Stream benthic macroinvertebrate communities respond to hemlock decline

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ABSTRACT

Eastern hemlock trees (*Tsuga canadensis* [L.] Carr.) often dominate riparian vegetation of central Appalachian headwater streams, and the invasive hemlock woolly adelgid (*Adelges tsugae* Annand; HWA) has decimated hemlock stands in this region. Although research concerning HWA impacts on soil, hydrology, and forest structure is emerging, associated changes in stream structure and function are not as well documented. We quantified HWA-invasion effects on benthic macroinvertebrate communities in 21 headwater streams across Ohio, West Virginia, and Virginia (USA) representing unimpacted, moderate invasion, and severe invasion, respectively. We observed differences in benthic macroinvertebrate community composition; severely invaded sites exhibited the highest diversity, whereas moderately invaded sites had the lowest diversity. The composition of macroinvertebrate functional feeding groups exhibited shifts as well. For example, the relative abundance of herbivorous invertebrates increased from 4% (±3%) at unimpacted sites to 23% (±14%) at severely impacted sites. Shifts in macroinvertebrate density, diversity, and functional-group composition were associated with sediment grainsize distribution (proportion bedrock and D_{84}), large-wood characteristics, and nutrient concentrations (PO_4 and NH_4). Our results suggest that in-stream physical and chemical alterations associated with HWA-invasion and subsequent hemlock decline are associated with changes in stream invertebrate diversity and trophic relationships. We demonstrate how a pervasive terrestrial invader can influence in-stream biotic communities.

BACKGROUND

- Many stream biota rely on riparian inputs, which can be modified by invaders within the riparian zone. One such invader, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), is an insect pest that causes death and decline of a foundational tree species common to riparian zones across the eastern US: the eastern hemlock (*Tsuga canadensis* [L.] Carr.)[1].
- Replacement forests are predicted to comprise of either previously occurring rhododendron (*Rhododendron maximum* L.) or mixed-hardwoods[2]. Impacts of HWA on streams are predicted primarily through comparison of paired hemlock- and hardwood-bound streams (**Table 1**) and can be contradictory.
- We used a chronosequence approach to more directly ask, **"How does hemlock decline (due to HWA invasion) relate to stream macroinvertebrates"**, and what are the underlying mechanisms of changes?

Table 1. Comparison of various properties and characteristics of streams running through hemlock forests and mixed-hardwood forests. Biotic parameters refer to benthic macroinvertebrates. ND = no difference measured between forest types; + and – refer to higher or lower parameter values, respectively; and FFG = functional feeding group.

Parameter	Hemlock Stream	Hardwood Stream
Light levels	–[3] / ND[4]	+[3] / ND[4]
Water chemistry[5]	ND	ND
In-stream primary productivity[3]	–	+
Macroinvertebrate density[5,6]	–	+
Taxa richness	+[5] / –[6]	–[5] / +[6]
FFG - Predator	+[5] / –[6]	–[5] / +[6]
FFG - Collector/gatherer	+[6] / ND[5]	–[6] / ND[5]
FFG - Shredder	–[6] / ND[5]	+[6] / ND[5]
FFG - Grazing algivore	–[5] / ND[6]	+[5] / ND[6]

STUDY SYSTEM & METHODS

- Twenty-one small Appalachian streams were selected across a range of hemlock decline condition (**Fig. 1**) to assess differences in stream macroinvertebrate communities.
- Hemlock decline was based on canopy health. Decline categories were determined by a previous study[7] and further collapsed here:

  HDC1 = uninvaded reference sites
  HDC2 = sites with moderate hemlock decline
  HDC3 = sites with severe hemlock decline

- Benthic invertebrates were sampled using a Surber sampler at three locations per site. Samples were stored in 70% ethanol, counted, identified to lowest possible taxonomic resolution[8], and assigned a functional feeding group (FFG)[9,10].
- Multivariate analysis of variance (MANOVA) tested for potential differences in density, diversity, and relative abundance of benthic insect FFGs among decline categories.
- Model-selection approach based on least-squares regression and Akaike Information Criterion adjusted for small sample sizes (ΔAICc) further investigated influences of hemlock decline and physicochemical factors.
- All data were analyzed in R[11].

