.g.,* Lapin 1994, Orwig and Foster 1998, Bonneau et al. 1999, Mayer et al. 2002). Other studies have focused on ecosystem changes attendant to loss of hemlock due to HWA (*e.g.,* Jenkins et al. 1999, Orwig and Foster 2000, Stadler et al. 2005). However, if other taxa are restricted to hemlock forests, or if dominance by hemlock precludes the colonization or occurrence of certain species, then removal of hemlock could result in changes in overall species diversity and composition within HWA-infested stands and across the landscape. However, studies of the impact of HWA on organisms other than economically important timber trees in eastern forests are rare (Tingley et al. 2002).

Here, we examine the changes in ant (Hymenoptera: Formicidae) community structure and composition occurring as HWA alters hemlock forests. Ants may be a useful indicator taxon for the impact of HWA on other hemlock-associated communities for several reasons. Ants are abundant and diverse in eastern (U.S.) forests (Cole 1940, Gotelli and Ellison 2002); they interact with plants (*e.g.,* Beattie and Culver 1981, Guo and Brown 1996) and invertebrates (Buckley 1987, Cushing 1997); and they can both drive (*e.g.,* Lyford 1963, Folgarait 1998, MacMahon et al. 2000) and respond to (Johnson 1992) ecosystem processes. Ant community structure changes in response to changes in plant community structure in deserts and grasslands (*e.g.* Bestelmeyer 2005), and ants have been used as indicators of ecosystem degradation and successful rehabilitation in arid environments (*e.g.,* Andersen et al. 2002).

As a first step to understanding how ant community structure could be affected by HWA impacts to hemlock forests, we examined how ant species richness and composition varied among intact hemlock stands, hemlock stands in varying states of degradation due to HWA and that have varying amounts of early-successional shrubs and hardwoods, and mid-successional deciduous stands – to which succession will proceed following the loss of hemlock in New England. Our results have implications for managing anticipated changes in local and regional biodiversity associated with the impact of HWA on New England forests. The observed compositional changes in ant communities associated with loss of hemlock also may be associated with substantial changes in soil ecosystem processes.

METHODS

SITES

We sampled eight sites in Connecticut (CT) and eight sites in Massachusetts (MA). The CT sites are a subset of those surveyed by Orwig et al. (2002) for HWA damage in southern New England, and are focal sites for studies of the impact of HWA on ecosystem processes (Jefts and Orwig 2005). These sites were all dominated by hemlock, and mortality due to HWA in these sites ranges from none to nearly 100% (Table 1). The MA sites were all 90 x 90 m plots

Table 1. Site characteristics. Latitude and longitude are in decimal degrees; elevation is in meters above sea level; overstory basal area is in m^2 (in a 20 x 20 m plot at the CT sites and a 30 x 30 m plot at the MA sites; percent hemlock is percent of total basal area that is live hemlock; GSF is global site factor—proportion of total solar radiation above the canopy that reaches ground level (in the center of the sample plot); AntS is number of ant species collected at each site.

Site	Lat.	Long.	Elev.	Overstory Basal Area	% Hemlock	GSF	AntS
Connecticut							
Selden Neck	41.40	72.40	64	41.8	31	0.043	10
Burnham Brook	41.46	72.33	132	8.4	2	0.067	10
Devil's Hopyard	41.47	72.34	72	38.1	65	0.056	10
Sunrise Resort	41.50	72.48	128	32.2	32	0.039	8
Salmon River	41.56	72.44	187	36.7	60	0.041	9
Ash Brook	41.78	72.40	174	20.8	29	0.110	12
Willington Hill	41.87	72.25	178	65.8	87	0.022	4
Crooked Road	41.98	72.27	228	60.2	65	0.065	7
Massachusetts							
Simes 1	42.47	72.22	207	49.6	82	0.073	4
Simes 2	42.47	72.22	210	44.2	68	0.034	3
Simes 3	42.47	72.22	214	40.5	56	0.053	4
Simes 4	42.47	72.21	225	51.4	77	0.038	7
Simes 5	42.47	72.21	220	52.2	78	0.081	4
Simes 6	42.47	72.21	224	71.9	70	0.080	3
Simes 7	42.48	72.21	229	44.8	6	0.083	8
Simes 8	42.47	72.22	220	26.4	0	0.041	11

located within the Simes Tract at the Harvard Forest. These plots are scheduled for experimental manipulations (logging, girdling to simulate slow death due to HWA, or no treatment) in 2005; plots 1-6 are in stands dominated by hemlock, whereas plots 7 and 8 are mid-successional hardwood "controls" (Barker-Plotkin et al. 2004). As of summer 2004, HWA had been found in two of the Simes plots (plots 5 and 6), but no impacts on tree vigor had yet been observed (Diana Barszcz and Scott Costa, pers. obs.).

