



Loss of a foundation forest species due to an exotic invader impacts terrestrial arthropod communities

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ARTICLE INFO

Article history:

Received 18 September 2012

Received in revised form 7 December 2012

Accepted 16 January 2013

Available online 24 February 2013

Keywords:

Hemlock woolly adelgid

Tsuga

Adelges tsugae

Macroarthropods

Invertebrates

ABSTRACT

The hemlock woolly adelgid (*Adelges tsugae*) is an invasive insect native to Asia that feeds on all species of hemlock (*Tsuga* spp.), and is rapidly spreading throughout the range of eastern hemlock (*T. canadensis*). Eastern hemlock is an essential component of forested communities, is particularly susceptible to the adelgid, and has already suffered extensive mortality throughout much of its range. Hemlock dominated forests in the central Appalachians are expected to shift to deciduous species following adelgid-induced hemlock mortality, leading to shifts in epigeic macroinvertebrates. In a 2-year study using pitfall traps, we compared abundance, diversity, and composition of ground dwelling arthropod taxa and feeding guilds associated with riparian zones dominated by eastern hemlock to those associated with deciduous trees in the southern Appalachians. Differences were detected for the Diplopoda (millipedes) and Isopoda (pillbugs and wood lice), and for Formicidae (ants) and Staphylinidae (rove beetles). Each was more abundant beneath deciduous canopies than eastern hemlock canopies. Our comparative evaluation of eastern hemlock and deciduous riparian zone arthropod communities depicts the potential end point of a likely successional trajectory of eastern North American forests invaded by hemlock woolly adelgid. Our results indicate probable shifts in arthropod communities as the hemlock woolly adelgid invasion progresses through the Central Appalachian region.

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1. Introduction

Invasion by exotic organisms is one of the most important causes of native species declines and habitat loss (Vitousek et al., 1997). However, knowledge regarding the cascading effects of the decline of foundation species due to exotic invasions is lacking (but see Gandhi and Herms, 2010). 'Foundation species' refers to individual species that define much of the structure of a community by creating locally stable conditions and modulating fundamental ecosystem processes (Dayton, 1972). Eastern hemlock is considered a foundation species in eastern North American forests based on several attributes (Ellison et al., 2005a, 2005b). Its litter decomposes slowly, and soils in eastern hemlock forests are deep and acidic with low rates of nitrogen mineralization and nitrification (Jenkins et al., 1999). The canopy is dense and understory plant associates are not diverse (Rankin and Tramer, 2002). Eastern hemlock fills vital roles by regulating nutrient and water cycling, air, soil, and stream temperatures, and also serves as habitat and a food source for wildlife (Telfer, 1972; Ellison et al., 2005a), including nesting habitat for migratory songbirds (Ross et al., 2004). Deep shade and slowly decomposing litter create microclimates important to terrestrial invertebrates and salamanders

(Welsh and Droege, 2001). As a foundation species, eastern hemlock influences the composition and structure of arthropod communities; these arthropods are important in ecosystem function, yet remain a relatively poorly studied component (Dunn, 2005).

The role of eastern hemlock as a foundation species in eastern North American forests is under threat due to invasion by an exotic forest herbivore, the hemlock woolly adelgid (HWA: *Adelges tsugae* Annand, Hemiptera: Adelgidae). The adelgid is a xylem feeding insect native to Asia that feeds on all *Tsuga* spp. Eastern (*T. canadensis* L.) and Carolina (*T. caroliniana* Engelm.) hemlocks are especially susceptible, and in eastern North America native predators are unable to regulate HWA populations (Wallace and Hain, 2000). HWA has the potential to functionally eliminate eastern hemlock from the landscape, resulting in drastic changes to forest composition and structure (Spaulding and Rieske, 2010). Simulations suggest a 52% reduction in eastern hemlock basal area within five years following adelgid infestation, while the total number of all stems in the mid and understory are expected to increase (Spaulding and Rieske, 2010). These changes will have far-reaching consequences for biogeochemical cycling and ecosystem function (Ford and Vose, 2007). Adelgid induced mortality causes asurge in needle loss from eastern hemlocks, leading to increases in dissolved organic carbon in litter leachate (tadler et al., 2005; Nuckolls, 2009). In northern latitudes adelgid-decimated forests result in a

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transition to dominance by black birch (*Betula lenta*) (Orwig and Foster, 1998). This change in dominant vegetation will result in eventual shifts in stand water balance and soil chemistry (Stadler et al., 2005; Daley et al., 2007).

Eastern hemlock loss can result in greater arthropod abundance and alpha diversity, while beta diversity may be reduced due to the reduction or loss of hemlock-associated or hemlock-dependent species (Rohr et al., 2009). In the southern Appalachians eastern hemlock sustains invertebrates distinct from other conifers, even *Tsuga* congeners (Dilling et al., 2007). The abundance of invertebrate detritivores associated with eastern hemlock has been attributed to deciduous leaf litter trapped in the complex structure of hemlock canopies (Turcotte, 2008). Eastern hemlock also supports an abundant and unique spider community (Mallis and Rieske, 2011). However, not all species are positively associated with hemlocks; for example, ant species richness is inversely related to eastern hemlock density in New England (Ellison et al., 2005b).

Exotic invaders can have dramatic effects by causing shifts in vegetative composition, altering trophic relationships and environmental conditions, and by displacing endemic species (Vitousek, 1990). The potential cascading effects of the loss of eastern hemlock due to HWA-induced mortality are many and far-reaching. While eastern hemlock is a prolific cone producer, it has a low germinative capacity and regenerates poorly (Godman and Lancaster, 1990), making it unlikely to effectively regenerate after HWA-induced mortality.

Our overall goal is to quantify the complex relationships between eastern hemlock forests and arthropod community structure in the context of adelgid-induced hemlock mortality. Here we focus on terrestrial arthropod communities in headwater stream riparian zones. We compare the current eastern hemlock associated terrestrial arthropod assemblage to the assemblage associated with the projected post-adelgid community of a mixed hardwood forest (Spaulding and Rieske, 2010). Our approach allows predictions about long-term effects of eastern hemlock loss on terrestrial arthropod biodiversity on a large spatial scale, expanding the scope from previous studies that utilize only one sample period or are limited to a single landscape (i.e. Rohr et al., 2009). We predict that eastern hemlock terrestrial arthropod communities will contain unique arthropod taxa that are at risk, and are threatened with local or regional extinction from adelgid-induced hemlock mortality. We also hypothesize that the relatively limited understory vegetative diversity and more uniform forest structure of hemlock dominated riparian zones will be associated with lower arthropod abundance and family richness than terrestrial arthropod communities associated with mixed deciduous riparian zones. The lower arthropod abundance and richness may manifest itself as reduced arthropod activity in eastern hemlock riparian zones due to lower diversity of understory vegetation and reduced temperatures at the soil interface caused by the dense canopy shading.

2. Methods

2.1. Study areas

Research sites were established in three locations in eastern Kentucky. The Red River Gorge Geological Area/Natural Bridge State Park State Nature Preserve is located in the Northern Forested Plateau Escarpment ecoregion of Kentucky (W83°37'44.115", N37°49'9.164"). Robinson Forest is situated in the Dissected Appalachian Plateau ecoregion (W83°9'30.578" N 37°27'38.68"), and Kentucky Ridge State Forest (W83°47'26.048" N 36°42'14.408") is located further south in the Cumberland Mountain Thrust Block ecoregion (Woods et al., 2002). The sites are located in the

Cumberland Plateau physiographic province of Kentucky, typified by steep, mountainous terrain underlain by shale and sandstone with abundant coal seams (McDowell, 1986). The dominant vegetation is mixed mesophytic forest (Davis, 1924; Braun, 1950). Annual precipitation ranges from 106 to 139 cm; temperatures vary from –6.2 °C to 8.3 °C in January and from 16.6 °C to 31.6 °C in July (Woods et al., 2002). Elevation varies from 167 to 1261 m (Woods et al., 2002).

