8-2015

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Notes/Citation Information

Published in Forests, v. 6, no. 8, p. 2719-2738.

Digital Object Identifier (DOI)
http://dx.doi.org/10.3390/f6082719

Forests **2015**, *6*, 2719-2738; doi:10.3390/f6082719

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Article

Benthic Collector and Grazer Communities Are Threatened by Hemlock Woolly Adelgid-Induced Eastern Hemlock Loss

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Academic Editor: Diana F. Tomback

Received: 5 May 2015 / Accepted: 20 July 2015 / Published: 6 August 2015

Abstract: Eastern hemlock (*Tsuga canadensis* (L.) is a foundation species in eastern North America where it is under threat from the highly invasive, exotic hemlock woolly adelgid (*Adelges tsugae*). Eastern hemlock is especially important in riparian areas of Central and Southern Appalachia, so we compared the spatial and temporal composition of benthic collector-gatherers, collector-filterers, and grazers in headwater streams with hemlock-dominated riparian vegetation to those with deciduous tree-dominated riparian vegetation to evaluate the extent to which adelgid-induced hemlock loss could influence composition and abundance of these two functional feeding groups. We found differences in benthic invertebrate abundance and family-level diversity based on riparian vegetation and sampling approach, and, often, riparian vegetation significantly interacted with location or season. Collector-gatherers and grazers were more abundant in eastern hemlock streams in the summer, when hemlock litter is readily available and deciduous litter is relatively sparse. Riparian eastern hemlock appears to exert considerable influence on benthic invertebrate functional feeding group composition in headwater stream communities, as expected with a foundation species. With the loss of eastern hemlock due to adelgid-induced mortality, we should expect to see alterations in spatial and temporal patterns of benthic invertebrate abundance and diversity, with potential consequences to both benthic and terrestrial ecosystem function.

Keywords: *Adelges tsugae*; *Tsuga canadensis*; riparian vegetation; headwater streams; benthic invertebrates; foundation species; invasive species

1. Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carrière; Pinales: Pinaceae) is a coniferous foundation species of eastern North American forests, and is a prominent component of riparian vegetation in Central Appalachia [1–3]. Foundation species, such as eastern hemlock, define much of the structure and function within a community by exerting a disproportionate influence on their surrounding environment, generating locally stable conditions and stabilizing fundamental ecosystem processes [4,5]. Eastern hemlock regulates nutrient cycling and stream base flows due to its persistent and elevated transpiration rates, and air, soil, and water temperatures beneath its dense canopy [6–9]. This canopy density significantly reduces light penetration, resulting in a paucity of understory associates [10]. Eastern hemlock needles and coarse woody debris decompose slowly, resulting in low rates of nitrogen mineralization and nitrification [11–13]. The slowly decomposing coarse woody debris generated from eastern hemlock remains prevalent in streams longer than that of deciduous tree and shrub species, creating in-stream microhabitats and altering sedimentation rates, flow dynamics, and nutrient cycling [12,14]. Fish community diversity in streams that drain eastern hemlock riparian zones is greater than streams with hardwood riparian zones [3]. Headwater streams with healthy eastern hemlock-dominated riparian zones support unique benthic invertebrate communities in New England [1,15], and, in Central Appalachia, the shredder component of these invertebrate communities is influenced by the presence of eastern hemlock [16]. Clearly, eastern hemlock exerts a measureable effect on an array of community and ecosystem interactions [5,17,18]. These communities are under threat by an invasive pest that is reshaping the riparian forests associated with these streams, the hemlock woolly adelgid (*Adelges tsugae* Annand; Hemiptera: Adelgidae).

Hemlock woolly adelgid is decimating eastern North American hemlocks [19–22], threatening headwater streams and potentially leading to extensive and permanent changes in the aquatic biota of these watersheds. Eastern hemlock exhibits little resistance to adelgid feeding and is not expected to regenerate, resulting in vegetative shifts to deciduous species [21,23]. Eastern hemlock mortality and the transition to hardwood dominance in headwater stream riparian areas could result in changes to the soil moisture regime with subsequent alterations to stream discharge, which may impact nutrient and carbon cycling in the southern Appalachians [8,9,22]. Benthic invertebrate community composition is correlated with surrounding forest composition [15,16,23], and streams draining eastern hemlock forests contain greater taxonomic richness than those associated with mixed deciduous forests [1]. Thus, changes in stream invertebrate communities due to adelgid-induced hemlock mortality could affect trophic interactions and energy cycling throughout the ecosystem.

