

## RESEARCH

# Canopy Vegetation Influences Ant (Hymenoptera: Formicidae) Communities in Headwater Stream Riparian Zones of Central Appalachia

Jonathan T. Johnson, Joshua K. Adkins, and Lynne K. Rieske<sup>1</sup>

Department of Entomology, University of Kentucky, S225 Ag North, Lexington, KY 40546-0091

<sup>1</sup>Corresponding author, e-mail: Irieske@uky.edu

Subject Editor: Evan Preisser

J. Insect Sci. 14(237): 2014; DOI: 10.1093/jisesa/ieu099

**ABSTRACT.** In the eastern United States, eastern hemlock *Tsuga canadensis* (L.) Carrière forests are threatened by the invasive hemlock woolly adelgid, *Adelges tsugae*, a pest that is causing widespread hemlock mortality. Eastern hemlock is an essential component of forested communities. Adelgid-induced hemlock mortality is causing a shift in forest composition and structure, altering ecosystem function and thereby influencing the arthropod community. Using pitfall traps at three sites, we monitored ground-dwelling arthropods at 30-d intervals in hemlock-dominated and deciduous-dominated forests in central Appalachia over 2 yr. Here, we focus on the ant community (Hymenoptera: Formicidae) collected in the summer months. Ants form a ubiquitous and integral component of the invertebrate community, functioning at various trophic levels as predators, herbivores, and omnivores, and fulfilling important roles in forest ecosystems. We found no difference in overall ant abundance between hemlock-dominated and deciduous-dominated forests but did detect significant differences in the genera *Prenolepis* between forest types ( $P < 0.01$ ) and *Aphaenogaster* across study locations ( $P = 0.02$ ). Three genera were unique to deciduous forests; one was unique to hemlock forests. Not surprisingly, total formicids and several genera demonstrated temporal differences in abundance, with greater numbers captured in July than in August. As hemlock woolly adelgid-induced mortality of eastern hemlock becomes more pervasive, changes in forest composition and structure are imminent, accompanied by shifts in hemlock associates.

**Key Words:** Arthropod, diversity, hemlock, *Tsuga canadensis*, hemlock woolly adelgid

Eastern hemlock, *Tsuga canadensis* (L.) Carrière, is an important foundation species in the sense that it defines the structure of the communities in which it occurs (Ellison et al. 2005a). Eastern hemlock creates densely shaded microclimatic conditions in riparian and cove habitats, regulating nutrient cycling and stream base flows, and maintaining air, soil, and water temperatures under its dense canopy (Godman and Lancaster 1990, Ford and Vose 2007, Nuckolls et al. 2009). Decomposition of eastern hemlock leaf litter is slow, resulting in localized differences in pH (Finzi et al. 1998), and a relative lack of vegetative community associates in the understory (Rankin and Tramer 2002). Hemlock is a crucial evergreen that provides essential habitat for songbirds (Tingley et al. 2002), and creates conditions which are conducive to distinct fish (Ross et al. 2003) and benthic invertebrate assemblages (Snyder et al. 2002, J.K.A. and L.K.R., unpublished data). Distinct salamander (Welsh and Droege 2001) and invertebrate communities (Rohr et al. 2009, Adkins and Rieske 2013) are associated with eastern hemlock riparian areas.

This ecologically important forest species is threatened throughout its range by the exotic invasive hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae). The adelgid depletes hemlock starch reserves, causing rapid tree mortality and leading to shifts in forest composition to hardwood species (Orwig and Foster 1998, Spaulding and Rieske 2010), with far-reaching consequences on structure, function, and diversity within affected forests. This transition to a hardwood canopy can lead to shifts in light penetration, nutrient availability, soil chemistry, and leaf litter composition (Jenkins et al. 1999, Webster et al. 2012). Faunal populations and communities that rely on eastern hemlock will be affected by the ecological changes associated with hemlock decline (Gandhi and Herms 2010).

The Formicidae (order: Hymenoptera) represent a portion of the invertebrate community that will likely be affected by changing forest canopy characteristics; loss of the eastern hemlock component may have direct effects on some members of this group. Ants are ubiquitous

and integral components of most ecosystems (Gotelli and Ellison 2002); they affect nutrient cycling, soil aeration, and plant distribution (Folgarait 1998). They are strongly influenced by environmental characteristics and microclimate, and generally select habitats with open canopies (Dolek et al. 2008, Klimes et al. 2012, Van Gils and Vanderwoude 2012). In central Appalachia, ant abundance differs between forests with eastern hemlock versus deciduous canopies (Adkins and Rieske 2013); Formicidae activity is most closely associated with deciduous understory vegetation. In New England, ant abundance and richness is greater in midsuccessional deciduous forests than in eastern hemlock forests unaffected by hemlock woolly adelgid (Ellison et al. 2005b). The objective of this study was to determine to what extent ant communities may be affected by hemlock woolly adelgid-induced eastern hemlock mortality. To this end, a comparison was made of the formicid community in hemlock-dominated forests with those found in deciduous-dominated forests, because deciduous forests represent a potential end point in the successional trajectory following adelgid-induced hemlock mortality (Orwig and Foster 1998, Spaulding and Rieske 2010).

