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Stream Macroinvertebrate Communities in Paired Hemlock and Deciduous Watersheds

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Abstract - *Tsuga canadensis* (Eastern Hemlock) is a common forest species that is declining throughout its range in the eastern United States because of the invasion of an exotic forest pest, *Adelges tsugae* (Hemlock Woolly Adelgid). This pest kills infected trees, and over time, infected stands are replaced by deciduous forests. The conversion of forests from hemlock to deciduous species is predicted to impact the hydrology, chemistry, and biology of associated headwater streams. In this study, we examined the macroinvertebrate communities of two adjacent headwater streams with differing hemlock influence in central Massachusetts. Abundance, taxa richness, diversity, and unique taxa were generally greater in the deciduous stream. Differences in the distribution of functional feeding groups were observed: the hemlock stream had a greater percentage of collector-gatherers while the deciduous stream had a greater percentage of shredders and predators. These findings suggest that macroinvertebrate communities in streams draining hemlock and deciduous watersheds may differ in structure and function, and that anticipated hemlock mortality may impact the region's stream ecology.

Introduction

Tsuga canadensis (L.) Carrière (Eastern Hemlock) is a highly shade-tolerant conifer that is dominant throughout much of central New England and often forms largely mono-specific stands (Rogers 1978). Hemlock forests in eastern North America have recently been invaded by *Adelges tsugae* Annand (Hemlock Woolly Adelgid) (Hemiptera: Adelgidae), an introduced insect that kills both saplings and adult trees (McClure 1991). Eastern Hemlocks do not regenerate following infestation, and stands killed by the adelgid are replaced by deciduous species (Orwig 2002, Orwig and Foster 1998). Forecasted hemlock mortality may impact the physical and biological characteristics of coupled aquatic ecosystems, such as headwater streams and wetlands (Ellison et al. 2005). For example, Eastern Hemlock evapotranspires less water than most deciduous trees and create a cool, moist, and dark forest understory (Hadley 2000), thus providing hydrologic and thermal stability to adjacent headwater streams (Snyder et al. 2002). In addition, hemlock stands may constrain food resources in streams by shading periphyton communities (Rowell and Sobczak 2008) and providing low-quality leaf litter for stream consumers (Maloney and Lamberti 1995). Hence, the loss of Eastern Hemlock in New

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England may result in significant changes in the hydrology and energy flow of the region's headwater streams. These changes may in turn impact the biota of headwater streams including populations of coldwater fishes, threatened stream salamanders, and aquatic insects.

Headwater streams drain more than 80% of the landscape and are important sources of organic carbon, inorganic nutrients, and organisms to downstream ecosystems (Lowe and Likens 2005, Nadeau and Rains 2007, Wipfli et al. 2007). Food resources in headwater streams draining forested watersheds are frequently dominated by allochthonous materials such as woody debris and leaves (Bilby and Likens 1980, Vannote et al. 1980), although periphyton can be significant seasonally and important for some headwater stream taxa (Mayer and Likens 1987). Decomposition rates, palatability to consumers, and the nutritional value of these terrestrially derived inputs vary with tree species (Maloney and Lamberti 1995, Webster and Benfield 1986). Stream macroinvertebrates are primary consumers of these allochthonous materials, and their distribution and productivity are tightly coupled to forest composition and the supply of bio-available organic matter (Cross et al. 2006, Cummins and Klug 1979, Eggert and Wallace 2003, Wallace et al. 1999).

The objective of this study was to identify differences between the macroinvertebrate communities of two streams. Specifically, we compared two adjacent streams with many comparable watershed attributes but contrasting riparian forest composition in regards to hemlock abundance. We predicted that the deciduous stream's macroinvertebrate community would have higher abundances, richness, and diversity than the hemlock stream's community due to greater food resources. In addition, we predicted that the deciduous stream would be dominated by leaf-shredding macroinvertebrates. While our comparative approach has been defended by some ecologists (e.g., Oksanen 2001) and employed in numerous stream-manipulation experiments (e.g., Wallace et al. 1999), we recognize this approach has also been criticized for a lack of replication at the scale of stream ecosystem (Hurlbert 2004). The ultimate goal of the study was to provide preliminary information that will help forecast how regional declines in Eastern Hemlock may impact New England's stream ecosystems.