Headwater streams supply energy downstream in the form of dissolved or particulate organic matter, nutrients, and benthic invertebrate prey items [24–27]. These small streams also export considerable energy to riparian areas in the form of emergent adult aquatic insects [28], which results in reciprocating energy dynamics between headwater streams and the riparian zone [29,30]. In temperate forests, headwater streams are often sustained by allochthonous coarse particulate organic matter (CPOM), which is converted to fine particulate organic matter (FPOM) via several pathways, one of which is by feeding activity of benthic shredders [31–33]. The resulting FPOM then serves as an energy resource for benthic collectors, which are further subdivided by their feeding mode; those that collect FPOM from the streambed are designated "collector-gatherers", whereas those that collect suspended FPOM from the water column are designated "collector-filterers" [34].

Benthic grazers, in contrast, utilize algae as a food resource, and since headwater streams are often densely shaded, primary productivity and grazer prevalence is often low in these habitats [31]. But since algal abundance and grazer abundance are intimately linked [35,36], any changes to riparian vegetation that alter stream light regimes and/or nutrient cycling could alter the complement of grazers in stream communities [35].

Collectors and grazers together represent half of the expected benthic invertebrate community within a hypothetical headwater stream [30]. Thus these two functional feeding groups represent a substantial pool of potential prey within aquatic and terrestrial food webs, which could be affected by hemlock woolly adelgid-induced loss of eastern hemlock [37].

We sought to gain a broad understanding of the extent to which adelgid-induced hemlock mortality might affect headwater stream communities, and focus here on benthic invertebrate collectors and grazers. We compare the spatial and temporal composition of collectors (both collector-gatherers and collector-filterers) and grazers over a two year period in headwater streams with hemlock dominated riparian vegetation to those with deciduous tree-dominated riparian vegetation, which represents one potential end point of the successional trajectory following adelgid-induced hemlock mortality [21]. This approach allows us to evaluate the extent to which adelgid-induced hemlock loss may influence the composition and abundance of these two functional feeding groups. Because of marked differences in stream inputs of allochthonous materials based on dominant riparian vegetation, we expected to find different communities of collectors in each stream type. This expectation is corroborated by previous findings that benthic shredders, which produce the FPOM utilized by collectors, are more abundant in eastern hemlock streams during summer months [16]. Finally, we expected that grazer abundance would be highest in deciduous streams prior to bud break and canopy formation, when shading would impede algal growth.

2. Results

2.1. Study Sites

Our sites (Figure 1) did not differ with respect to watershed area and were similar in stream depth, discharge, and elevation at the confluence between the two riparian zone vegetation designations [16]. Co-dominant canopy species based on basal area consisted of eastern hemlock, 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), with a substantial *Rhododendron maximum* (L.) component in the understory. Riparian vegetation classified as deciduous-dominated contained significantly lower eastern hemlock basal area in the overstory (3.1 + 1.3 (S.E.) *versus* 12.6 + 2.2 (S.E.) m^2/ha), but not the understory, relative to those classified as hemlock-dominated, but eastern hemlock basal area was similar across the three study locations [16].

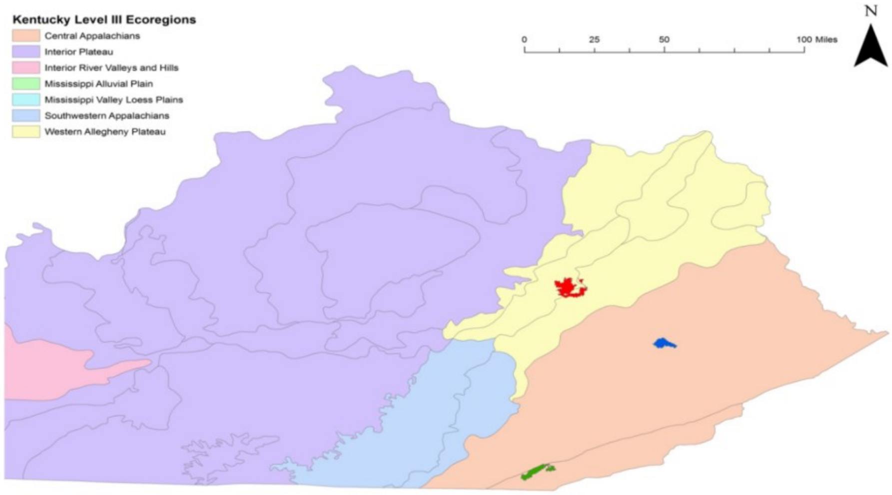

Figure 1. Location of sites in the Cumberland Plateau physiographic province of eastern Kentucky (USA) used to evaluate effects of dominant riparian vegetation on benthic collectors and grazers, including Red River Gorge ( ), Robinson Forest ( ), and Kentucky Ridge State Forest ( ).

