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# Invasive woolly adelgid appears to drive seasonal hemlock and carcass inputs to a detritus-based stream

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## Introduction

Ecosystems are experiencing rapid ecological changes due to human-driven alterations in climate, land-use, nutrient availability, and introduction of pests and pathogens. Many of these environmental changes are predicted to result in non-random loss of species that will alter community composition (Vitousek et al. 1997, Loreau et al. 2001, Ellison et al. 2005). For example, in eastern U. S. forests, current declines in eastern hemlock (*Tsuga canadensis*) resulting from infestation of the woolly adelgid (*Adelges tsugae*) are altering riparian tree community composition (Orwig et al. 2002). Declines in eastern hemlock in southern Appalachian forests are projected to result in long-term increases in tulip poplar (*Liriodendron tulipifera*) or rhododendron (*Rhododendron maximum*; Ellison et al. 2005), but short-term seasonal effects of woolly adelgid infestation on allochthonous inputs to streams have not been studied.

The life cycle of the woolly adelgid contains 2 generations. Overwintering adult woolly adelgids deposit eggs in ovisacs from February to late March, and larvae emerge in early April (McClure 1989, 1991, McClure & Cheah 1999). These larvae develop into the adult stage and deposit a second generation of eggs in June. Emergent larvae remain inactive until October, when feeding resumes (McClure 1989, 1991, McClure & Cheah 1999). Larvae feed on sap from the base of hemlock needles (McClure 1987), which causes the needles to fall off. Needle inputs from infested riparian hemlock trees may serve as an important resource to stream ecosystems.

Terrestrial litter subsidies are important organic matter and energy resources for recipient stream ecosystems (Fisher & Likens 1973, Vannote et al. 1980, Hall et al. 2001), and the chemical quality of litter can be altered by terrestrial herbivores (Hutchens & Benfield 2000, Chapman et al. 2003, 2006). Herbivory on evergreens results in higher litter quality and accelerated decomposition and nutrient cycling in terrestrial environments compared to herbivory on deciduous trees (Chapman et al. 2003, 2006), and eastern hemlock litter from infested trees has been reported to contain higher nitrogen concentrations than litter from uninfested trees (Stradler et al. 2006).

Here we present data from a 2-year litter trap study, conducted during the early stages of woolly adelgid infestation and hemlock decline. We assess the contribution of eastern hemlock to direct litterfall and lateral inputs to streams as well as entrainment of woolly adelgid carcasses by leaf packs in a second-order reach of Ball Creek, a headwater stream located at Coweeta Hydrologic Laboratory (Coweeta), Macon County, North Carolina, U. S. (35°00'N; 83°30'W).

**Key words:** eastern hemlock (*Tsuga canadensis*), eastern U. S. forests, invasive species, life cycle, litterfall, streams, woolly adelgid (*Adelges tsugae*)

## Materials and methods

We estimated litter inputs from August 2004 to August 2006 using directfall (0.1 $m^2$, n = 10) and lateral (0.5 × 0.2 × 0.3 m, n = 10) traps. Six directfall traps were randomly placed along the circumference of a 10-m diameter circle that incorporated both the riparian zone on either side of Ball Creek, and 4 directfall traps were randomly placed along 30-m reaches on either side of Ball Creek. Lateral traps were randomly placed in 5-m segments along both margins of the 75-m stream reach. Contents within traps were collected approximately monthly, except during peak litterfall (October-November) when traps were emptied every 2 weeks. Hemlock needles were separated from total litterfall, and both hemlock and the remaining litter material were oven-dried (60 °C for 48 h) and weighed to determine dry mass (DM).

A random composite of hemlock needles was collected from multiple directfall litter traps over several dates and ground using a Spex Mill. The ratio of carbon to nitrogen (C:N) concentrations of hemlock needles was measured using a Carlo Erba 1500N CHN analyzer (Carlo Erba, Milan, Italy).

To measure woolly adelgid carcass entrainment by submerged leaf packs, we used 15-g leaf packs (n = 480) containing litter from 4 dominant riparian species along the 75-m reach of Ball Creek (Kominoski et al. 2007). Leaf packs were randomly retrieved on days 7, 14, 28, 70, 118, 169, 183, and 190. Retrieved packs were placed on ice and transported to the labo-

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ratory for processing within 12 h. Litter was rinsed over nested sieves (1 mm and 250 µm) to collect macroinvertebrates. Abundance of woolly adelgid carcasses was determined for all leaf packs retrieved on harvest days 14, 70, and 118. Woolly adelgid biomass was estimated using mean length and width calculations for 10 individuals within each size class and length-mass regressions (BENKE et al. 1999).