Study sites were chosen using GIS and remote sensing techniques. Presence of riparian eastern hemlock was determined using the vegetation database from the Kentucky GAP Analysis (Wethington et al., 2003). Surface hydrology modeling of 30 m resolution digital elevation models from the Kentucky Office of Geographic Information was implemented to determine watershed boundaries. The watersheds were delineated and extracted from the digital elevation models using the Hydrology Tools of ESRI ArcGIS Spatial Analyst (ESRI, 2008). Candidate study sites with similar watershed areas and appropriate eastern hemlock riparian vegetation were visited and assessed for suitability. Three eastern hemlock dominated streams and three deciduous dominated streams were selected at each of the three sites for a total of eighteen streams.

2.2. Riparian vegetation

Woody vegetation composition and structure was assessed by establishing two 0.04-ha fixed-radius whole plots within each stream's riparian zone, one on each side of the stream. Ten subplots, five 0.004-ha and five 0.0004-ha, were nested within each 0.04-ha whole plot to enhance precision of the vegetation assessments. Whole plots (0.04-ha) were utilized to assess overstory and midstory vegetation (all trees ≥ 12.7 cm diameter at 1.5 m high; DBH), 0.004-ha subplots were used to assess saplings and shrubs (<12.7 cm DBH, >137 cm high), and 0.0004-ha micro plots were used to assess seedlings, shrubs (<137 cm height) and vines. One of each subplot size was positioned at the whole plot center and in each cardinal direction, 7.7 m from the plot center. Thus, a surveyed reach contained two 0.04-ha whole plots, ten 0.004-ha subplots, and ten 0.0004-ha microplots (Coleman et al., 2008). Measurements of vegetation and plot data followed the Common Stand Exam protocol of the USDA Forest Service's Natural Resource Information System: Field Sampled Vegetation Module (USDA, 2009) and included tree height and diameter at breast height (DBH). Diameter measurements were then used to determine basal area of the overstory riparian vegetation within each whole plot (Spurr, 1962).

2.3. Riparian arthropods

Pitfall traps were used to assess terrestrial arthropod activity density within the riparian zone of each stream. Activity density is defined as the number of individuals moving randomly within a given area (Thiele, 1977; Spence and Niemela, 1994) and is well correlated with absolute abundance (Adis, 1979). Three large capacity pitfall traps (Houseweart et al., 1979; Coleman and Rieske, 2006) consisting of a 150 mm plastic funnel, a 1-liter plastic bottle, and a 30 × 30 × 0.6 cm apron fashioned from tempered hardboard, and each containing approximately 250 ml of 1:1 70% ethyl alcohol:ethylene glycol were spaced approximately 10 m apart along the accessible side of each stream reach, resulting in a total of 54 pitfall traps. Pitfall traps spaced at ≥ 10 -m intervals do not affect abundance or composition of collected invertebrates (Ward et al., 2001), implying sample independence. Traps were installed and opened in September 2008 and the contents collected at monthly intervals through September 2010. Contents were removed and stored in 70% ethyl alcohol and returned to the lab. Specimens

were sorted and identified to order or family level; the twenty most abundant taxa were broadly categorized as detritivore, herbivore, omnivore, or predator, based on the most common feeding mode within each taxon (Triplehorn and Johnson, 2005; Rohr et al., 2009). Because this was a long term study on a broad geographic scale we used family-level identifications, which are deemed taxonomically sufficient when addressing a study of the scope and magnitude of ours (Birkhofer et al., 2012). This approach provides a good estimate of the invertebrate diversity within a community when using a given sampling method and has been utilized in a number of invertebrate studies (Hoback et al., 1999; Riggins et al., 2009; Rohr et al., 2009). Surface temperature (daily maximum, minimum, and mean) was recorded in the leaf litter adjacent to pitfall traps using iButton data loggers (Model DS1921-G, Maxim Integrated Products, Sunnyvale, CA). One iButton per trap was installed at Robinson Forest in 2009; in 2010 traps at the remaining sites were similarly equipped.

2.4. Analysis

Three sampling intervals representing spring (April and May), summer (July and August), and fall (October and November) over two years were used to assess the influence of riparian vegetation (eastern hemlock vs. deciduous) on terrestrial arthropod assemblages and activity. Arthropod abundance (recorded as activity density) was calculated and diversity, evenness, and richness were derived by stream location, riparian vegetation, and season. Richness is the total number of taxa within each sample. We used the Simpson index as our measure of diversity, which utilizes the relative abundance of each taxon and the total insect abundance within a sample (Magurran, 1988). Pielou's Index of Evenness (J), which incorporates the Shannon index and taxa richness in the sample (Magurran, 1988), was calculated (Southwood and Henderson, 2000). Additionally, Jaccard's coefficient (J) was calculated to determine overlap between the combined taxa lists of the two riparian vegetation types (Krebs, 1989).

Riparian arthropod population parameters (Pielou's evenness index and Simpson's index) for the 20 most abundant taxa and their associated feeding guild were analyzed using a generalized linear mixed model optimized for Poisson distributed data (SAS, 2006) with a split plot design to determine the effects of riparian vegetation composition, stream location, and season on terrestrial arthropod communities. All interactions were evaluated. However, the three-way interaction was not significant ($P = 0.05$), thus it was removed from the model. Tukey's HSD was used as a post hoc means separation procedure when appropriate. Maximum, minimum, and mean temperature data from 2010 were analyzed similarly. Differences were considered statistically significant at an alpha level of $P < 0.05$.

The influence of riparian overstory and understory vegetation on arthropod taxa and feeding guild abundance for the 20 most abundant taxa was evaluated using canonical correspondence analysis (CCA), a multivariate approach that tests for arthropod associations along environmental gradients (Palmer, 1993), and provides insight as to which components of the riparian vegetation community most influence terrestrial arthropod activity. CCAs partition variation in community structure in response to quantitative environmental variables (Anderson et al., 2011) and are useful for determining the relationships between arthropod taxa and environmental parameters (ter Braak and Verdonschot, 1995; Coleman and Rieske, 2006; Riggins et al., 2009). Only the pitfall traps that corresponded with the upstream and downstream vegetation assessment plots were used for this analysis; the midstream trap was disregarded. We assessed the correlations terrestrial arthropod abundance to riparian slope and elevation, and vegetation community data including stem count, diameter, tree height,

crown height, and basal area in eastern hemlock vs. deciduous riparian vegetation. A second CCA was implemented to assess the relationships between feeding guilds and riparian zone vegetation. A Monte Carlo permutation with 300 iterations was used to evaluate the influence of random events on the relationship between environmental variables and taxa abundance (Elliott et al., 1999). The strongest intraset correlation values are presented to determine the environmental variable with the highest correlation (ter Braak, 1986). Weights are included to demonstrate the association of arthropod taxa with the ordination axes, and we present eigenvalues to explain variance in relation to environmental variables. Relationships of arthropod taxa to riparian vegetation are presented graphically as a biplot representing the correlation structure of the data in a low dimensional form (Gabriel, 1981; ter Braak, 1986; McCune and Medford, 1999). Environmental gradients, in the form of riparian vegetation data, are characterized as radiating lines from the plot center, the length and direction of which relate to the strength of the relationships between environmental variables (Palmer, 1993).