ANT SAMPLING

We used standard methods for sampling diversity of ground-nesting ants (Agosti and Alonso 2000). At each site, we established a square grid of 25 pitfall traps (20 x 20 m with 5 m spacing in CT; 10 x 10 m with 2.5 m spacing in MA). Each pitfall trap consisted of a 95mm-diameter plastic cup filled with 20 mm of dilute soapy water. Traps were buried so that the upper lip of each trap was flush with the surface of the substrate, and left in place for 48 hours during dry weather. Trap contents were fixed in the field in 95% EtOH. After the pitfall traps were collected, we removed the traps, refilled the holes, and set out a grid of 25 bait stations each consisting of 50 g of Pecan Sandies on a 12.5 x 7 cm index card. Baits were allowed to accumulate ants for 1 hour in the middle of the day, and then representative individuals were collected with a suction aspirator. We also collected 3 1-liter leaf litter samples from each grid and sifted them in the field to collect litter-dwelling ants. Finally, we actively searched in and around each grid for 1 hour and hand-collected any ants that were found on the substrate, in the leaf litter, or on low-growing vegetation. At each site, two complete ant surveys (pitfalls, baits, litter, and hand-samples) were conducted separated by approximately 42 days. The same grids were re-sampled in the second survey. The CT sites were sampled in June–August, 2004, and the MA sites were sampled in July and August in both 2003 and 2004 (with only one sample in 2004). All ants were identified to species; identifications were confirmed by Stefan Cover of the Museum of Comprative Zoology.

VEGETATION SAMPLING

To obtain an "ant's-eye" view of the vegetation at each site, we recorded the number of stems of all herbs and shrubs in 50 x 50 cm square quadrats centered on each pitfall trap. We sampled vegetation in mid-July, the peak of the growing season, to ensure that we recorded the vast majority of both early and late emerging plants. In addition, diameter at breast height (DBH) of all trees greater than 5 cm DBH in each grid was also recorded. Total basal area and percent basal area in hemlock were determined from these data.

CANOPY MEASUREMENTS

Available light levels beneath the forest canopy were estimated from hemispherical canopy photographs, which were taken after full leaf flush of the canopy at each site. Photographs were taken 1 m above ground level using an 8mm fish-eye lens on a Nikon F-3 camera. Although this does not precisely correspond to an ants-eye view at ground level, differences among sites in ground-level light interception are closely correlated with these measurements (Chazdon and Field 1987, Rich et al. 1993). The camera was leveled and oriented to magnetic north for each photograph. Images were digitized at 300dpi and analyzed using HemiView 3.1 (Delta-T, Cambridge, United Kingdom). We summed weighted values of direct site factor

(DSF) (total direct beam solar radiation) and indirect site factor (total diffuse solar radiation) to compute a global site factor (GSF) (total solar radiation) for each forest site (Rich et al. 1993). GSF values are expressed as percent of total possible solar radiation (i.e., above the canopy) during the growing season (April through October), corrected for latitude and solar track.

RESULTS

In total, 22 species of ants in three subfamilies were collected across the 16 sites (Figure 1). Of these, four are common generalist species of eastern forests (*Camponotus pennsylvanicus* (de Geer), *Aphaenogaster rudis* (Enzmann) *s.l.*, *Temnothorax longispinosus* (Roger), and *Myrmica punctiventris* (Roger)) and four are southern species near their northern range boundary (*Prenolepis impairs* (Say), *Acanthomyops interjectus* (Mayr), *Camponotus chromaiodes* Bolton, and *Stenamma schmitti* Wheeler). The average species richness (á-diversity) at a site was 7 species, and ranged from 3 to 12 species (Table 1). The average pair-wise Jaccard dissimilarity (one measure of landscape-level, or β-diversity) among sites was 0.73 (range = 0.2 – 0.93), indicating substantial differences among sites.