Methods

Study site

We selected two adjacent streams draining the extensively studied Prospect Hill Tract of Harvard Forest in north central Massachusetts. The 340-ha Prospect Hill Tract is located in the towns of Petersham and Phillipston at an elevation of 270 to 420 m (as described in Motzkin et al. 1999). Soils are primarily acidic sandy loams and glacial tills overlying schist and gneiss bedrock. Variability in the relief, soil depth, and the presence of a hardpan all result in erratic patterns of soil drainage (Foster et al. 1992). The property is approximately 90% forested, primarily second growth, and characterized as the transition hardwood forest type with common species including: *Quercus rubra* L. (Northern Red Oak), *Acer rubrum* L. (Red Maple), *Betula lenta* L. (Sweet Birch), *B. papyrifera* Marsh. (Paper Birch), *Fraxinus americana* L. (White Ash), *Pinus strobus* L. (Eastern White Pine), and Eastern Hemlock (Westveld 1956).

The two comparison streams are both first-order tributaries of Bigelow Brook, a tributary of the Swift River that drains into the Quabbin Reservoir. The two watersheds are adjacent to one another and comparable in gradient, total area, underlying geology, and water chemistry (Table 1); however, one stream's riparian area is dominated by Eastern Hemlock, while the other's is composed primarily of deciduous species (Red Maple, Paper Birch, and Northern Red Oak) with diffuse patches of Eastern Hemlock. The hemlock stream had slightly lower pH than the deciduous stream; however, this difference is likely a function of hemlock abundance. Both streams have small springs as their source, consistent summer flow, and mean summer water temperatures between 10 and 12 °C. Inorganic N and P concentrations are low in both streams (Table 1), and high discharge events dominate fluvial losses of dissolved C, N, and P in the hemlock-dominated stream. Summer photosynthetically active radiation values are ≈3-fold greater in the deciduous stream (Rowell and Sobczak 2008). The hemlock stream's hydrology, chemistry, and macroinvertebrate community have been previously characterized (Collins et al. 2007).

Field collection

Invertebrate samples were taken from four randomly chosen locations in each stream during a two-week period in late July and early August of 2005. At each location, one sample was taken from the nearest riffle area and one from the nearest depositional area; thus, eight samples were taken from each stream. Moss was sampled when present on the substratum. Peak emergence of insects usually occurs in early to late spring; hence, it is likely that our sampling regime underestimated the abundance, richness, and diversity of the streams' macroinvertebrate communities. Samples were taken by thoroughly disturbing the substrate within a 0.25-m^2 quadrat for a 30-second period and collecting all dislodged material in standard D-frame kick nets (250-µm mesh) placed downstream. Samples were live-picked, with care being taken to collect all sizes of individuals. Live-picking has been used extensively in rapid biological assessments and environmental monitoring with favorable results (Chessman and Robinson 1987, Courtemanch 1996,

Table 1. Physical and chemical characteristics of the two study streams. Riparian hemlock was estimated using half-meter resolution satellite imagery within a 10-m buffer on either side of the streams. Temperature was measured during sample collection. Photosynthetically active radiation (PAR) data is from Rowell and Sobczak (2008). Water chemistry data represent the mean values from two sampling dates in July of 2007.

Characteristic	Hemlock	Deciduous
Watershed area (ha)	24	27
Riparian hemlock (%)	88	36
Mean summer temperature (˚C)	10.8	11.2
pH	5.2	5.4
Dissolved organic carbon (mg/L)	1.4	1.5
Nitrate (mg/L)	0.018	0.013
Phosphate (µg/L)	0.9	1.0
PAR (µmol m^{-2} s^{-1})	22	64

Growns et al. 1997, Marchant et al. 2006, Metzeling et al. 2003). While live-picking has traditionally been assumed to underestimate small and cryptic taxa (Humphrey et al. 2000), comparisons between live-picking and laboratory sorting have shown that this method is effective at detecting even relatively fine-scale differences between watersheds (Growns et al. 1997, Metzeling et al. 2003). In this study, each sample was live-picked for three hours rather than the 30 minutes to one hour generally used in rapid assessments of stream communities; thus, we believe that our samples accurately portray any differences between streams. All invertebrates were preserved in 70% ethanol and brought back to the laboratory.