## Materials and Methods

Three research sites were established in eastern Kentucky in the Cumberland Plateau physiographic province (Adkins and Rieske 2013). This area is characterized by steep, mountainous terrain underlain by shale and sandstone (McDowell 1986). The first site, the Red River Gorge Geological Area, Natural Bridge State Park State Nature Preserve (RRG), is located in the Northern Forested Plateau Escarpment ecoregion (83° 37' 44.115" W, 37° 49' 9.164" N). The second site, Robinson Forest (RF), is situated in the dissected Appalachian Plateau ecoregion (83° 9' 30.578" W, 37° 27' 38.68" N). Lastly, Kentucky Ridge State Forest (KYR) (83° 47' 26.048" W, 36° 42' 14.408" N) is located further south in the Cumberland Mountain Thrust Block ecoregion (Woods et al. 2002). The dominant vegetation is a

mixed mesophytic forest (Davis 1924, Braun 1950). Annual precipitation ranges from 106 to 139 cm; temperatures vary from  $-6.2$  to  $8.3^{\circ}\text{C}$  in January and from  $16.6$  to  $31.6^{\circ}\text{C}$  in July (Woods et al. 2002). Elevation varies from 167 to 1,261 m (Woods et al. 2002).

Study sites were selected using Geographic Information Systems (GIS) and remote sensing techniques. Three eastern hemlock dominated streams and three deciduous dominated streams were selected at each of the three sites for a total of eighteen riparian zones in the study (Adkins and Rieske 2013).

Riparian vegetation composition and structure were assessed by evaluating woody plant vegetation in two 0.04-ha fixed-radius whole plots within each stream's riparian zone, one on each side of the stream (Coleman et al. 2008, Adkins and Rieske 2013). Whole plots (0.04 ha) were utilized to assess overstory and midstory woody vegetation (trees  $\geq 12.7$  cm in diameter at 1.5 m above ground level; Diameter at Breast Height (DBH)), 0.004-ha subplots were used to quantify shrubs and saplings ( $< 12.7$  cm DBH,  $> 137$  cm high), and 0.0004-ha microplots were used to assess seedlings, shrubs ( $< 137$  cm in height), and vines. Measurements of vegetation and plot data followed the Common Stand Exam protocol of the U.S. Department of Agriculture Forest Service's Natural Resource Information System: Field Sampled Vegetation Module (USDA 2009, Adkins and Rieske 2013). Riparian zones designated as eastern hemlock dominated had an average eastern hemlock basal area of  $12.6$  (SE =  $2.2$ )  $\text{m}^2/\text{ha}$ , whereas deciduous dominated stands had an average eastern hemlock basal area of  $4.7$  (SE =  $1.6$ )  $\text{m}^2/\text{ha}$  (Adkins and Rieske 2013).