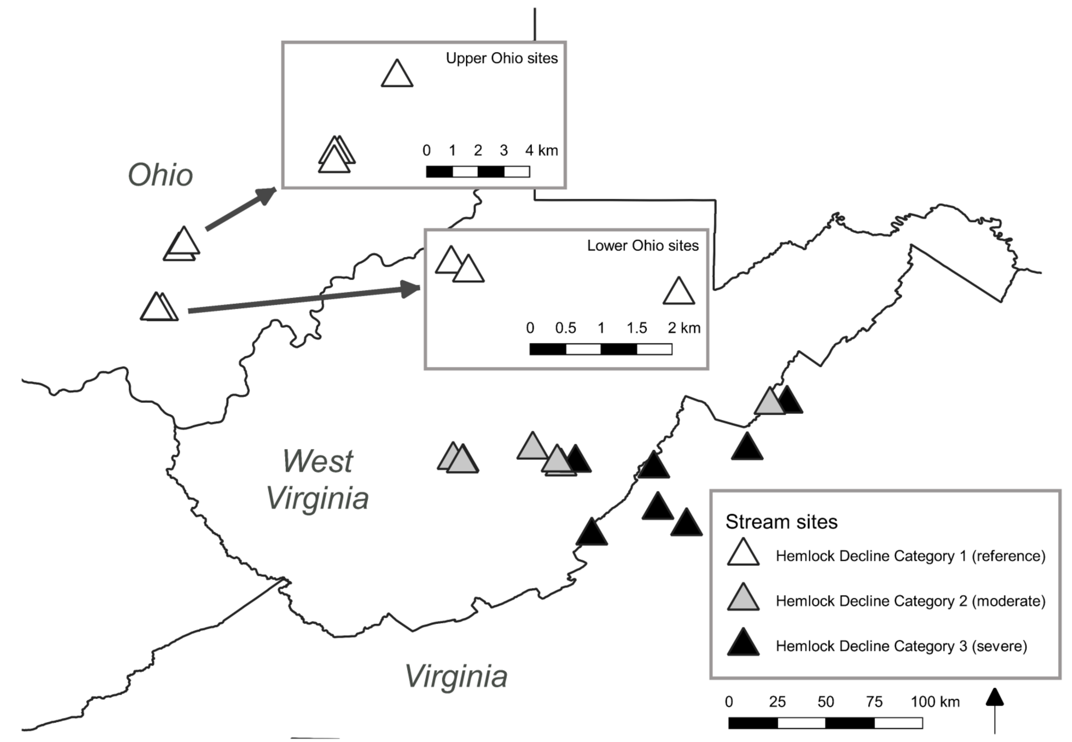

Figure 1. Locations and hemlock decline categories (HDCs) of study sites across Appalachian Mountain regions of Virginia, West Virginia, and Ohio. Insets show the relative locations of the clustered Ohio sites.

RESULTS

Invertebrate community composition varied by hemlock decline category (**Fig. 2**) at the genus level (PERMANOVA: p = 0.004).