Laboratory methods and analysis

In the laboratory, invertebrates were sorted and identified to the genus level (with the exception of Chironomidae, which were identified to the subfamily/tribe level) using dissecting and compound microscopes. Taxa were then segregated among the grazer, shredder, collector-gatherer, collector-filterer, and predator functional feeding groups based on the ecological information known for each taxon (Merritt and Cummins 1996, Stewart et al. 1993, Wiggins 2000). In addition, taxa unique to each stream were identified. We calculated mean abundance (number of individuals/m^2), richness (number of taxa/sample), and Shannon's diversity index of macroinvertebrates in each stream and compared them using a Student's t-test. In addition, the composition of the two streams was compared at the order level and among functional feeding groups.

Results

Community composition

The deciduous stream had a significantly higher mean richness (24.4 vs. 11.0, P-value < 0.001; Fig. 1A), more unique taxa (17 vs. 3; Table 2), and more taxa (45 vs. 31; Table 2) than the hemlock stream. The deciduous stream also had a significantly higher mean diversity (2.3 vs. 1.7, P-value = 0.008; Fig 1B). The deciduous stream had a higher mean abundance (397.3/m^2 vs. 288.5/m^2) than the hemlock stream, although the difference between the two streams was not significant (P-value = 0.223; Fig. 1C). The structure of the streams' macroinvertebrate communities, in terms of composition by order, also differed (Fig. 2). The deciduous stream's community was dominated by Diptera and Trichoptera (46% and 43%, respectively), and the hemlock stream's community was composed primarily of Diptera (59%), Trichoptera (19%), and Ephemeroptera (19%).

Functional feeding groups

The functional composition of the two streams' macroinvertebrate communities were very different (Fig. 3). In both streams, the collector-gatherer feeding group dominated; however, their relative importance varied between streams, with the collector-gatherer group comprising 62% of the hemlock community and only 32% of the deciduous stream community. Shredder and predator feeding groups were notably lower in the hemlock stream, comprising only 17% and 15%, respectively, versus 28% and 22%, repectively, in the deciduous stream. In both streams, the percentage of grazers was low (≈1% in both streams).

There were large differences in the composition and relative abundances of the taxa comprising the predator, shredder, collector-filterer, and collector-gatherer feeding groups (Fig. 4). In both streams, the predator feeding