Ant species richness was lowest in dense hemlock stands and increased significantly as hemlock basal area declined (Table 1, Figure 2). This change in species richness appears to be an actual effect of hemlock, as ant species richness was not significantly associated with other, potentially confounding factors, including latitude ($P = 0.19$), elevation ($P = 0.33$), or richness (number of species) and diversity (Simpson's index) of understory vegetation ($P = 0.07$).

The increase in species richness in early-successional mixed stands of shrubs and hardwoods (CT stands impacted by HWA) and in mid-successional (80-125 year-old) deciduous stands (MA stands without HWA) was due almost entirely to the occurrence in these stands of *Formica* spp., which were entirely absent in dense hemlock stands. This pattern is independent of subgenera: *Formica aserva* Forel (subgenus *sanguniea*) is an actively-foraging, slave-making ant. The similarly active *Formica neogagates* Viereck (subgenus *neogagates*) forms small colonies. *Formica subsericea* Say and *F. subaenescens* Emery (both subgenus *fusca*) are generalists and somewhat less active foragers. As with the overall relationship between species richness and hemlock basal area, the effect on *Formica* appears to be an actual effect of hemlock, as there was no consistent relationship with insolation ($P = 0.73$) – an otherwise common driver of ant activity (Figure 3).

DISCUSSION

We examined changes in ant diversity and composition in stands with a known history of HWA impact (the CT stands) (Orwig et al. 2002), in stands so far undamaged by HWA (Simes plots 1-6 in MA), and in mid-successional hardwood stands (Simes plots 7-8 in MA) that represent the anticipated stand structure 80-100 years from now, after HWA has eliminated hemlock from our landscape (Barker-Plotkin et al. 2004). At the stand level, a shift from hemlock to hardwood resulted in an increase in ant species diversity (Figure 2). Because geographic (latitude and elevation) or habitat (understory vegetation structure, composition, and insolation) did not significantly affect ant species richness, we conclude that the low levels of

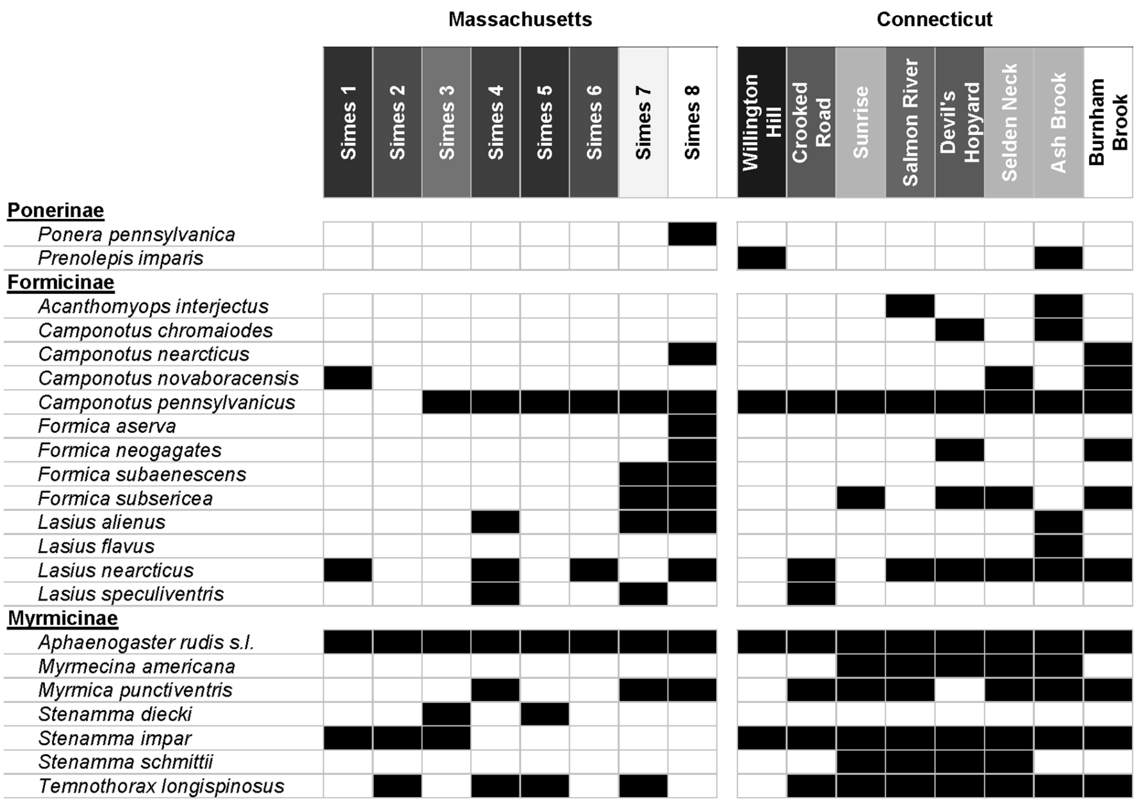

Figure 1. Species by site matrix of ant species at the 16 sampled sites. Shading of the site name is proportional to the percent hemlock cover (black = 100%; white = 0%).