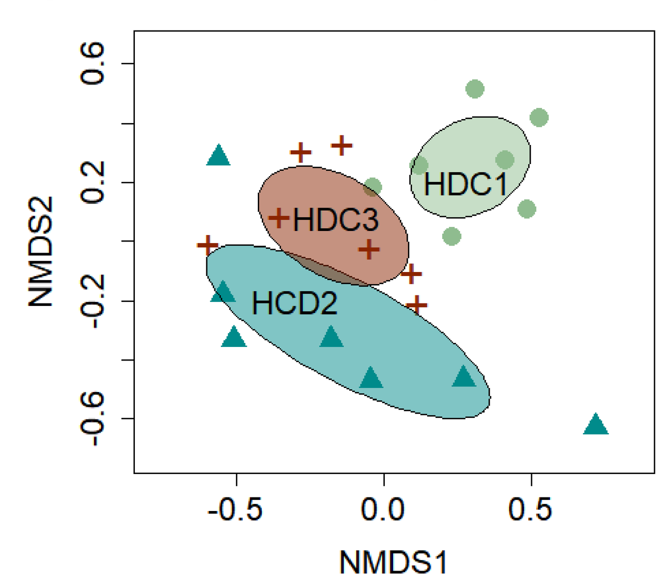

Figure 2. Non-metric multidimensional scaling ordination of 21 sites based on benthic invertebrate community composition (stress value = 0.204). Ellipses indicate location of centroids by decline category (α = 95%).

RESULTS – Invertebrate Density & Diversity

- Mean invertebrate density and Simpson's diversity were highest at sites with severe decline and lowest at moderate levels of decline (**Fig. 3**; Tukey's HSD: p = 0.0154 and p = 0.0174, respectively).
- Density was best predicted by D_{84} and PO_4 (adj-R^2 = 0.39, F = 6.86, p = 0.007).
- Simpson's diversity index was best predicted by NH_4, PO_4, and large-wood volume (adj-R^2 = 0.50, F = 7.06, p = 0.003).

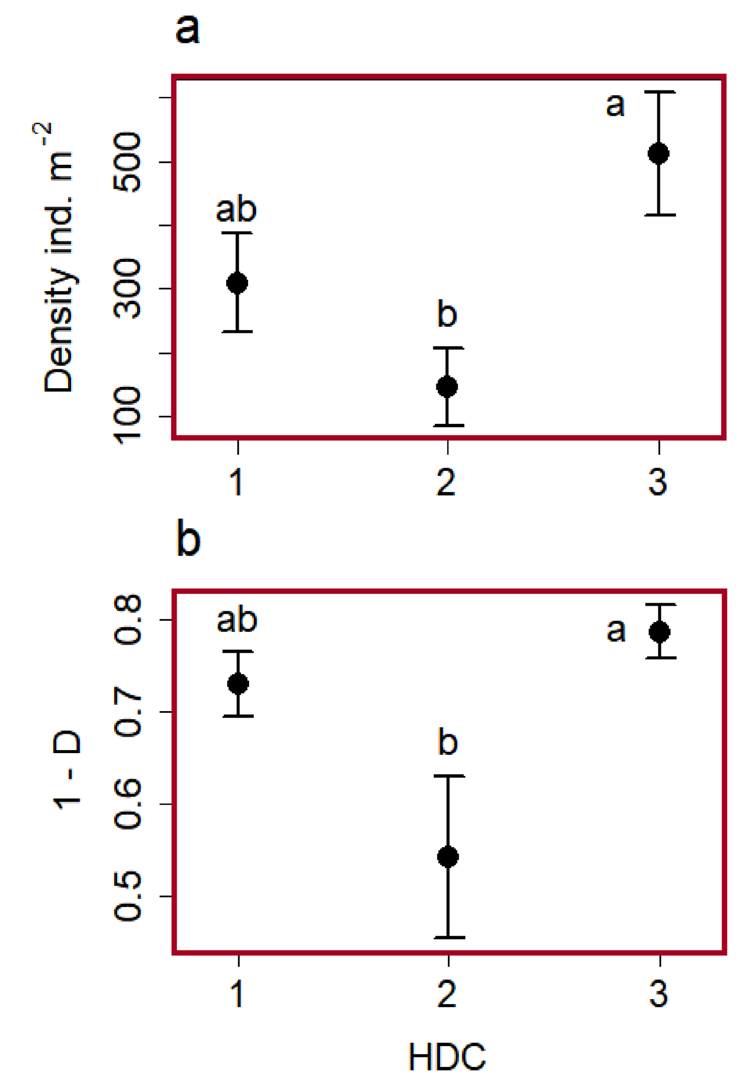

Figure 3. Mean (±1SE) values for measures relevant to diversity of benthic invertebrates by hemlock decline category (HDC). (a) density ind. m^{-2} and (b) Simpson's Index (1-*D*). Simpson's Index was e^x transformed for statistical analysis; raw data are displayed here.