Large capacity pitfall traps (Houseweart et al. 1979, Coleman and Rieske 2006, Adkins and Rieske 2013) were used to assess terrestrial arthropod activity within the riparian zone of each stream. Traps consisted of a 150-mm plastic funnel, a 1-liter Nalgene holding bottle, and a 30- by 30- by 0.6-cm apron fashioned from tempered hardboard. Approximately 250 ml of 1:1 70% ethyl alcohol: ethylene glycol was used as a killing and preserving agent. Three traps were placed along the accessible side of the stream in each riparian zone, spaced  $\sim 10$  m apart. Traps spaced at  $\geq 10$  m intervals do not affect abundance or composition of invertebrates collected from adjacent traps (Ward et al. 2001), implying sample independence. Traps ( $N = 54$ ) were installed and opened in September 2008 and the contents were collected at monthly intervals through September 2010. The contents of each trap were removed and returned to the laboratory, where they were stored in 70% ethanol. Formicid specimens collected during the summer months (July and August) in 2009 and 2010 were included, as they contained the greatest number of individuals. Samples were sorted, counted, and identified to the lowest taxonomic resolution possible using appropriate keys (Ross et al. 1971, MacGown 2012). Abundance (recorded as activity density) was calculated for each formicid taxon identified on a per-trap basis. The Shannon–Weaver diversity index, which uses relative abundance of each taxon and total insect abundance within a sample (Magurran 1988) was calculated as  $H' = -\sum p_i \log p_i$ , where  $p_i$  = relative abundance of each taxon, calculated as the proportion of individuals of a given taxon to the total number of individuals in the community:  $n_i/N$ ,  $n_i$  = number of individuals (abundance) of each taxon;  $N$  = total number of all individuals. From this, Pielou's Index of Evenness ( $J$ ), which incorporates the Shannon index and taxa richness in the sample (Magurran 1988), was calculated as  $J = H'/\ln(S)$ , where  $S$  = taxa richness (Southwood and Henderson 2000). The Simpson index was calculated as  $D = 1 - [\sum (n_i/N)^2]$ , where  $n$  = the total number of organisms of a particular taxa and  $N$  = the total number of individuals (Magurran 1988). Additionally, Jaccard's coefficient ( $J$ ) was calculated to determine overlap between the combined taxa lists of the two riparian vegetation types, as  $J = A \cdot [(B + C) - A]^{-1}$ ; where  $A$  = the number of taxa found in both riparian zone designations,  $B$  = the number of taxa found only in eastern hemlock dominated riparian zones, and  $C$  = the number of taxa found only in deciduous dominated riparian zones (Krebs 1999). Data were analyzed using a generalized linear mixed model to assess the influence of overstory vegetation (eastern

**Table 1. Formicidae abundance in pitfall traps ( $N = 54$ ) monitored in eastern hemlock and deciduous dominated riparian zones of central Appalachia over two summers**

Subfamily	Genus	Overstory vegetation		Total
		Hemlock	Deciduous	
Formicinae	<i>Camponotus</i>	157	37	194
	<i>Prenolepis</i>	0	63	63
	<i>Formica</i>	27	2	29
	<i>Lasius</i>	17	12	29
	<i>Acanthomyops</i>	2	2	4
	Subtotal	203	116	319
Myrmecinae	<i>Aphaenogaster</i>	270	233	503
	<i>Tetramorium</i>	14	4	18
	<i>Myrmecina</i>	1	0	1
	Subtotal	285	237	522
Ponerinae	<i>Ponera</i>	0	2	2
	Subtotal	0	2	2
Dolichoderinae	<i>Dorymyrmex</i>	0	2	2
	Subtotal	0	2	2
Total Formicidae		488	357	845

hemlock vs. deciduous), sample month, and study site (RRG, RF, and KYR) on formicid occurrence and associated population parameters. Initially, sample year was included in the model, but because it was not significant, it was excluded from the final analysis.

## Results

Focusing only on pitfall trap samples with  $\geq 10$  formicid individuals, sampling in July and August over 2 yr yielded a total of 845 Formicidae in four subfamilies, including Formicinae (38%), Myrmecinae (62%), Ponerinae ( $< 1\%$ ), and Dolichoderinae ( $< 1\%$ ), representing 10 genera (Table 1). Formicid abundance did not differ between riparian zones dominated by eastern hemlock and their deciduous counterparts ( $P = 0.91$ ; Table 2); 488 were collected from eastern hemlock dominated riparian zones and 357 from deciduous dominated riparian zones. The number of genera was greater in deciduous dominated forests (9 vs. 6), but the difference was not statistically significant ( $P = 0.15$ ; Table 2). Further, no differences were discovered between the two forest types with respect to ant diversity (Shannon–Weaver or Simpson's indices) or evenness (Table 2).

Greater numbers of ants were collected in July than in August (Table 2), driven by the numerically dominant genera, *Aphaenogaster* (Fig. 1a) and *Camponotus* (Fig. 1b). Generic richness across both years was statistically greater in samples collected during July than during August, but numerically this difference was small ( $\bar{x} = 0.7$  vs.  $0.2$ ; Table 2).

The genus *Aphaenogaster* (subfamily Myrmecinae) ( $n = 503$ ) represented  $\sim 60\%$  of the specimens collected, with abundance similar between hemlock dominated and deciduous dominated riparian areas (270 vs. 233) (Table 1) and abundance greater in July than in August (Table 2, Fig. 1a).

*Camponotus* ( $n = 194$ ) was the next most abundant genus. Although they were more numerous in hemlock riparian areas than in deciduous areas (157 vs. 37 individuals), because of high variance, the difference was not significant. Greater numbers of *Camponotus* were captured in July than in August (Tables 1 and 2, Fig. 1b).