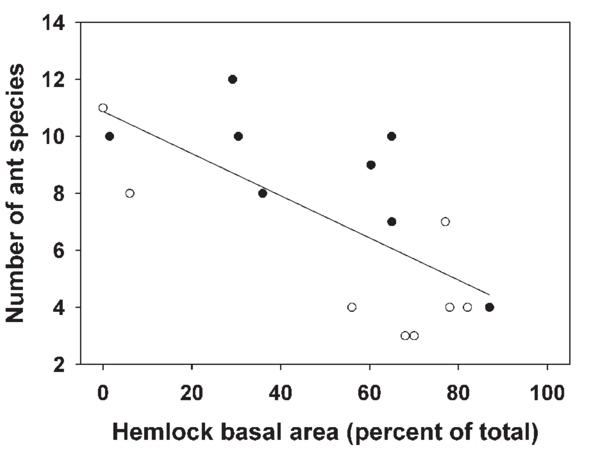

Figure 2. Relationship ($r^2 = 0.50$, $P = 0.002$) between ant species richness and percent of hemlock (basal area) in the eight sampled stands in Connecticut (solid circles) and the eight sample plots in Massachusetts (open circles).

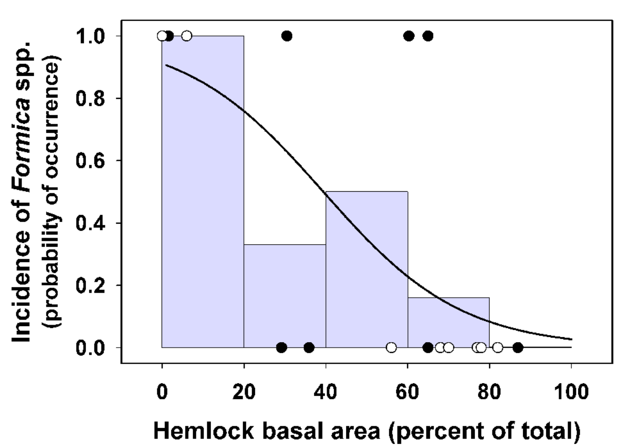

Figure 3. Incidence of *Formica* spp. at the 16 sites. Points are the raw data (solid circles: Connecticut stands; open circles: Massachusetts stands); bars are proportion of sites in each of five basal area classes in which *Formica* spp. were found; the line is the best-fit logistic regression ($P = 0.045$) to the incidence data, and predicts the probability of encountering *Formica* for any given percent of hemlock basal area.

ant species richness observed in hemlock results from effects of hemlock itself on the system. Such effects could include changes in local microclimate or soil properties (Mladenoff 1987, Finzi et al. 1998a and 1998b, Ferrari 1999, Hadley 2000). The increase in species richness observed in early- and mid-successional hardwood stands could be associated with a greater number of homopterans in these forests (Buckley 1987). Homoptera are often tended by formicine ants, and the rate and impacts of colonization by *Formica* spp. into HWA-infested stands may alter homoptera population dynamics, consequent nutrient throughfall (*cf.* Stadler et al. 2005), and ecosystem structure and dynamics in these forests. The proximate and mechanistic causes and the system-wide effects of this compositional shift in ant diversity merit further study.

An oft-professed goal of ecosystem management is to increase biodiversity (*e.g.*, Tilman et al. 1997, Chapin et al. 2000, Garber-Yonts et al. 2004); the increase in ant species richness as hemlock declines superficially suggests that HWA exerts a net positive effect on faunal diversity in New England forests. However, the increase in ant species richness at local (stand) scales would be more than offset by the reduction in regional biodiversity (expressed as dissimilarity among sites). In other words, by converting a regionally diverse assemblage of forests stands, HWA homogenizes our forests – their plants, their ants, and presumably other associated fauna. This biotic impoverishment affects us all.

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