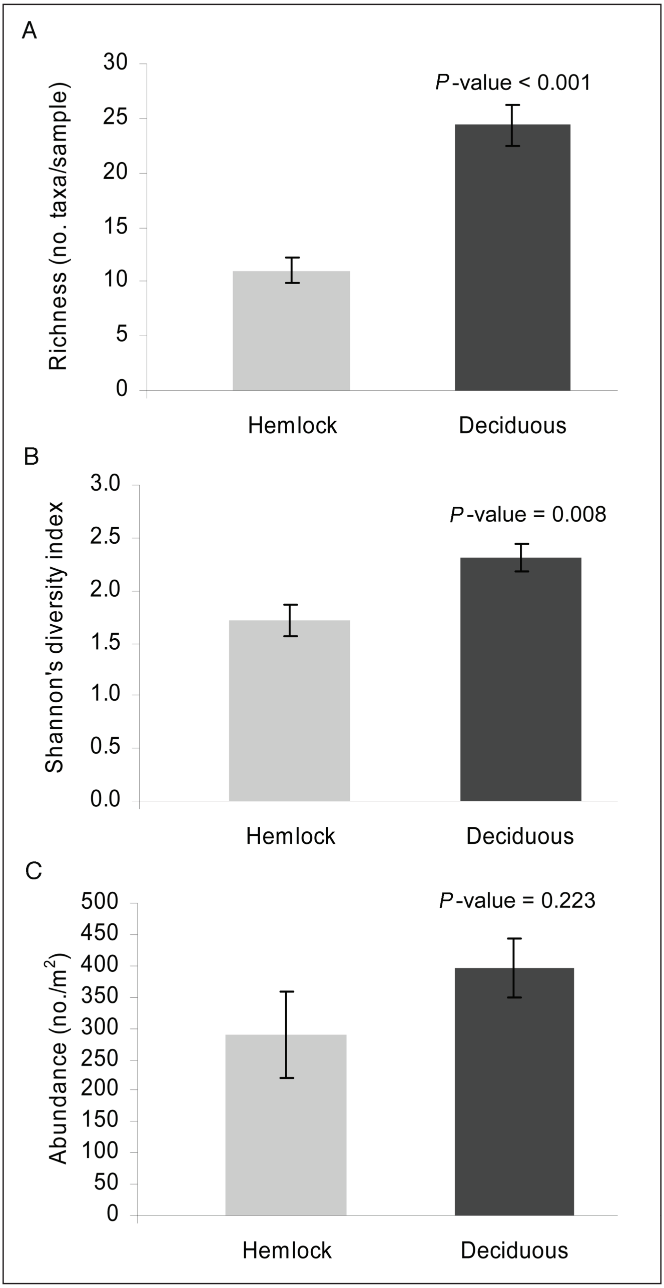

Figure 1. Comparison of three community structure metrics: A) richness (number of taxa/sample), B) Shannon's diversity index, and C) abundance (number of individuals/m^2) between a hemlock-dominated stream and a deciduous-dominated stream during summer 2005 at Harvard Forest, MA.

Table 2. Classifications and abundances (number of individuals/m^2) (± SD) of taxa found in a hemlock-dominated stream and a deciduous-dominated stream during the summer of 2005 at Harvard Forest, MA. FFG = functional feeding group.

			Abundance ± SD	
Taxa	Order	FFG	Hemlock	Deciduous
Simulium sp.	Diptera	Filterer	-	0.3 ± 0.7
Diplectrona sp.	Trichoptera	Filterer	-	5.8 ± 9.8
Dolophilodes sp.	Trichoptera	Filterer	-	0.8 ± 1.5
Parapsyche sp.	Trichoptera	Filterer	8.0 ± 11.8	35.5 ± 58.6
Wormaldia sp.	Trichoptera	Filterer	0.8 ± 1.5	11.8 ± 26.2
Chelifera sp.	Diptera	Gatherer	-	0.3 ± 0.7
Chironomini	Diptera	Gatherer	6.5 ± 15.3	22.3 ± 19.6
Clinocera sp.	Diptera	Gatherer	0.3 ± 0.7	4.3 ± 5.5
Dixa sp.	Diptera	Gatherer	-	0.3 ± 0.7
Orthocladiinae	Diptera	Gatherer	11.0 ± 13.9	6.8 ± 6.1
Ptychoptera sp.	Diptera	Gatherer	-	0.3 ± 0.7
Tanytarsini	Diptera	Gatherer	113.3 ± 119.0	73.3 ± 94.8
Ameletus sp.	Ephemeroptera	Gatherer	-	0.5 ± 1.4
Eurylophella sp.	Ephemeroptera	Gatherer	56.8 ± 49.9	16.8 ± 20.8
Amphinemura sp.	Plecoptera	Gatherer	2.3 ± 4.1	-
Lype sp.	Trichoptera	Gatherer	0.5 ± 1.4	0.3 ± 0.7
Ectopria sp.	Coleoptera	Grazer	-	1.5 ± 2.3
Optioservus spp.	Coleoptera	Grazer	-	0.3 ± 0.7
Molanna sp.	Trichoptera	Grazer	3.5 ± 9.1	3.3 ± 5.8
Neophylax sp.	Trichoptera	Grazer	-	0.3 ± 0.7
Agabus spp.	Coleoptera	Predator	0.5 ± 1.4	0.5 ± 0.9
Celina sp.	Coleoptera	Predator	0.3 ± 0.7	-
Cymbiodyta sp.	Coleoptera	Predator	-	0.3 ± 0.7
Hydrobius sp.	Coleoptera	Predator	-	2.3 ± 4.8
Dicranota sp.	Diptera	Predator	0.5 ± 1.4	7.5 ± 4.6
Hexatoma sp.	Diptera	Predator	1.3 ± 2.8	5.0 ± 4.1
Hybomitra sp.	Diptera	Predator	0.8 ± 1.5	4.5 ± 7.2
Limnophila spp.	Diptera	Predator	-	0.5 ± 0.9
Palpomyia sp.	Diptera	Predator	3.3 ± 7.6	3.0 ± 3.2
Pedicia sp.	Diptera	Predator	1.0 ± 1.5	0.5 ± 1.4
Psuedolimnophila sp.	Diptera	Predator	-	0.5 ± 1.5
Tanypodinae	Diptera	Predator	24.3 ± 26.1	48.5 ± 32.3
Gerris sp.	Hemiptera	Predator	-	0.5 ± 1.4
Microvelia sp.	Hemiptera	Predator	0.8 ± 2.1	1.0 ± 1.5
Sialis sp.	Megaloptera	Predator	1.3 ± 1.8	2.0 ± 3.2
Cordulegaster sp.	Odonata	Predator	0.3 ± 0.7	2.0 ± 3.9
Lanthus sp.	Odonata	Predator	0.3 ± 0.7	0.8 ± 1.0
Sweltsa spp.	Plecoptera	Predator	-	1.3 ± 2.3
Oligostomis sp.	Trichoptera	Predator	0.5 ± 0.9	6.3 ± 8.8
Rhyacophilia spp.	Trichoptera	Predator	2.3 ± 2.7	2.5 ± 3.2
Haliplus sp.	Coleoptera	Shredder	-	0.3 ± 0.7
Tipula spp.	Diptera	Shredder	0.5 ± 0.9	2.8 ± 2.6
Pyralidae	Lepidoptera	Shredder	0.3 ± 0.7	0.3 ± 0.7
Leuctra sp.	Plecoptera	Shredder	2.3 ± 2.7	4.5 ± 3.2
Ironoquia sp.	Trichoptera	Shredder	0.3 ± 0.7	-
Lepidostoma sp.	Trichoptera	Shredder	20.3 ± 21.6	73.8 ± 58.3
Psilotreta sp.	Trichoptera	Shredder	13.5 ± 21.7	14.0 ± 9.3
Pycnopsyche sp.	Trichoptera	Shredder	5.3 ± 9.9	13.0 ± 22.1