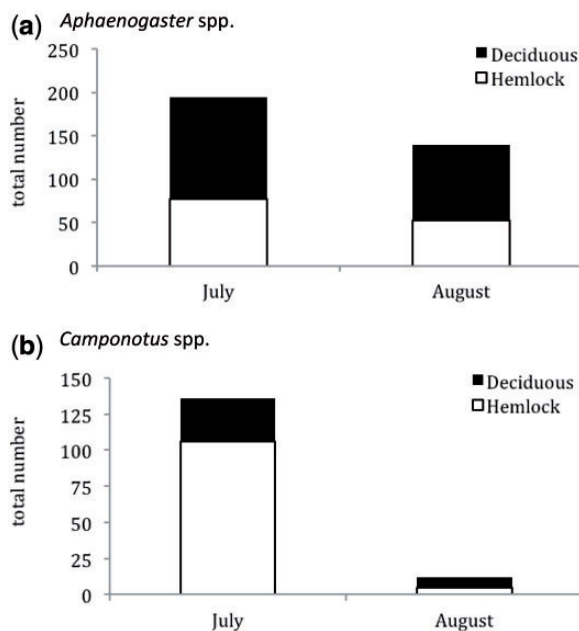
Ants in the genus *Prenolepis* ( $n = 63$ ) (subfamily Formicinae) were the third most abundant genus (Table 1). They were unique to deciduous dominated riparian areas and were the only taxon to demonstrate significant differences between dominant vegetation; none were recorded from pitfall traps in hemlock dominated riparian areas (Table 2 and Fig. 2).

Less than 30 individuals were captured in the remaining seven genera, representing  $< 1\%$  of the total (Table 1). Two individuals from the genus *Ponera* (subfamily Ponerinae) and two individuals from the

**Table 2. Abundance and diversity (mean [SE] per trap, N = 54) of ant genera sampled in pitfall traps from the forest floor of eastern hemlock and deciduous dominated forests over summer months in eastern Kentucky**

	Overstory vegetation		Month	
	Hemlock	Deciduous	July	August
<i>Aphaenogaster</i>	2.5 (0.6)a	2.2 (0.5)a	3.4 (0.7)a	1.3 (0.4)b
<i>Camponotus</i>	1.5 (0.8)a	0.3 (0.1)a	1.7 (0.8)a	0.1 (0.0)b
<i>Prenolepis</i>	0.0 (0.0)a	0.6 (0.3)b	0.5 (0.2)a	0.1 (0.1)a
<i>Lasius</i>	0.2 (0.1)a	0.1 (0.1)a	0.3 (0.1)a	0.0 (0.0)b
<i>Formica</i>	0.3 (0.3)a	0.0 (0.0)a	0.3 (0.3)a	0.0 (0.0)a
<i>Tetramorium</i>	0.1 (0.1)a	0.0 (0.0)a	0.2 (0.1)a	0.0 (0.0)a
<i>Acanthomyops</i>	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a
<i>Myrmecina</i>	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a
<i>Ponera</i>	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a
<i>Dorymyrmex</i>	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a	0.0 (0.0)a
Total Formicidae	4.5 (1.3)a	3.3 (0.7)a	6.4 (1.4)a	1.5 (0.4)b
Shannon Index	0.4 (0.1)a	0.6 (0.1)a	0.6 (0.1)a	0.4 (0.1)a
Simpson Index	0.2 (0.0)a	0.4 (0.0)a	0.6 (0.0)a	0.5 (0.1)a
Evenness	0.5 (0.1)a	0.6 (0.1)a	0.4 (0.0)a	0.3 (0.1)a
Generic richness	0.4 (0.1)a	0.5 (0.1)a	0.7 (0.1)a	0.2 (0.1)b

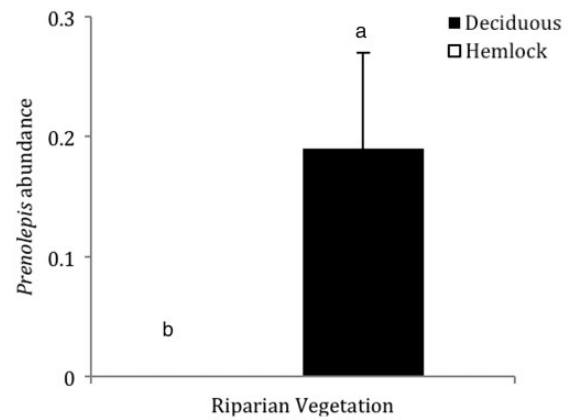
Means within rows followed by the same letter are not significantly different ( $\alpha = 0.05$ ).