Analyses were conducted with SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, U.S.) using an alpha of 0.10. Data were log-transformed when necessary to meet assumptions of homoscedasticity. One-way analysis of variance (ANOVA) was used to determine monthly variation in proportion and dry mass of hemlock litter inputs (directfall and lateral). T-tests were used to compare annual proportion and dry mass of hemlock litter in directfall and lateral traps. One-way ANOVA was also used to test differences in abundance and biomass of woolly adelgid carcasses entrained by leaf packs over time.

## Results and discussion

Mean annual proportion of hemlock litter was higher in directfall (0.16 ± 0.04) than lateral traps (0.08 ± 0.04; $p < 0.10$), and mean annual dry mass of hemlock was higher in directfall (4.32 g DM/m$^2$ ± 1.09) than lateral traps (0.32 ± 0.13; $p < 0.10$). The proportion of hemlock dry mass to directfall and lateral inputs varied among months ($F_{11,209} = 14.8$, $p < 0.0001$; $F_{11,209} = 2.64$, $p = 0.008$, respectively) and was higher in April than in March, September, or October ($p < 0.05$; Fig. 1). Absolute hemlock litter dry mass, as directfall and lateral inputs, varied among months ($F_{11,209} = 9.07$, $p < 0.0001$; $F_{11,209} = 3.31$, $p = 0.001$, respectively). For directfall, dry mass was greater in October than any other month ($p < 0.05$; Fig. 2), and dry mass in lateral traps was higher in October than May, June, August, or September ($p < 0.05$).

Abundance and biomass of woolly adelgid carcasses entrained in submerged leaf packs increased through time ($F_{2,93} = 2.79$, $p = 0.07$ and $F_{2,101} = 53.0$, $p < 0.0001$, respectively; Fig. 3). Leaf packs in spring and summer had higher woolly adelgid biomass than leaf packs in winter ($p < 0.05$), and leaf packs in summer had higher woolly adelgid biomass than those in spring ($p < 0.05$; Fig. 3). Predator abundance and biomass also increased from winter to summer in stream leaf packs (J. S. Kominoski, unpubl.).

Hemlock litter inputs and carcass entrainment were directly linked to woolly adelgid emergence and feeding patterns. We observed the highest proportions of direct-

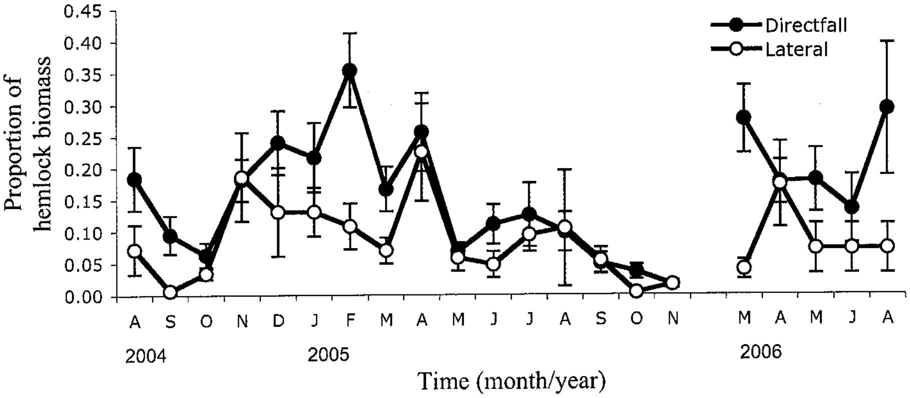

**Fig. 1.** Proportion of hemlock biomass in directfall and lateral traps from August 2004 to August 2006 at Ball Creek, Coweeta Hydrologic Laboratory, N.C., U.S. Values are means ± 1 SE. Note gap in monthly sampling.