group was dominated by the chironomid subfamily Tanypodinae; however, in the deciduous stream, there were also large tipulid populations (*Dicranota* spp. and *Hexatoma* sp.). Shredder abundance was ≈3-fold greater in the deciduous stream. In both streams, the primary shredders (by abundance) were the Trichopterans, *Lepidostoma* sp. and *Pycnopsyche* sp.; however, the abundances of both these taxa were higher in the deciduous stream. In the collector-gatherer feeding group, the two streams had the same dominant taxa,

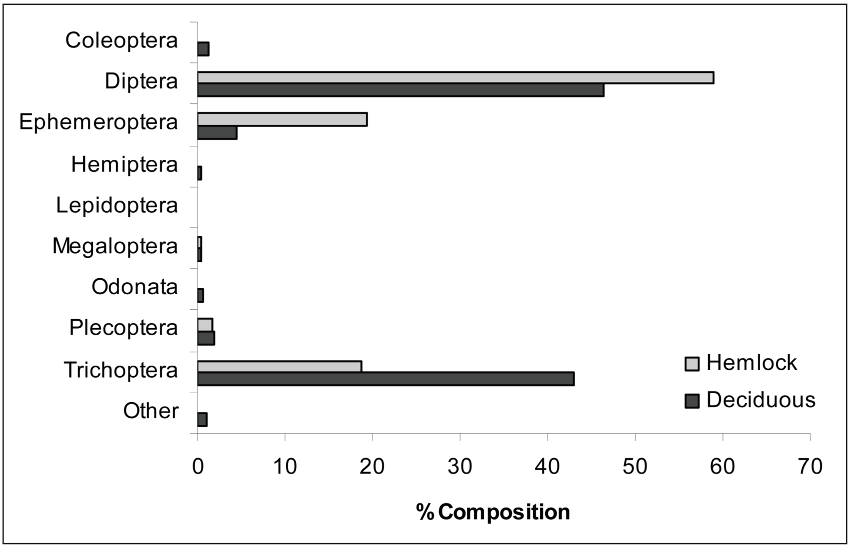

Figure 2. Relative abundance (% total) by order of macroinvertebrate communities in headwater streams draining hemlock and deciduous forests at Harvard Forest, MA.