RESULTS – Functional Feeding Groups

- Relative abundance of collector-gatherers, shredders, and predators did not vary by decline category (Tukey's HSD: all p > 0.05).
- Relative abundance of non-shredder herbivorous invertebrates (i.e., scrapers, grazers, and herbivorous pierces) increased from 4% (±3%) at unimpacted sites to 23% (±14%) at severely impacted sites (**Fig. 4**; Tukey's HSD: p = 0.0129).
- The best-supported model for non-shredder herbivore proportion included D_{84} and proportion bedrock (adj-R^2 = 0.45, F = 8.38, p = 0.003).

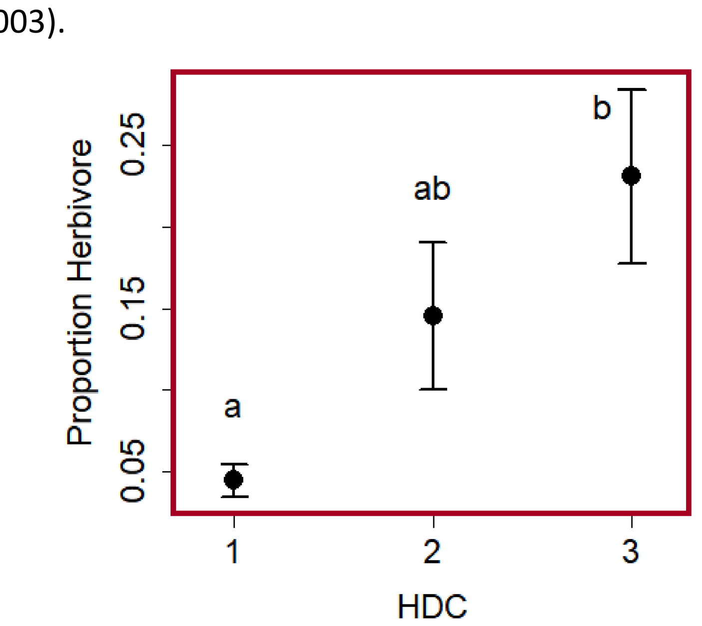

Figure 4. Mean (±1SE) proportion herbivores of benthic macroinvertebrates by hemlock decline category (HDC). Proportion herbivore was logit(x + 0.005) transformed prior to statistical analysis; raw data are displayed here.

DISCUSSION POINTS

- Hemlock detritus (i.e., needles and twigs) provides poor-quality substrate for microbial colonization and growth[12], which can reduce lability and limit grazer use compared to deciduous detritus.
- Seasonality should be considered as well. We sampled in summer, when invertebrates of multiple FFGs are more abundant in hemlock streams than in deciduous streams[13], which may explain why we did not observe greater relative abundance of shredders at the severely invaded sites (one of our hypotheses).
- A companion study[14] found fewer but larger log jams at severely invaded sites, possibly due to larger hemlock trees toppling. These jams can increase retention of sediments and nutrients, altering benthic habitat and likely contributing to the differences in macroinvertebrate assemblages seen in this study.

CONCLUSIONS

Loss of eastern hemlock – a foundational tree species – via HWA invasion promoted shifts in the diversity, density, and functional-feeding group composition of benthic macroinvertebrate communities. Variability in bed material (proportion bedrock and D_{84}), large-wood characteristics, and nutrient concentrations (PO_4 and NH_4) emerged as important mechanisms. **Streams formerly in eastern hemlock headwaters will likely support divergent macroinvertebrate assemblages with implications for both food webs and ecosystem functioning.**

NEXT STEPS

- Construct aquatic-terrestrial food-web models using ^{13}C and ^{15}N isotopes to investigate differences in energy flow and food-web architecture.

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