3. Results

3.1. Study sites and riparian vegetation

Our study sites did not differ in watershed area or elevation at the confluence with the next largest stream between riparian vegetation designations (Table 1a). Watershed area did not differ across locations, but elevation at the confluence was greatest at Kentucky Ridge (Table 1b). In addition to eastern hemlock, the dominant canopy species in terms of basal area consisted of American beech (*Fagus grandifolia* Ehrhart), white oak (*Quercus alba* L.), tulip poplar (*Liriodendron tulipifera* L.), black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), and sourwood (*Oxydendrum arboretum* (L.) DC). There was also a substantial amount of *Rhododendron maximum* (L.) in the understory, particularly in the deciduous streams (Table 2). There were significantly fewer eastern hemlock stems within the riparian zones classified as "deciduous dominated" in both the overstory and understory (Table 1a). Overstory deciduous stems did not vary by riparian zone designation, but the density of understory deciduous stems in the deciduous riparian zones was more than double that of the eastern hemlock riparian zones (Table 1a). The number of overstory eastern hemlock stems and overstory and understory deciduous stems did not vary by location. However, we observed significant differences in understory eastern hemlock stems across each location, with the highest number at Kentucky Ridge, and the lowest at Robinson Forest (Table 1b). Maximum surface temperature in the leaf litter adjacent to pitfall traps was significantly higher in deciduous dominated riparian zones than in eastern hemlock riparian zones, but vegetation did not influence mean or minimum leaf litter temperature (Table 1a).

3.2. Riparian arthropods

Detritivores were the most abundant arthropod feeding guild represented in pitfall traps, followed by predators, omnivores and herbivores (Table 3). A total of 31,013 arthropods from 164 taxa were collected from pitfall traps across all sites (Table 3). The Jaccard value comparing overlap of the two invertebrate communities reveals a 62% similarity in community composition. Twenty-eight taxa were unique to eastern hemlock dominated riparian zones while 35 were unique to deciduous riparian zones. The most abundant unique taxon in deciduous riparian zones was the Philopotamidae (caddisflies) ($N = 33$ adults), likely incidental catches that were not used in our analysis. The most numerous taxon unique to eastern hemlock was Ctenophthalmidae ($N = 10$ individuals);

Table 1

Sites in eastern Kentucky (USA) used to evaluate the effects of the hemlock woolly adelgid on riparian arthropod communities ($N = 3$ plots per site) by (a) forest type, and (b) location. Means (s.e.) within columns followed by the same letter are not significantly different ($\alpha = 0.05$).

	Watershed	Stream confluence	Overstory stem count (#/ha)		Understory stem count (#/ha)		Litter temperature ($^{\circ}\text{C}$)		
	Area	Elevation (m)	Eastern hemlock	Deciduous	Eastern hemlock	Deciduous	Maximum	Mean	Minimum
<i>(a) Forest type</i>									
Eastern hemlock	69.4 (5.1)a	393 (33)a	7.8 (1.0)a	10.2 (0.9)a	14.5 (2.2)a	13.3 (2.6)b	21.5 (1.0)b	16.0 (1.0)a	10.7 (1.0)a
Deciduous	61.1 (3.4)a	391 (37)a	3.6 (1.0)b	9.3 (0.8)a	4.7 (1.6)b	29.6 (5.3)a	24.7 (1.0)a	16.3 (1.0)a	10.3 (1.0)a
Statistics	$(F_{1,14}/P)$	$(F_{1,14}/P)$	$(X^2_{df=1}/P)$		$(X^2_{df=1}/P)$		$(F_{1,82}/P)$		
	1.8/0.19	0.02/0.43	8.3/<0.01	0.9/0.27	12.6/<0.01	6.9/<0.01	11.5/<0.01	0.3/0.57	0.4/0.51
<i>(b) Location</i>									
Red River Gorge	59.8 (3.0)a	322 (8)b	5.3 (1.4)a	11.2 (1.0)a	9.7 (2.6)b	16.3 (3.4)a	22.4 (1.2)a	16.0 (1.2)a	10.8 (1.2)a
Robinson Forest	69.3 (8.1)a	322 (7)b	6.3 (1.3)a	9.3 (1.2)a	3.9 (1.1)c	18.7 (5.5)a	22.6 (1.1)a	16.1 (1.1)a	10.2 (1.1)a
Kentucky Ridge	66.7 (3.9)a	533 (7)a	5.6 (1.4)a	8.8 (1.0)a	15.3 (3.1)a	29.3 (6.9)a	25.7 (1.5)a	16.5 (1.5)a	10.3 (1.5)a
Statistics	$(F_{2,14}/P)$	$(F_{2,14}/P)$	$(X^2_{df=2}/P)$		$(X^2_{df=2}/P)$		$(F_{2,82}/P)$		
	0.8/0.45	264.2/< 0.01	0.4/0.79	2.7/0.26	7.0/0.03	2.9/0.22	1.3/0.29	0.1/0.93	0.4/0.67

Table 2

Basal area (m^2/ha) of the most abundant riparian tree species within the overstory (≥ 12.7 cm diameter at 1.5 m high) and understory (< 12.7 cm DBH, > 137 cm high) across locations and dominant vegetation type.

	<i>A. rubrum</i>	<i>B. lenta</i>	<i>F. grandifolia</i>	<i>L. tulipifera</i>	<i>O. arboreum</i>	<i>Q. alba</i>	<i>T. canadensis</i>	<i>R. maximum</i>
<i>Overstory</i>								
Hemlock dominated	1.6 (0.5)	2.4 (0.9)	5.1 (2.0)	4.0 (0.8)	1.1 (0.3)	4.0 (1.4)	12.6 (2.2)	–
Deciduous dominated	1.3 (0.6)	1.1 (0.5)	5.0 (1.2)	5.5 (1.2)	0.3 (0.1)	4.4 (3.3)	4.7 (1.6)	–
Kentucky Ridge	1.0 (0.3)	2.3 (0.8)	3.5 (0.9)	3.5 (1.2)	0.9 (0.4)	2.4 (0.8)	11.5 (4)	–
Robinson Forest	2.1 (0.6)	0.7 (0.2)	7.7 (2.1)	5.0 (1.0)	0.1 (0.0)	2.0 (0.9)	7.6 (1.4)	–
Red River Gorge	1.4 (0.8)	0.1 (0.0)	3.6 (1.9)	5.7 (1.4)	0.8 (0.3)	8.6 (2.2)	9.3 (3.5)	–
<i>Understory</i>								
Hemlock dominated	0.4 (0.3)	0.4 (0.4)	0.4 (0.2)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.6 (0.2)	0.9 (0.5)
Deciduous dominated	0.3 (0.1)	2.5 (1.9)	0.7 (0.2)	0.6 (0.2)	0.1 (0.1)	0.0 (0.0)	0.3 (0.2)	2.0 (1.0)
Kentucky Ridge	0.7 (0.2)	2.1 (1.4)	1.0 (0.4)	0.4 (0.2)	0.1 (0.0)	0.2 (0.1)	0.6 (0.2)	2.0 (0.4)
Robinson Forest	0.1 (0.0)	0.1 (0.0)	0.4 (0.2)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
Red River Gorge	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)	0.7 (0.3)	0.1 (0.0)

Table 3

Arthropod feeding guilds of the 20 most abundant taxa captured in pitfall traps from eastern hemlock and deciduous dominated streams across study location and season in eastern Kentucky (USA); KYR: Kentucky Ridge State Forest, RF: Robinson Forest, RRG: Red River Gorge.