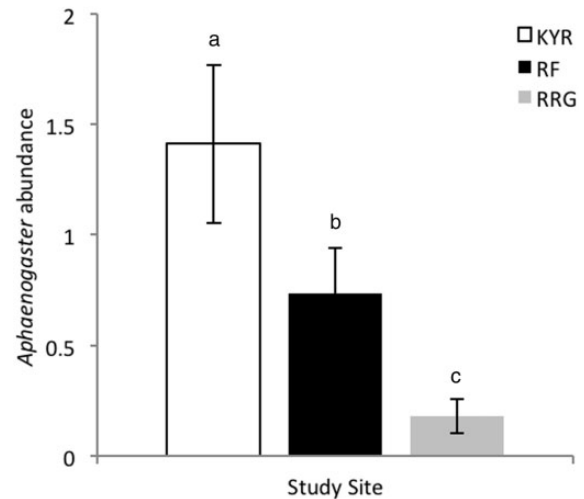
**Fig. 1.** Occurrence of numerically dominant ants from July and August pitfall trap collections (N = 54) from hemlock dominated versus deciduous dominated riparian areas of central Appalachia. The abundance of a) *Aphaenogaster* spp. and b) *Camponotus* spp. did not differ among study locations or dominant riparian canopy vegetation.

genus *Dorymyrmex* (subfamily Dolichoderinae) were found only in deciduous dominated areas. Similarly, there was a single individual in the genus *Myrmecina* that was found in a single trap from a hemlock dominated area (Table 1).

In addition to the lack of differences in overall formicid abundance or any subfamily abundance between dominant riparian vegetation or between study sites, there was no significant vegetation by study site interactions, regardless of taxonomic level. There was a significant difference in the genus *Aphaenogaster* among study sites, with the majority captured at Kentucky Ridge, the southernmost site, and the fewest were captured at Red River Gorge, the northernmost site, and intermediate numbers captured at Robinson Forest (RF) (Fig. 3).



**Fig. 2.** Occurrence of *Prenolepis imparis* in hemlock dominated versus deciduous dominated riparian areas of central Appalachia. N = 54,  $F_{1,48} = 7.41$ ,  $P < 0.01$ , different letters indicate significant differences.



**Fig. 3.** Abundance of *Aphaenogaster* ants in riparian areas of three study sites in southeastern Kentucky. KYR: Kentucky Ridge State Forest; RF: Robinson Forest; RRG: Red River Gorge. N = 54;  $F_{2,48} = 5.81$ ,  $P < 0.01$ , different letters indicate significant differences.

## Discussion

As hemlock woolly adelgid-induced mortality of eastern hemlock becomes more severe and more pervasive in the eastern United States, changes in forest composition and structure are imminent, accompanied by concomitant shifts in hemlock associates. Differences in ground-dwelling ant communities within eastern hemlock-dominated and deciduous-dominated forests of central Appalachia were investigated using pitfall traps monitored during the summers of 2009 and 2010. Overall formicid abundance did not differ between forest types. A greater number of formicid genera were found in deciduous dominated forests relative to hemlock dominated forests, though differences were not statistically significant. Three genera were unique to deciduous forests, and one was unique to hemlock forests. Elevation varied considerably among the study sites (167–1,261 m), which would lead to differences in plant communities and subsequent variation in formicid communities. In spite of this, there was very little difference in ant abundance across sites. Not surprisingly, total formicids and several genera demonstrated temporal differences in abundance, with greater numbers captured in July than in August.

The Jaccard value comparing overlap of the 10 formicid genera that were collected between eastern hemlock and deciduous dominated

riparian zones demonstrates that the two riparian zone designations were 60% similar with respect to formicid community composition. Deciduous riparian zones had a greater number of unique taxa ( $n = 3$ ) than eastern hemlock riparian zones ( $n = 1$ ).

The most abundant genus, *Aphaenogaster*, was equally distributed in hemlock and deciduous forests and was more abundant in July than August. *Aphaenogaster* is a common genus that occurs in all habitats but is especially common in mesic forested ecosystems (MacKay and MacKay 2002, MacGown 2012). Rohr et al. (2009) found that *Aphaenogaster* were more closely associated with hardwood forests in Virginia's Shenandoah National Park; those results were not supported by findings from this study, which found equivalent abundances. It is possible that the hardwood sites in Rohr et al. (2009) were located in more mesic areas that would support greater *Aphaenogaster* abundances than we observed. *Aphaenogaster* nest in soil under decaying logs or rocks, in colonies that are moderate to very large (MacKay and MacKay 2002). These ants are omnivores, feeding on dead insects and also tending Homoptera or collecting nectar.