2.2. Benthic Invertebrate Collectors and Grazers

We collected 9532 invertebrates. Our sampling generated 28 collector taxa; 6 were classified as collector-filterers and 22 were classified as collector-gatherers. There were 9 taxa classified as grazers (Table 1).

The Hydropsychidae were most abundant collector-filterers in kick net samples (n = 1347), Surber samples (n = 518), and the Hester-Dendy samples (n = 69). The Chironomidae were the most common collector-gatherer (kick net and Hester-Dendy samples); in the Surber samples the Ephemerellidae were predominant (n = 417). The Heptageniidae were the most abundant grazers in kick net (n = 1202) and Surber samples (n = 518), but they were absent from Hester-Dendy samples. The most abundant grazer taxon in the Hester-Dendy samples was the Elmidae but only 4 individuals were collected (Table 1).

We found differences in benthic invertebrate abundance and family-level diversity based on riparian vegetation and sampling approach, and, often, riparian vegetation was involved in significant two-way interactions with location or season (Table S1). In particular, in samples collected via kick net we found significant ($p < 0.1$) vegetation by season interactions in the Elmidae, Shannon diversity index at the family level, and overall grazer abundance. In each instance values were elevated in hemlock streams during summer (Table 2 and Figure 2a–c). Additionally there was a weakly significant vegetation × season interaction for collector-gatherers sampled via kick nets, with the lowest abundance in summer. In Hester-Dendy samples, significant vegetation × season interactions were detected for the Heptageniidae, an Ephemeroptera categorized as a grazer, with abundance in summer greater in eastern hemlock streams than in their deciduous counterparts (Table 2 and Figure 2d). Collector-gatherer abundance collected via Hester-Dendy's in the fall was greater in hemlock streams than in deciduous streams (Table 2 and Figure 2e).

Table 1. Number of individuals from predominant collector-filterer, collector-grazer, and grazer families collected from kick net, Surber, and Hester-Dendy samples from eastern hemlock and deciduous dominated headwater streams, 2008–2010.

Functional Group	Family	Kick Net		Surber		Hester-Dendy		Total
		Deciduous	Hemlock	Deciduous	Hemlock	Deciduous	Hemlock	
Collector-Filterers	Hydropsychidae	612	735	252	266	36	33	1934
	Simuliidae	65	139	74	68	14	23	383
	Polycentropodidae	74	107	63	53	9	24	330
	Philopotamidae	44	36	8	10	1	4	103
	Isonychiidae	1	1	0	0	1	0	3
	Leptoceridae	0	3	0	0	0	0	3
	Brachycentridae	2	1	0	0	0	0	3
Total		798	1022	397	397	64	84	2759
Collector-Gatherers	Chironomidae	300	447	111	91	90	78	1117
	Ephemerellidae	241	174	324	93	49	68	949
	Leptophlebiidae	159	219	58	51	20	18	525
	Baetidae	124	102	32	11	19	11	299
	Ameletidae	62	49	51	59	7	2	230
	Siphlonuridae	68	58	31	19	18	11	205
	Ephemeridae	34	21	14	7	1	0	77
	Psychomyiidae	3	49	0	0	6	11	69
	Dixidae	12	15	4	2	11	7	51
	Caenidae	6	2	1	0	0	0	9
	Limnephilidae	0	0	4	5	0	0	9
	Rhyacophilidae	0	0	1	2	0	0	3
	Hydrophilidae	0	1	0	0	0	1	2
Total		1054	1182	634	340	232	213	3655

Table 1. *Cont.*

Functional Group	Family	Kick Net		Surber		Hester-Dendy		Total
		Deciduous	Hemlock	Deciduous	Hemlock	Deciduous	Hemlock	
Grazers	Heptageniidae	608	594	690	316	44	43	2295
	Elmidae	139	121	57	41	4	4	366
	Uenoidae	36	43	26	43	1	3	152
	Psephenidae	58	36	24	15	0	1	134
	Dryopidae	12	41	6	16	3	13	91
	Glossosomatidae	11	13	13	6	0	2	45
	Goeridae	7	8	8	7	0	0	30
	Odontoceridae	0	0	0	0	0	4	4
	Helicopsychidae	0	1	0	0	0	0	1
Total		871	857	824	444	52	70	3118

Table 2. Abundance (mean (S.E.)) of benthic collectors and grazers collected in (a) kick nets; (b) Surber; and (c) Hester-Dendy Samplers from headwater streams with eastern hemlock or deciduous dominated riparian vegetation across two years in Kentucky (USA). For location, vegetation, and season, means within rows followed by the same letter are not significantly different ($\alpha = 0.1$).