	Total	Location			Forest type		Season		
		KYR	RF	RRG	Hemlock	Non	Fall	Spring	Summer
<i>Feeding guild^a</i>									
Detritivore	14346	5110	5398	3838	8401	5945	1358	5632	7356
Herbivore	2924	241	803	1880	1038	1886	32	1673	1219
Omnivore	3313	1543	889	881	1512	1801	286	939	2088
Predator	7349	2380	2732	2237	3443	3906	1979	1538	3832

^a Triplehorn and Johnson (2005).

these ectoparasitic Siphonaptera (fleas) likely originated from a small mammal passing near the traps. Ground-dwelling arthropod abundance in deciduous dominated riparian zones was $2.8 \times$ greater than in hemlock dominated riparian zones (22,959 in deciduous sites vs. 8054 in hemlock sites, but there were no statistical differences in overall arthropod abundance, richness, diversity or evenness between hemlock dominated and deciduous dominated riparian zones (Tables 2a and 3a). Similarly, there were no differences in arthropod population parameters based on sample location. However, there were differences based on season for all but evenness and Simpson's diversity index, and there were significant location \times season interactions for richness and evenness (Tables 2a and 3a).

Seasonal differences were evident for each feeding guild (Table 4b), and there were significant differences across locations and between riparian vegetation types for omnivores, which include Oribatida (mites), Opiliones (harvestmen), Phoridae (scuttle flies), and Formicidae (ants) (Table 4b). Omnivores were more

abundant in deciduous than eastern hemlock riparian zones, and were more abundant at Kentucky Ridge than the other sites (Table 5b). Interactions between vegetation and season were detected for herbivores, which consisted only of Scolytidae (bark beetles), and predators, which include Chilopoda (centipedes), Araneae (spiders), Carabidae (ground beetles), and Staphylinidae (rove beetles). Herbivores were most abundant in deciduous riparian zones in the spring (mean (s.e.) = 10.9 (3.9)) (Table 5b). Predators were more abundant in deciduous riparian zones than eastern hemlock riparian zones during the summer ($t_{100} = -2.1$, $p = 0.04$). There was a significant vegetation \times location interaction for predators in which the abundance of predators in eastern hemlock riparian zones at Red River Gorge was lower than at Robinson Forest ($t_{100} = 2.8$, $p < 0.01$) but no other pairwise differences were detected (Tables 2b and 3b).

Over 70% of captured arthropods were from eight taxa, including Hypogastruridae (springtails, 24%), Carabidae (13%), Scolytidae

Table 4
Effects of location, forest type/vegetation, and season on arthropod abundance in hemlock and deciduous dominated riparian zones of eastern Kentucky (USA).

	Location $F_{2,48}/P$	Forest type $F_{1,48}/P$	Season $F_{2,100}/P$	Forest type \times location $F_{2,48}/P$	Forest type \times season $F_{2,100}/P$	Location \times season $F_{4,100}/P$
<i>(a) Population parameters</i>						
Abundance	0.1/0.89	0.1/0.81	21.4/<0.01	1.4/0.25	0.6/0.57	1.6/0.18
Richness	2.3/0.09	2.0/0.15	69.4/<0.01	0.1/0.91	0.2/0.79	3.8/<0.01
Evenness	1.9/0.15	2.7/0.10	1.8/0.16	1.3/0.27	0.3/0.77	2.4/0.05
Simpson diversity	2.1/0.13	2.2/0.13	2.1/0.12	1.0/0.36	0.2/0.82	1.9/0.11
<i>(b) Feeding guild</i>						
Detritivore	0.4/0.65	1.5/0.23	14.1/<0.01	1.0/0.37	2.0/0.14	2.0/0.14
Herbivore	2.8/0.07	0.1/0.79	5.0/<0.01	1.0/0.37	9.2/<0.01	0.8/0.45
Omnivore	5.9/<0.01	4.1/0.04	48.4/<0.01	1.3/0.27	1.1/0.38	2.1/0.13
Predator	0.8/0.45	0.5/0.51	23.8/<0.01	4.6/0.02	3.9/<0.01	1.6/0.21
<i>(c) Taxon abundance</i>						
Hypogastruridae	0.2/0.82	0.2/0.70	3.8/0.03	1.5/0.24	2.1/0.13	2.4/0.05
Carabidae	1.1/0.36	0.1/0.73	18.3/<0.01	5.7/0.01	1.9/0.16	3.0/0.02
Scolytidae	2.8/0.07	0.1/0.79	5.0/0.01	1.0/0.37	0.8/0.45	9.2/<0.01
Isotomidae	2.0/0.15	3.2/0.08	16.7/<0.01	1.3/0.30	1.4/0.25	2.8/0.03
Formicidae	3.2/0.05	7.5/0.01	49.5/<0.01	0.6/0.53	4.6/0.01	0.6/0.68
Araneae	0.4/0.70	3.0/0.09	11.3/<0.01	0.1/0.95	0.4/0.67	2.2/0.07
Rhaphidophoridae	0.2/0.85	0.1/0.76	62.0/<0.01	2.6/0.09	0.1/0.98	2.2/0.07
Staphylinidae	7.9/<0.01	5.3/0.03	16.8/<0.01	1.0/0.37	0.3/0.72	4.5/<0.01
Diplopoda	16.3/<0.01	7.3/0.01	7.9/<0.01	0.1/0.99	0.9/0.43	2.3/0.06
Sminthuridae	1.3/0.29	0.5/0.48	14.4/<0.01	1.0/0.37	0.1/0.91	0.4/0.84
Phoridae	0.1/0.94	0.4/0.52	17.2/<0.01	3.3/0.05	1.3/0.29	1.6/0.17
Oribatida	5.6/0.01	0.1/0.94	1.1/0.32	1.0/0.37	1.5/0.24	0.1/0.97
Nitidulidae	0.7/0.50	3.0/0.09	33.3/<0.01	0.3/0.78	0.6/0.56	1.8/0.13
Entomobryidae	8.6/<0.01	1.9/0.17	1.1/0.34	0.8/0.46	1.5/0.23	0.2/0.91
Sciaridae	2.2/0.12	0.2/0.68	8.4/<0.01	4.1/0.02	0.9/0.40	1.1/0.35
Isopoda	2.9/0.06	5.6/0.02	2.8/0.07	0.4/0.71	0.4/0.68	0.6/0.65
Mycetophilidae	5.7/0.01	0.1/0.84	14.6/<0.01	2.0/0.15	0.2/0.86	2.1/0.09
Opiliones	2.2/0.12	0.8/0.36	28.4/<0.01	2.2/0.12	0.1/0.89	1.6/0.18
Tipulidae	0.3/0.75	1.8/0.19	19.6/<0.01	1.3/0.28	0.2/0.79	1.1/0.36
Chilopoda	2.4/0.1	0.2/0.69	16.0/<0.01	2.5/0.09	1.3/0.28	1.9/0.11

Table 5
Abundance and diversity [mean (s.e.) derived from trap-level data] of arthropods sampled from the forest floor of hemlock and deciduous dominated riparian zones in Eastern Kentucky (USA). For each main effect, means within rows followed by the same letter are not significantly different ($\alpha = 0.05$).