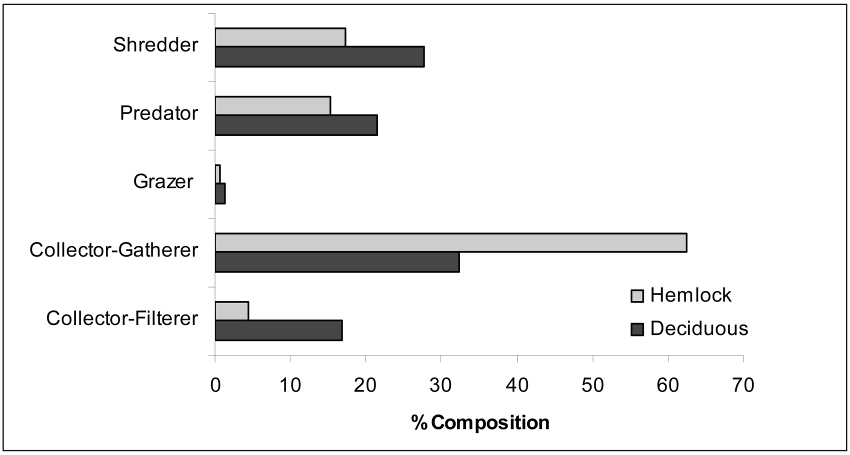

Figure 3. Relative abundance (% total) by functional feeding group of macroinvertebrate communities in headwater streams draining hemlock and deciduous forests at Harvard Forest, MA.

the chironomid tribe Tanytarsini, but with rather substantial differences in their abundance and in the composition of the remaining taxa. The hemlock stream had more Tanytarsini along with a greatly increased abundance of the Ephemeropteran genus *Eurylophella*.

Discussion

We found ecologically important differences between the macroinvertebrate communities of adjacent deciduous and hemlock streams. We believe that these differences are a function of differences in the streams' riparian vegetation; however, we recognize that our study was spatially and temporally limited.

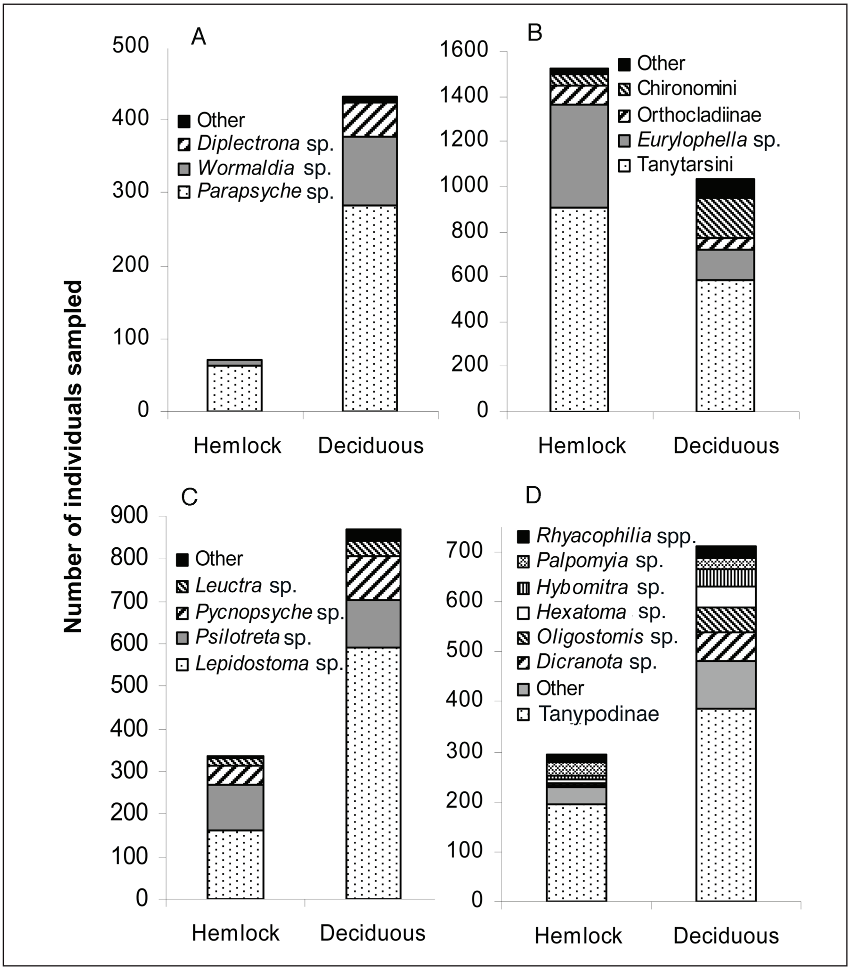

Figure 4. Number of individuals sampled in four functional feeding groups: A) collector-filterer, B) collector-gatherer, C) shredder, and D) predator in headwater streams draining hemlock and deciduous forests at Harvard Forest, MA. Taxa with less than 5% relative abundance were pooled together and designated "other."