*Camponotus* abundance in hemlock and deciduous forests was also statistically equivalent, though numerically greater numbers were captured from hemlock forests; they were also more abundant in July than in August. *Camponotus* are habitat generalists; the lack of differences in abundance between the two riparian forest types in this study is not unexpected. Over 20 species are found in the eastern United States (MacGown 2012) and over 900 species worldwide. Females ("majors" or "queens") are required for definitive identification (Mackay and Mackay 2003), and many species are polymorphic (MacGown 2012). *Camponotus* are referred to collectively as "carpenter ants" because of their habit of nesting in association with dead and decaying wood, where they form large but loose colonies. They do not eat wood. They are omnivorous, and forage for honeydew and plant secretions, as well as small invertebrates.

The most numerous unique taxon in deciduous riparian zones was *Prenolepis*. In North America, *Prenolepis* is monospecific, with several recognized subspecies (Bolton 2013a,b). In this study, *Prenolepis imparis* (Say) was found exclusively in the more open deciduous dominated sites; none were captured in hemlock sites, and there was no temporal difference in *P. imparis* abundance. *P. imparis* is widely distributed and generally abundant in the United States (Wheeler 1930). It is usually associated with oak woodlands or beech-maple forests (Tschinkel 1987), where it occurs in small, well-defined colonies, sometimes displaying aggressive behavior and relying heavily on trail pheromones during foraging (Talbot 1943). *P. imparis* are sometimes referred to as "winter ants" because they remain active at low temperatures, even in northern latitudes (Talbot 1943). Their appearance in this study in the more open, warmer deciduous plots is somewhat unexpected, especially since they are generally absent from samples during the summer months in Maryland (Fellers 1989), and workers seal their nests from April to November in Florida (Tschinkel 1987). Diurnal activity patterns further reflect avoidance of warmer temperatures and minimize competition among the woodland formicid community (Fellers 1989). Given that, it is surprising that *P. imparis* was captured in pitfall traps in summer months in central Appalachia in this study, even at low numbers. Monitoring these sites during the winter months when temperatures are cooler would provide greater insights into these puzzling results. Sometimes referred to as "false honey ants" due to the storage product in corpulent workers that facilitates brood production (Tschinkel 1987), *P. imparis* feeds on decaying fruit, nectar, honeydew, and arthropod carrion.

In this study, only one genus was unique to hemlock forests, and only a single individual was found. Similar to *Prenolepis*, *Myrmecina* is also thought to be monospecific in eastern North America. *Myrmecina americana* Emery is found in rich forests of the southeast, typically nesting in small colonies in soil under logs and at bases of trees (MacGown 2013). It does not appear to be associated with a specific forest type or successional stage (AntWeb 2013).

Many of the findings reported here corroborate those of Ellison et al. (2005b), who found shifts in ant community structure between these two forest types in New England, including greater ant richness and diversity in deciduous dominated stands. However, there are notable differences in results between the two studies. In New England, *P. imparis* was found only in a single hemlock-dominated site, reflecting its affinity for cooler temperatures, and *Formica* spp. were found exclusively in deciduous stands (Ellison et al. 2005b). In contrast, *P. imparis* was confined to deciduous sites in this study, and *Formica* spp. was found only in low numbers, and primarily in hemlock-dominated areas.

Ants appear to select areas of open and light canopies over those with denser canopies and darker conditions, suggesting that the composition of ant communities may be driven by forest structure (Dolek et al. 2008, Klimes et al. 2012, Van Gils and Vanderwoude 2012) and influenced by litter characteristics (Karban et al. 2013). Eastern hemlock canopies generate exceptionally deep shade (Canham et al. 1994) with acidic litter and soils (Jenkins et al. 1999), which may manifest itself in altered formicid abundance, diversity, or evenness.

Ants affect physical and chemical changes in soil strata, influence energy flow and nutrient dynamics (Jones et al. 1994, Meyer et al. 2013), and lead to vegetation changes (Folgarait 1998). Thus, a shift to deciduous dominance could lead to alterations in competitive interactions and resource partitioning between competing groups of ants (Fellers 1989). It is probable that as forest composition and structure shift due to hemlock woolly adelgid induced hemlock mortality, there will be associated shifts in formicid abundance and community structure, furthering the effects of the adelgid invasion.

## Acknowledgments

The authors thank Ignazio Graziosi, Melanie Sprinkle, and Lee Townsend for technical assistance, and two anonymous reviewers, whose comments strengthened this manuscript. This project was supported by MacIntire Stennis funds from the Kentucky Agricultural Experiment Station and is published as Experiment Station 13-08-77.