	Location ^a			Forest type		Season		
	KYR	RF	RRG	Hemlock	Deciduous	Fall	Spring	Summer
<i>(a) Population parameters</i>								
Abundance	47.6 (6.2)a	50.0 (7.3)a	46.0 (4.5)a	48.6 (5.8)a	47.1 (4.1)a	19.0 (1.2)c	50.9 (7.4)b	73.7 (7.0)a
Richness	9.1 (0.4)a	10.0 (0.4)a	10.3 (0.4)a	9.5 (0.4)a	10.1 (0.4)a	6.2 (0.2)b	10.4 (0.4)a	12.8 (0.5)a
Evenness	0.7 (0.1)a	0.8 (0.1)a	0.7 (0.1)a					
Simpson diversity	0.7 (0.1)a	0.7 (0.1)a	0.7 (0.1)a	0.6 (0.1)a	0.7 (0.1)a	0.6 (0.1)a	0.7 (0.1)a	0.7 (0.1)a
<i>(b) Feeding guild</i>								
Detritivore	23.7 (3.9)a	25.0 (6.2)a	17.8 (2.5)a	25.9 (4.8)a	18.3 (2.0)a	6.3 (0.5)c	26.1 (6.3)b	34.1 (4.3)a
Herbivore	1.1 (0.2)a	3.7 (0.6)a	8.7 (2.1)a	2.7 (0.6)a	6.3 (1.3)a	0.1 (0.1)b	7.7 (2.0)a	5.6 (0.8)a
Omnivore	7.1 (1.0)a	4.1 (0.6)b	4.1 (0.4)b	4.7 (0.6)b	5.6 (0.6)a	1.3 (0.2)c	4.3 (0.6)b	9.7 (1.0)a
Predator	11.0 (1.6)a	12.6 (1.2)a	10.4 (1.2)a	10.6 (0.9)a	12.1 (1.3)a	9.2 (0.9)b	7.1 (0.5)b	17.7 (2.0)a
<i>(c) Taxon abundance</i>								
Hypogastruridae	12.7 (3.4)a	9.8 (2.4)ab	7.9 (2.1)b	1.6 (0.6)a	18.1 (2.7)b	0.2 (0.1)b	11.5 (2.7)a	18.8 (3.7)a
Carabidae	7.0 (1.4)a	6.9 (1.0)a	5.2 (1.0)a	2.7 (0.3)a	10.0 (1.3)a	5.1 (0.8)b	2.8 (0.4)c	11.2 (1.7)a
Scolytidae	1.1 (0.2)a	3.7 (0.6)a	8.7 (2.1)a	2.7 (0.6)a	6.3 (1.3)a	0.1 (0.1)b	7.7 (2.1)a	5.6 (0.8)a
Isotomidae	3.5 (0.4)a	3.5 (0.5)a	2.1 (0.3)a	1.0 (0.2)a	5.0 (0.4)a	1.1 (0.2)b	4.0 (0.4)a	3.9 (0.5)a
Formicidae	3.8 (0.6)a	2.6 (0.6)b	2.2 (0.3)b	2.2 (0.4)b	3.5 (0.4)a	1.0 (0.2)b	1.3 (0.3)b	6.3 (0.7)a
Araneae	2.7 (0.2)a	2.8 (0.2)a	2.6 (0.2)a	2.9 (0.2)a	2.5 (0.2)a	1.9 (0.1)b	3.2 (0.2)a	3.0 (0.2)a
Rhaphidophoridae	2.5 (0.3)a	2.4 (0.3)a	2.2 (0.3)a	1.6 (0.2)a	3.1 (0.3)a	2.0 (0.2)b	0.4 (0.1)c	4.7 (0.4)a
Staphylinidae	1.1 (0.2)b	2.5 (0.3)a	2.3 (0.3)a	1.6 (0.2)b	2.3 (0.2)a	1.8 (0.3)b	1.0 (0.1)c	3.0 (0.3)a
Diplopoda	0.6 (0.1)b	1.9 (0.2)a	2.0 (0.2)a	1.2 (0.1)b	1.8 (0.2)a	1.3 (0.1)b	0.9 (0.1)c	2.2 (0.3)a
Sminthuridae	1.3 (0.3)a	1.1 (0.4)a	0.6 (0.1)b	0.3 (0.1)a	1.7 (0.3)a	0.1 (0.1)c	2.2 (0.5)a	0.6 (0.1)b
Phoridae	0.7 (0.1)a	0.9 (0.2)a	1.2 (0.2)a	0.4 (0.01)a	1.4 (0.2)a	1.1 (0.2)a	1.1 (0.2)a	1.6 (0.2)a
Oribatida	2.0 (0.5)a	0.3 (0.1)b	0.3 (0.1)b	0.8 (0.2)a	1.0 (0.3)a	0.1 (0.1)a	0.9 (0.3)a	1.6 (0.4)a
Nitidulidae	0.3 (0.1)a	0.6 (0.1)a	1.1 (0.2)a	0.3 (0.1)a	1.1 (0.2)a	0.1 (0.1)b	0.1 (0.1)b	1.8 (0.2)a
Entomobryidae	0.9 (0.2)a	0.4 (0.1)b	0.3 (0.1)b	0.7 (0.1)a	0.3 (0.1)a	0.7 (0.2)a	0.4 (0.1)a	0.5 (0.1)a
Sciaridae	0.7 (0.2)a	0.5 (0.1)a	0.3 (0.1)a	0.2 (0.1)a	0.8 (0.2)a	0.2 (0.1)c	0.9 (0.2)a	0.4 (0.1)b
Isopoda	0.2 (0.1)c	0.4 (0.1)b	0.7 (0.2)a	0.3 (0.1)b	0.6 (0.2)a	0.3 (0.1)b	0.3 (0.1)b	0.7 (0.2)a
Mycetophilidae	0.6 (0.1)a	0.4 (0.1)b	0.3 (0.1)b	0.2 (0.1)a	0.7 (0.1)a	0.2 (0.1)b	0.8 (0.1)a	0.3 (0.1)b
Opiliones	0.7 (0.1)a	0.2 (0.1)a	0.4 (0.1)b	0.4 (0.1)a	0.5 (0.1)a	0.1 (0.1)c	0.9 (0.1)a	0.2 (0.1)b
Tipulidae	0.3 (0.1)a	0.3 (0.1)a	0.4 (0.1)a	0.2 (0.1)a	0.4 (0.1)a	0.1 (0.1)b	0.7 (0.1)a	0.2 (0.1)b
Chilopoda	0.3 (0.1)a	0.4 (0.1)a	0.2 (0.1)a	0.3 (0.1)a	0.3 (0.1)a	0.3 (0.1)a	0.1 (0.1)b	0.5 (0.1)a

^a KYR: Kentucky Ridge State Forest; RF: Robinson Forest, RRG: Red River Gorge Geological Area + Natural Bridge State Park State Nature Preserve.

(9%), Isotomidae (springtails, 6%), Formicidae (6%), Araneae (6%), Rhaphidophoridae (camel crickets, 5%), and Staphylinidae (4%). The 20 most abundant taxa represent 90% of total arthropods captured (Table 5c). Of these 20 taxa, Formicidae, Staphylinidae, Diplopoda, and Isopoda (pill bugs and wood lice) were influenced by riparian vegetation type (Table 4c); each was more abundant in deciduous dominated riparian zones than in eastern hemlock riparian zones (Table 5c). There was a significant vegetation × season interaction for Formicidae (Table 4c), driven primarily by elevated ant abundance during fall and spring in deciduous sites relative to hemlock sites. However, in summer Formicidae abundance did not differ between riparian zone types ($t_{100} = 0.66$, $p = 0.51$). Oribatida, Entomobryidae, and Isopoda, which comprise 1.8%, 1%, and <1% of the total, respectively, were the only taxa that did not differ seasonally (Table 4c).