The deciduous stream supported higher richness and abundance of macroinvertebrates, and had more unique taxa than the hemlock stream. In addition, we found the composition of the communities in the two streams differed, both at the taxonomic and functional levels. These findings support and geographically extend many of the findings in Snyder et al.'s (2002) benchmark study on macroinvertebrates in numerous streams draining deciduous and hemlock-dominated watersheds in the Delaware Water Gap National Recreation Area; however, our findings differ in some regards. Importantly, Snyder et al. (2002) found that hemlock streams supported more taxa of macroinvertebrates relative to deciduous streams.

Snyder et al. (2002) attributed higher species richness of streams draining hemlock forests to increased stability of daily and seasonal temperature and flow regimes. We believe the hydrologic stability that hemlock stands provide may allow increased abundance of taxa well adapted to the stream's environmental conditions; however, increased environmental stability may also lead to a reduction in the heterogeneity of habitats, which is an important determinate of diversity (Death and Winterbourn 1995, Miller and Stout 1989, Power et al. 1988). We propose that in some streams with riparian areas dominated by deciduous species, localized and seasonal variation in riparian litter inputs, light levels, and water temperatures may augment the diversity of microhabitats relative to hemlock-dominated streams, thus allowing increased niche partitioning. Environmental conditions in streams flowing through hemlock stands may be optimal for some taxa, but not for many taxa with the potential to colonize hemlock-dominated streams. Thus, the conversion from hemlock to deciduous forest may result in an increase in the diversity of aquatic macroinvertebrate communities; however, this change may be accompanied by the loss of some hemlock-adapted taxa.

Hemlock and deciduous forests differ in the quality, quantity, and diversity of food resources they provide to stream biota. Streams draining deciduous forests receive more light annually than those draining hemlock forests because of reduced shading during leaf-off, and reduced canopy density during leaf-out (Hadley 2000, Rowell and Sobczak 2008). Light is often a limiting resource for primary production in headwater streams (Hill and Knight 1988); thus, increases in light availability may stimulate in-stream primary production, increase autochthonous food resources, and provide a broader food base for macroinvertebrates.

Eastern Hemlock also influences allochthonous food resources by contributing litter of poorer quality relative to many deciduous forest species. Maloney and Lamberti (1995) found that hemlock needles decayed more slowly and supported fewer macroinvertebrates than leaves of most deciduous riparian plant species. Based on studies with other conifer species, primarily of the genus *Pinus*, it appears that conifer needles are a nutritionally poor food resource, and are generally avoided by shredders (Webster and Benfield 1986, Whiles and Wallace 1997). Because allochthonous inputs are a critical energy source for forested headwater streams (Eggert and Wallace 2003, Wallace et al. 1999), it is likely that a transition from the low-quality inputs from Eastern Hemlock to the relatively high-quality inputs from deciduous species will result in changes in headwater stream macroinvertebrate communities.

We predicted that differences in the riparian vegetation would result in differences in the functional composition of the two streams, particularly in regards to the shredder feeding group. Our findings and those of Snyder et al. (2002) support this prediction. In this study, the difference can primarily be attributed to greater abundances of shredding trichopteran taxa, particularly *Lepidostoma* sp. *Lepidostoma* is often associated with leaf packs and debris dams (Wiggins 2000). We found that predators comprised a greater proportion of the deciduous stream's community; this finding differs from those of Snyder et al. (2002). Both streams' collector-gatherer communities were dominated by the chironomid tribe Tanytarsini; however, in the hemlock stream, *Eurylophella* mayflies also comprised a large proportion. Several species of *Eurylophella* have been shown to inhabit aquatic mosses (Funk and Sweeney 1994) which are prevalent along many hemlock-dominated streams. Snyder et al. (2002) also found *Eurylophella* weakly associated with hemlock stands.

Overall, our findings suggest that macroinvertebrate communities in streams flowing through hemlock-dominated and deciduous-dominated riparian zones differ in both structure and function, and that anticipated hemlock mortality may impact central New England's stream ecology. An emerging body of literature suggests that headwater streams can influence the ecology and biogeochemistry of connected downstream ecosystems (Lowe and Likens 2005, Nadeau and Rains 2007, Wipfli et al. 2007). Further research over broader geographic and longer temporal scales is needed to understand more precisely how potential alterations in the macroinvertebrate communities of New England's headwater streams may influence downstream ecosystems.

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