## References Cited

- Adkins, J. K., and L. K. Rieske. 2013. Loss of a foundation forest species due to an exotic invader impacts terrestrial arthropod communities. *Forest Ecol. Manage.* 295: 126–135.
- AntWeb. Available from <http://www.antweb.org> (accessed 27 August 2013).
- Bolton, B. 2013a. AntWeb: genus: *Aphaenogaster*. (<http://www.antweb.org/description.do?rank=genus&name=aphaenogaster&project=worldants>) (accessed June 2013).
- Bolton, B. 2013b. AntWeb: species: *Myrmecina americana*. (<http://www.AntWeb.org/california.jsp>) (accessed 22 August 2013).
- Braun, E. 1950. *Deciduous forests of eastern North America*. Blackburn Press, Philadelphia, PA.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. Forest Res.* 24: 337–349.
- Coleman, T. W., and L. K. Rieske. 2006. Arthropod response to prescription burning at the soil-litter interface in oak-pine forests. *Forest Ecol. Manage.* 233: 52–60.
- Coleman, T. W., S. R. Clarke, J. R. Meeker, and L. K. Rieske. 2008. Forest composition following overstory mortality from southern pine beetle and associated treatments. *Can. J. Forest Res.* 38: 1406–1418.
- Davis, D. 1924. The geography of the mountains of eastern Kentucky: a reconnaissance study of the distribution and activities of man in that part of the Cumberland Plateau embraced by the Commonwealth, 180 pp. Kentucky Geological Survey Report, Series 6, vol. 18, Lexington, KY.
- Dolek, M., A. Freese-Hager, H. Bussler, A. Floren, A. Liegl, and J. Schmidl. 2008. Ants on oaks: effects of forest structure on species composition. *J. Insect Conser.* 13: 367–375.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloepfel, J. D. Knoepp, G. M. Lovett, et al. 2005a. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3: 479–486.
- Ellison, A. M., J. Chen, D. Diaz, C. Kammerer-Burnham, and M. Lau. 2005b. Changes in ant community structure and composition associated with