Arthropod abundance differed by location for six taxa (Table 4c). Of these, Formicidae, Staphylinidae, Diplopoda, and Isopoda differ by location and by vegetation, but there were no significant vegetation by location interactions for these taxa (Tables 2c and 3c). Vegetation by location interactions were detected for Carabidae, Phoridae, and Sciaridae (Table 4c). The Carabidae represent our second most abundant taxon, and were found in greater abundance in deciduous riparian zones of each location. Phorids and sciarids are fungivorous dipterans (flies) which were collected in very low numbers via pitfall traps, indicating some measure of attraction to the trap contents of the pitfall traps (Greenslade and Greenslade, 1971).

3.3. Riparian vegetation and arthropod activity

Terrestrial arthropod activity corresponds with our environmental parameters describing riparian zone vegetation and physiographic data. When all environmental variables were incorporated into the CCA, the Monte Carlo test was significant for the first axis ($P < 0.05$), indicating a linear relationship between terrestrial arthropod community composition and riparian vegetation for this ordination axis (McCune and Grace, 2002). The CCA ordination accounted for 5.7% of the variation within the dataset (Fig. 1). The first ordination axis is most strongly linked to understory hemlock stem count (intraset correlation value 0.53), and negatively associated with understory deciduous basal area and understory deciduous stems. The Hypogastridae, our most abundant taxon, was negatively correlated with axis 1 (Hypogastridae axis 1 weight = -0.58), indicating a negative relationship with understory hemlock stem count. Likewise, Carabidae (-0.12) and Isotomidae (-0.09) are negatively correlated with axis 1, but less so than Hypogastridae. Scolytidae had the highest positive weight associated with axis 1 (0.69), indicating a strong positive association with understory hemlock stem density, but in the generalized linear mixed model scolytids did not differ by riparian vegetation type. Of the four taxa that were significantly affected by vegetation type, the Diplopoda were most strongly associated with axis 1 (weight = 0.27); Staphylinidae (0.15) and Isopoda (0.03) are also positively associated with understory hemlock (axis 1). Formicidae were negatively correlated with understory hemlock stems (-0.31)

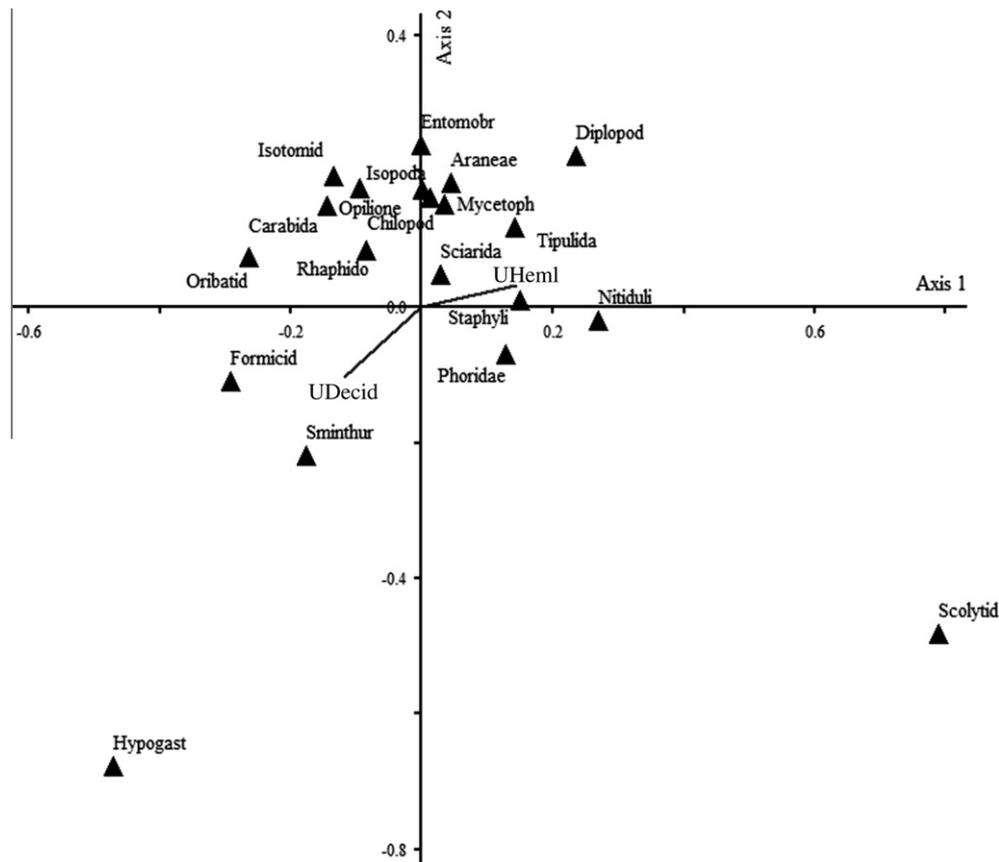


Fig. 1. First and second ordination axes from the canonical correspondence analysis depicting relationships between riparian vegetation structure and terrestrial arthropod taxa in eastern hemlock and deciduous dominated riparian zones. The environmental variables shown are those with the greatest association with the ordination axes. Axis one accounts for 2.6% of the explained variation, while axis 2 accounts for 2.0%. “UHeml” indicates understory hemlock stems, and “UDecid” indicates understory deciduous stems.