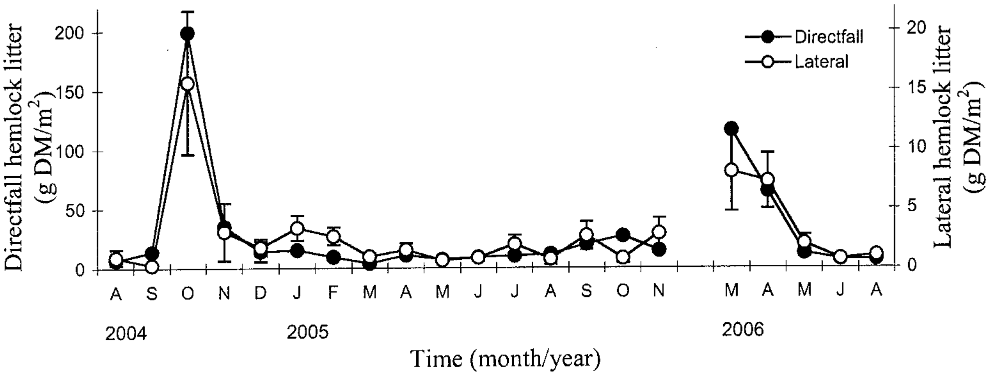

**Fig. 2.** Hemlock litter biomass in directfall and lateral traps from August 2004 to August 2006 at Ball Creek, Coweeta Hydrologic Laboratory, N.C., U.S. Values are means ± 1 SE. Note gap in monthly sampling.

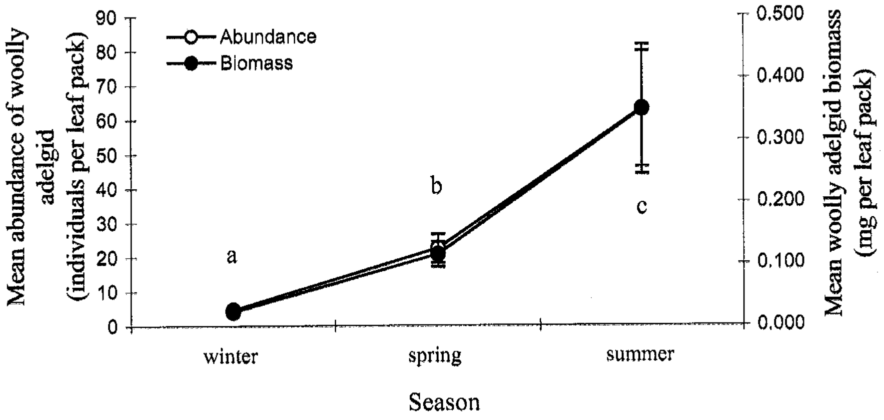

**Fig. 3.** Mean abundance (individuals per leaf pack) and biomass (mg per leaf pack) of hemlock woolly adelgid (*Adelges tsugae*) carcasses in leaf packs incubated in Ball Creek (Coweeta Hydrologic Laboratory, N.C., U.S.) during January-May 2004. Different letters denote significant differences using ANOVA. Values are means ± 1 SE.

fall and lateral inputs of hemlock litter in mid-April (during larval emergence and feeding) and woolly adelgid carcass entrainment increased steadily following this period. Increases in abundance and biomass of woolly adelgid carcasses in leaf packs from winter to summer are in accordance with the woolly adelgid life cycle, and subsequent increases in abundance and biomass of stream predators during this time suggest that carcasses may provide a high quality resource for stream consumers.

Both hemlock litter and woolly adelgid carcasses provide substantial allochthonous subsidies to streams. Hemlock litter C:N levels were lower than other labile, high quality litter species reported from Coweeta. For example, Kominoski et al. (2007) measured higher C:N for tulip poplar, a fast-decomposing species, from the same watershed. Hemlock litter from infested trees likely has low C:N because the litter has not senesced, and therefore foliar nitrogen has not been reabsorbed, resulting in litter with high nutrient concentrations (Chapin 1980). Woolly adelgid carcasses contribute terrestrially (specifically hemlock) derived energy and nutrients to stream ecosystems, which are retained in part through leaf pack entrainment. This resource increased during spring and summer to high densities (>60 individuals per leaf pack), and concomitant increases in stream predators (J. S. Kominoski, unpubl.) suggest that infested hemlock trees may support higher abundances of stream consumers during a time when most resources are typically low in abundance and quality.

Biological invaders alter ecosystem-level properties and therefore serve to integrate population and ecosystem ecology (Vitousek 1990). Understanding the biology of invasive pests and their effects on host species and subsequent ecosystem processes are vital to predict spatial and temporal ecological patterns associated with species invasions. Our dataset represents a quantitative record of hemlock litter and carcass inputs to a detritus-based stream during a period of early hemlock senescence due to woolly adelgid infestation. Even in the absence of pre-infestation baseline data on hemlock inputs, our findings suggest that the life cycle of woolly adelgids affects seasonal trends of hemlock needle and adelgid carcass inputs to streams draining adelgid-infested, forested catchments. Further research quantifying hemlock needle inputs to streams in uninfested hemlock forests is needed to understand and compare the relative contribution of hemlock organic matter and energy to stream ecosystems prior to eastern hemlock decline.

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