- hemlock decline in New England, pp. 280–289. In **B. Onken and R. Reardon** (eds.), *Proceedings of the Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*. USDA Forest Service, Morgantown, WV.
- Fellers, J. 1989.** Daily and seasonal activity in woodland ants. *Oecologia* 78: 69–76.
- Finzi, A. C., N. van Breemen, and C. D. Canham. 1998.** Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.* 8: 440–446.
- Folgarait, P. J. 1998.** Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.* 7: 1221–1244.
- Ford, C. R., and J. M. Vose. 2007.** *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecol. Appl.* 17: 1156–1167.
- Gandhi, K. J. K., and D. A. Herms. 2010.** Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invas.* 12: 389–405.
- Godman, R., and K. Lancaster. 1990.** Eastern Hemlock, In **R. Burns and B. Honkala** (eds.), *Silvics of North America*. US Dept. of Agriculture Forest Service, Washington, DC.
- Gotelli, N. J., and A. M. Ellison. 2002.** Assembly rules for New England ant assemblages. *Oikos* 99: 591–599.
- Houseweart, M. W., D. T. Jennings, and J. C. Rea. 1979.** Large capacity pitfall trap. *Entomol. News* 90: 51–54.
- Jenkins, J. C., J. D. Aber, and C. D. Canham. 1999.** Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can. J. Forest Res.* 29: 630–645.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994.** Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- Karban, R., T. M. Mata, P. Grof-Tisza, G. Cruetsinger, and M. A. Holyoak. 2013.** Non-trophic effects of litter reduce ant predation and determine caterpillar survival and distribution. *Oikos* 122: 1362–1370.
- Klimes, P., C. Idigel, M. Rimandai, T. M. Fayle, M. Janda, G. D. Weiblen, and V. Novotny. 2012.** Why are there more arboreal ant species in primary than in secondary tropical forests? *J. Anim. Ecol.* 81: 1103–1112.
- Krebs, C. J. 1999.** *Ecological methodology*. Harper and Row, New York, NY.
- MacGown, J. A. 2012.** *Ants (Formicidae) of the Southeastern United States*. Mississippi Entomological Museum. ([mississippientomologicalmuseum.org.msstate.edu](http://mississippientomologicalmuseum.org.msstate.edu)) (accessed October 2012–August 2013).
- Mackay, W. P., and E. E. Mackay. 2002.** *The ants of New Mexico* (Hymenoptera: Formicidae), 400 pp. The Edwin Mellen Press, Lewiston, NY.
- Mackay, W. P., and E. E. Mackay. 2003.** *The Ants of North America*. Centennial Museum, Laboratory for Environmental Biology, University of Texas, El Paso, TX. (<http://www.utep.edu/lb/antgenera.htm>) (accessed June 2013).
- Magurran, A. E. 1988.** *Ecological diversity and its measure*. Princeton University Press, Princeton, NJ.
- McDowell, R. C. 1986.** *The geology of Kentucky - a text to accompany the geologic map of Kentucky*. In USGS Professional Paper 1151-H, Department of the Interior. US GPO, Washington, D.C.
- Meyer, S. T., M. Neubauer, E. J. Sayer, I. R. Leal, M. Tabarelli, and R. Wirth. 2013.** Leaf-cutting ants as ecosystem engineers: topsoil and litter perturbations around *Atta cephalotes* nests reduce nutrient availability. *Ecol. Entomol.* 38: 497–504.
- Nuckolls, A. E., N. Wurzburger, C. R. Ford, R. L. Hendrick, J. M. Vose, and B. D. Kloeppel. 2009.** Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of Southern Appalachian forests. *Ecosystems* 12: 179–190.
- Orwig, D. A., and D. R. Foster. 1998.** Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *J. Torrey Bot. Soc.* 125: 60–73.
- Rankin, W., and E. J. Tramer. 2002.** The gap dynamics of canopy trees of a *Tsuga canadensis* forest community. *Northeastern Nat.* 9: 391–406.
- Rohr, J. R., C. G. Mahan, and K. C. Kim. 2009.** Response of arthropod biodiversity to foundation species declines: The case of the eastern hemlock. *Forest Ecol. Manage.* 258: 1503–1510.
- Ross, H. H., G. Rotramel, and W. Laberge. 1971.** A synopsis of common economic Illinois ants, with keys to the genera (Hymenoptera: Formicidae). Illinois Natural History Survey Biological Notes no. 71, 28 pp. Urbana, IL.
- Ross, R., R. Bennett, C. Snyder, D. Smith, J. Young, and D. Lemarie. 2003.** Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. *Ecol. Freshwater Fish* 12: 60–65.
- Snyder, C., J. Young, D. P. Lemarié, and D. R. Smith. 2002.** Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Can. J. Fisheries Aquat. Sci.* 59: 262–275.
- Southwood, T.R.E., and P. A. Henderson. 2000.** *Ecological methods*, 3rd ed. Wiley-Blackwell, Hoboken, NJ.
- Spaulding, H. L., and L. K. Rieske. 2010.** The aftermath of an invasion: Structure and composition of Central Appalachian hemlock forests following establishment of the hemlock woolly adelgid, *Adelges tsugae*. *Biol. Invas.* 12: 3135–3143.
- Talbot, M. 1943.** Population studies of the ant, *Prenolepis imparis* Say. *Ecology* 24: 31–44.
- Tingley, M.W.W., D.A.A. Orwig, R. Field, and G. Motzkin. 2002.** Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *J. Biogeogr.* 29: 1505–1516.
- Tschinkel, W. 1987.** Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*. *Insectes Soc.* 34: 143–164.
- (USDA) U.S. Department of Agriculture. 2009.** Natural resource information service (NRIS): field sampled vegetation (FSVeg) common stand exam. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Van Gils, H.A.J.A., and C. Vanderwoude. 2012.** Leafcutter ant (*Atta sexdens*) (Hymenoptera: Formicidae) nest distribution responds to canopy removal and changes in microclimate in the southern Columbian Amazon. *Fla. Entomol.* 95: 914–924.
- Ward, D. F., T. R. New, and A. L. Yen. 2001.** Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *J. Insect Conserv.* 5: 47–53.
- Webster, J., K. Morkeski, C. Wajculewski, B. R. Niederlehner, and E. F. Benfield. 2012.** Effects of hemlock mortality on streams in the southern Appalachian mountains. *Am. Midland Nat.* 168: 112–131.
- Welsh, H. H., and S. Droege. 2001.** A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. *Conserv. Biol.* 15: 558–569.
- Wheeler, W. M. 1930.** The ant *Prenolepis imparis* Say. *Ann. Entomol. Soc. Am.* 23: 1–26.
- Woods, A., J. Omernik, W. Martin, G. Pond, W. Andrews, S. Call, J. Comstock, and D. Taylor. 2002.** *Ecoregions of Kentucky*. U.S.G.S., Reston, VA.

Received 13 June 2013; accepted 12 September 2013.