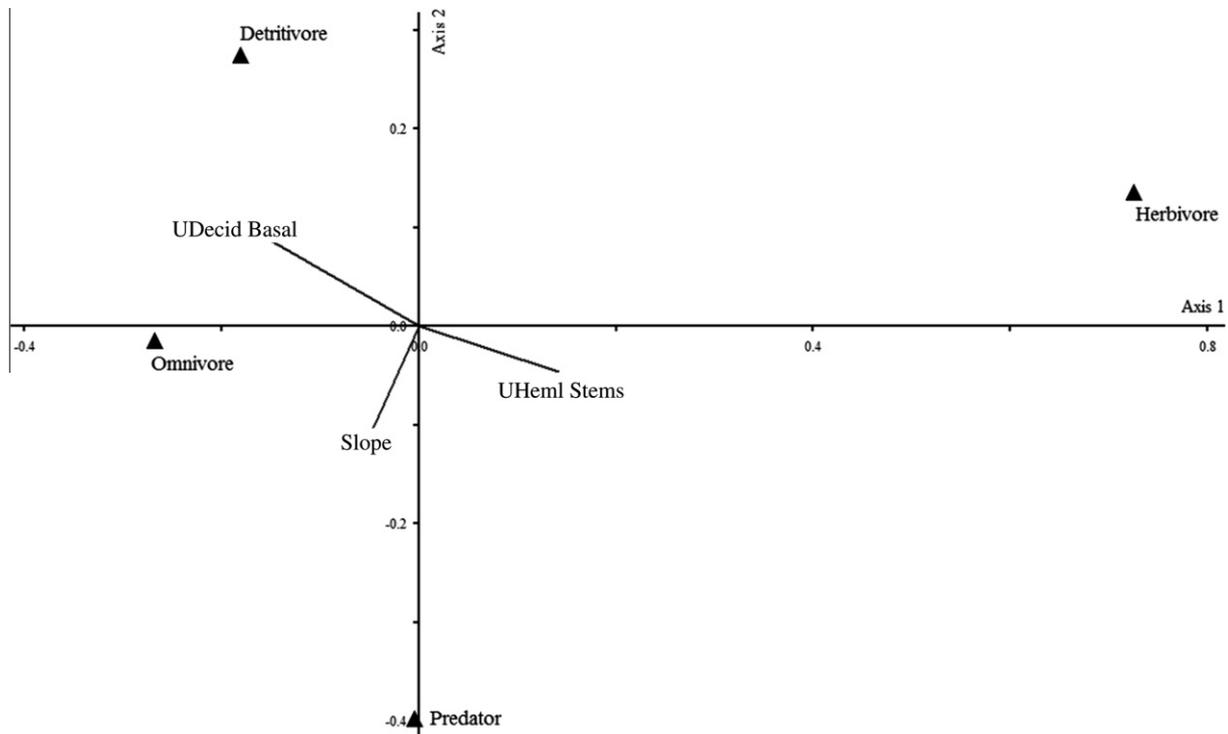


Fig. 2. First and second ordination axes from the canonical correspondence analysis depicting relationships between riparian vegetation structure and terrestrial arthropod feeding guilds in eastern hemlock and deciduous dominated riparian zones. The environmental variables shown are those with the greatest association with the ordination axes. Axis one accounts for 8.1% of the explained variation, axis two accounts for 3.7%. “UHeml Stems” indicates understory hemlock stems, “UDecid Basal” indicates understory deciduous basal area.

and are found on the “non-hemlock” side of axis 1. This first ordination axis accounts for just under half the explained variability (2.6%) with an eigenvalue of 0.006. The Monte Carlo species-environment correlation for the first axis was significant ($P = 0.04$) indicating a linear relationship between riparian vegetation parameters and terrestrial arthropods. While axis 2 and 3 account for 2.0% and 1.1% of the overall variation, the Monte Carlo tests of species-environment correlations for these axes are not significant (axis 2: $P = 0.16$, axis 3: $P = 0.34$), making interpretation of species-environment relationships in the context of these ordination axes dubious.

The CCA for feeding guilds (Fig. 2) yielded similar results. The Monte Carlo test was significant for each of the three ordination axes ($P < 0.05$). The CCA ordination accounted for 14% of the overall variation within the dataset. Axis 1 accounted for 8.1% of this variation, and was most strongly linked to understory deciduous basal area (intraset correlation = -0.45). The herbivore guild had a strong inverse correlation with understory deciduous basal area (weight = 0.73), but these were comprised entirely of Scolytidae. Omnivores (weight = -0.27) and detritivores (weight = -0.18) were linked with understory deciduous basal area. The link between the first ordination axis and predators is very low (weight = 0.004) indicating that understory deciduous basal area has very little influence on predator abundance or activity. Axis 1 accounts for more than half of the explained variability within our dataset. Axis 2 explains 3.7% of the variation within the dataset, and is most strongly linked with riparian slope (intraset correlation = -0.38). Predators are most strongly linked to this ordination axis (weight = -0.39) while detritivores (weight = 0.27) and herbivores (weight = 0.14) have an inverse correlation. Omnivores have a direct but weak correlation with axis 2 (weight = -0.02). Finally, axis 3 explains 2.4% of the variation within the dataset, and like axis 1 is most associated with understory

deciduous basal area (intraset correlation = 0.36). Because of the similarity to axis 1 and the low amount of variation explained by axis 3, interpretation is not provided.

4. Conclusions

Our study depicts discernible differences between arthropod communities associated with eastern hemlock dominated riparian zones and those associated with deciduous dominated riparian zones. Adelgid-induced hemlock mortality is expected to produce drastic changes in forest composition and structure, with alarming consequences for hemlock associates, including invertebrates (Dilling et al., 2007; Rohr et al., 2009; Mallis and Rieske, 2011), fish (Ross et al., 2003), migratory songbirds (Tingley et al., 2002), and forest vegetation (Spaulding and Rieske, 2010). Our comparative approach does not describe short term changes and unforeseen alterations in successional trajectories, or compare the ecological histories of the communities within these two distinct habitat types. It does provide a means of estimating potential long-term changes in arthropod community structure as a result of eastern hemlock mortality (see Rohr et al., 2009). We detected very few taxa that were unique to either forest type, but found differences in activity-density (presumably due to differences in abundance) in some terrestrial arthropod groups. These trends suggest that an adelgid-induced shift from eastern hemlock dominance to deciduous dominance within these riparian areas could lead to shifts in the relative abundance and community dominance of certain arthropod groups. While finer level taxonomic shifts were not monitored in this study, differences in coarser taxonomic resolutions were evident between the two forest types over this two year sampling period. This comparative approach has been used extensively to evaluate the influence of eastern hemlock on forest

arthropod communities by comparing abiotic conditions and biotic communities between eastern hemlock and deciduous dominated forests (Snyder et al., 2002; Ross et al., 2003; Ellison et al., 2005b; Rohr et al., 2009; Mallis and Rieske, 2010, 2011).

The use of family level identifications could be viewed as a limitation in our evaluation of terrestrial arthropod communities. However, 'taxonomic sufficiency' (*sensu* Ellis, 1985) recognizes that, within a community, changes at the species level are often reflected at coarser taxonomic levels. The use of coarser taxonomic identifications reduces the inputs associated with large scale community level studies (Williams and Gaston, 1994; Balmford et al., 1996; Hoback et al., 1999; Coleman and Rieske, 2006; Riggins et al., 2009; Rohr et al., 2009). Williams and Gaston (1994) discovered that family richness is a good predictor of species richness for a variety of taxa including butterflies, passerine birds, and bats in North and Central America.

Family level identifications of benthic fauna are appropriate for calculating diversity and stream quality indices (Hilsenhoff, 1988; Barbour et al., 1999; Bailey et al., 2001) and multivariate analysis of community data (Reynoldson et al., 1997), and can reliably detect moderate ecosystem impacts (Ferraro and Cole, 1992). Identifications beyond the family level may not yield much more information and may not be worth the time and effort (Resh and Unzicker, 1975). Investigations of invertebrate communities may also make use of family level data in order to answer broad ecological questions. For example, Rohr et al. (2009) utilized family level invertebrate data to evaluate differences in feeding guilds between eastern hemlock dominated and deciduous dominated forest stands. Coleman and Rieske (2006) used family level arthropod data to assess differences in arthropod abundance, richness, and diversity between forested sites that experienced single and multiple controlled burns. Targeting coarser taxonomic resolution, rather than insisting upon species level identification for woody plant surveys, reduces costs of field work 60–85% (Balmford et al., 2012). Clearly, accepting coarser taxonomic sufficiency provides us with an effective approach to conduct large landscape scale studies over long periods of time to answer broad questions regarding arthropod community responses to change. However, care must be taken in interpreting results. The use of coarser level taxonomic identifications in ecological monitoring can be misleading (Longcore, 2003), as not all genera in a given invertebrate family function in the same trophic role (e.g. Formicidae, Hölldobler and Wilson, 1990).

We found no statistically significant differences in arthropod family abundance between the two forest types, but arthropod family abundance in deciduous riparian zones was almost three times greater than in more structurally uniform hemlock riparian zones, a trend which may support our hypothesis that arthropod abundance correlates with structural complexity and diversity of vegetation. While there are a number of other physical and chemical properties that differ between the two forest types in other studies (see Ellison et al., 2005a), these conditions rely on the presence of the foundation species, eastern hemlock. The Jaccard value comparing overlap of the 164 invertebrate taxa that were collected between eastern hemlock and deciduous dominated riparian zones reveals that the two riparian zone designations were 62% similar in community composition. Deciduous riparian zones had a greater number of unique taxa ($n = 35$) than eastern hemlock riparian zones ($n = 28$), as expected. Excluding the incidental Ctenophthalmidae captured in the eastern hemlock pitfall traps, which were likely vectored by small mammals, the most numerous unique taxon in eastern hemlock riparian zones were the Phryganeidae, and in deciduous riparian zones, the Philopotamidae. The immature forms of these caddisfly families are aquatic. Phryganeids are shredders that break down coarse leaf material and to a lesser extent function as predators. Philopotamids are collector-filterers, utilizing finer particulate

matter within streams (Merritt and Cummins, 1996). These feeding groups occupy different niches within the benthic community and play very different roles within streams (Wallace, 1996). While the adult caddisflies we collected in pitfall traps are likely incidental, their presence does suggest a potential functional change that may occur as the eastern hemlock forest type shifts to a deciduous dominated forest due to adelgid-induced hemlock mortality.

Our canonical correspondence analyses offer some explanation of the differences between eastern hemlock dominated and deciduous dominated riparian zones. While the explained variation is less than 15% in the canonical correspondence analyses, ter Braak and Verdonschot (1995) note that percentage-explained inertia in ecological studies is generally low and often less than 10%. Our CCAs accounted for 5.7% and 14.0% of the explained variation in our data, and our Monte-Carlo permutation tests for taxa-environmental relationships were each highly significant ($p < 0.05$), indicating the presence of strong environmental influences. Thus, the CCAs allow us to understand finer scale arthropod-plant relationships within our forest types. For example, we captured a greater number of ants, which dominated our omnivore guild, in deciduous dominated than eastern hemlock dominated riparian zones (Table 5), reflecting the relationship between ant abundance and forest structure, and corroborating results from other studies (Ellison et al., 2005b; Dolek et al., 2008). While our dataset does not go beyond the family level, formicid species richness in adelgid-free eastern hemlock forests is reportedly lower than in adjacent deciduous forests (Ellison et al., 2005b). In southern New England forests this was attributed to the foundation effects exerted by eastern hemlock, including local microclimates and soil conditions (Ellison et al., 2005a, 2005b), and to the typically greater abundance of sap-feeding homopterans, which are often tended by ants, in deciduous dominated forests (Buckley, 1987).

Forest ants select open and light forests over those with denser canopies, suggesting that ant faunal composition is driven by forest structure (Dolek et al., 2008). A defining characteristic of eastern hemlock canopies is the deep shade they generate, which can be less than 2% of full sun (Canham et al., 1994). Our arthropod taxon CCA reveals a negative relationship between formicid abundance and understory hemlock stems (Fig. 1), which reduce sunlight penetration. This trend was also detected by our feeding guild CCA (Fig. 2). Furthermore, we detected a significant interaction of vegetation and season in formicid abundance. While ant abundance in eastern hemlock and deciduous streams in fall and spring differs, these differences were not evident in summer when abundance is high in both eastern hemlock and deciduous riparian zones, perhaps due to longer days and increased strength of solar radiation. These seasonal differences may be due to more sunlight reaching the forest floor during the spring and fall months in deciduous forests, while there was less seasonal variation in sunlight in eastern hemlock dominated forests. Because of the variability of trophic roles within the Formicidae, our current efforts are focused on gaining greater taxonomic resolution within the family, shedding more insight into the influence of vegetation composition and structure on this abundant and diverse component of the forest arthropod community.

The predatory Staphylinidae were significantly more abundant in deciduous dominated riparian zones, yet were correlated with understory hemlock stems in our CCA. This apparent discrepancy can be explained by the fact that axis 1 (Fig. 1) is associated with only the understory component of our riparian vegetation, a finer resolution than the broad generalized mixed model which compares eastern hemlock vs. deciduous riparian zones. Eastern hemlock was present in the understory of both riparian zone designations, but there was a significant difference between eastern hemlock and deciduous dominated riparian zones in terms of understory eastern hemlock stem density (14.5 (2.2) vs. 4.7

(1.6)). Local habitat characteristics do influence arthropod activity (Dauber et al., 2005), and understory hemlock stems may interact with deciduous overstories to produce favorable microclimatic factors for terrestrial arthropod taxa such as Staphylinidae. Our guild level CCA found that predators as a group are more strongly linked to slope than components of riparian vegetation.

In our study detritivores were dominated by millipedes and isopods, which are instrumental in processing leaf material and form an important link in energy flow (Lavelle et al., 2006). Millipedes (Class Diplopoda) have been correlated with eastern hemlock (Rohr et al., 2009), but we found that millipedes and isopods were more abundant in deciduous dominated riparian zones (Table 5). The guild level CCA reveals that detritivores are most directly linked with the understory deciduous basal area component of our riparian zone vegetation. The use of these detritivore taxa as indicators in the wake of ecosystem change has been suggested, particularly in the context of soil characteristics such as pH (Snyder and Hendrix, 2008). The loss of eastern hemlock and associated shifts in dominant forest canopy species will likely drive changes in ecosystem processes such as nutrient mineralization (Jenkins et al., 1999), which could potentially be reflected in changes in diplopod abundance.

Our study offers an appraisal of the terrestrial invertebrate communities of eastern hemlock and deciduous dominated riparian zones, which may represent projected replacement forests resulting from eastern hemlock mortality. Our data suggest no statistical differences in overall activity-density, diversity, or richness between arthropod communities of eastern hemlock and deciduous dominated riparian zones. Although total arthropod activity density is numerically greater in deciduous riparian zones, we found significant differences in the abundance of only four taxa. Differences in abundance and activity of arthropods such as millipedes and isopods, as well as Formicidae and Staphylinidae, were readily apparent in our study, and it would appear that these groups will benefit from the replacement of eastern hemlock by deciduous tree species. Ground and soil dwelling arthropods such as these are often sensitive to subtle changes in their environment and may be useful as indicator taxa. Their numbers and composition should be scrutinized intently prior to and following habitat perturbations to establish accurate benchmarks so that restoration of imperiled ecosystems remains a viable strategy (Landres et al., 1999).

Acknowledgements

The authors thank Josh Adams, Paul Ayayee, Daniel Bowker, Josh Clark, Tom Coleman, Zachary Cornett, Murphey Coy, Joe Hacker, Cat Hoy, Amber Jones, Tom Kuhlman, Rachael Mallis, Heather Spaulding, Melanie Sprinkle, Matt Thomas, and Sarah Wightman for field and laboratory assistance. Luke Dodd and Xia Yu provided statistical guidance, and John Obrycki, Lee Townsend, and two anonymous referees reviewed an earlier version of this manuscript. We also thank the University of Kentucky Robinson Forest Field Station, USDA Forest Service, Kentucky Division of Forestry, and the Kentucky State Nature Preserves Commission. This project was funded in part by grant funds from the Kentucky Water Resources Research Institute and the Tracy Farmer Center for the Environment and through funds provided by McIntire Stennis, and is published as Kentucky Agricultural Experiment Station publication number 12-08-001.

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