	Vegetation		Location			Season		
	Deciduous	Hemlock	Kentucky Ridge	Robinson Forest	Red River Gorge	Fall	Spring	Summer
a. Kick net								
Chironomidae	1.0 (0.2) b	1.5 (0.3) a	0.4 (0.1) b	1.8 (0.4) a	1.6 (0.3) a	1.1 (0.4) b	2.3 (0.4) a	0.4 (0.1) b
Ephemerellidae	0.8 (0.2) a	0.6 (0.1) a	0.2 (0.1) a	0.6 (0.1) a	1.3 (0.3) a	0.3 (0.1) b	1.6 (0.3) a	0.1 (0.0) b
Leptophlebiidae	0.6 (0.1) b	0.8 (0.1) a	0.4 (0.1) a	0.6 (0.1) a	0.9 (0.1) a	1.0 (0.2) a	0.8 (0.1) a	0.2 (0.0) b
Siphlonuridae	0.2 (0.1) a	0.2 (0.1) a	0.3 (0.1) a	0.3 (0.1) a	0.1 (0.0) a	0.0 (0.0) b	0.5 (0.1) a	0.0 (0.0) b
Ameletidae	0.2 (0.1) a	0.2 (0.1) a	0.2 (0.1) a	0.4 (0.1) a	0.1 (0.0) a	0.0 (0.0) a	0.5 (0.1) a	0.0 (0.0) a
Ephemeridae	0.1 (0.0) a	0.1 (0.0) a	0.0 (0.0) b	0.0 (0.0) b	0.2 (0.1) a	0.2 (0.1) a	0.1 (0.0) a	0.0 (0.0) a
Psychomyiidae	0.0 (0.0) a	0.2 (0.1) a	0.0 (0.0) a	0.0 (0.0) a	0.2 (0.1) a	0.2 (0.2) a	0.1 (0.0) a	0.0 (0.0) a
Heptageniidae	2.1 (0.4) a	2.0 (0.3) b	1.4 (0.2) b	0.8 (0.2) b	3.7 (0.6) a	1.0 (0.1) b	4.4 (0.6) a	0.4 (0.1) b

Table 2. *Cont.*

	Vegetation		Location			Season		
	Deciduous	**Hemlock**	**Kentucky Ridge**	**Robinson Forest**	**Red River Gorge**	**Fall**	**Spring**	**Summer**
Elmidae	0.5 (0.1) a	0.4 (0.1) b	0.1 (0.0) b	0.1 (0.0) b	1.0 (0.1) a	0.5 (0.1) ab	0.6 (0.1) a	0.3 (0.1) b
Psephenidae	0.2 (0.0) a	0.1 (0.0) a	0.2 (0.0) b	0.0 (0.0) c	0.3 (0.1) a	0.2 (0.0) a	0.2 (0.0) a	0.1 (0.0) a
Uenoidae	0.1 (0.0) a	0.1 (0.1) a	0.1 (0.1) a	0.0 (0.0) a	0.2 (0.1) a	0.0 (0.0) b	0.4 (0.1) a	0.0 (0.0) b
Dryopidae	0.0 (0.0) a	0.1 (0.0) a	0.0 (0.0) b	0.0 (0.0) b	0.2 (0.1) a	0.1 (0.0) a	0.0 (0.0) b	0.1 (0.1) a
Hydropsychidae	2.1 (0.3) a	2.5 (0.3) a	1.9 (0.3) b	0.3 (0.1) c	4.4 (0.5) a	3.4 (0.6) a	1.8 (0.3) b	2.0 (0.3) b
Simuliidae	0.2 (0.0) a	0.5 (0.1) a	0.2 (0.1) a	0.3 (0.1) a	0.5 (0.2) a	0.0 (0.0) b	0.9 (0.2) a	0.0 (0.0) b
Polycentropodidae	0.3 (0.1) a	0.4 (0.1) a	0.2 (0.0) b	0.1 (0.0) b	0.6 (0.1) a	0.3 (0.1) a	0.5 (0.1) a	0.1 (0.0) b
Philopotamidae	0.2 (0.1) a	0.1 (0.0) a	0.1 (0.0) a	0.2 (0.1) a	0.1 (0.1) a	0.2 (0.1) a	0.2 (0.1) a	0.0 (0.0) a
Simpson	0.5 (0.0) a	0.5 (0.0) a	0.5 (0.0) a	0.3 (0.0) b	0.6 (0.0) a	0.5 (0.0) a	0.6 (0.0) a	0.3 (0.0) b
Shannon	0.7 (0.0) b	0.8 (0.0) a	0.7 (0.0) b	0.5 (0.0) c	1.0 (0.0) a	0.8 (0.0) b	1.0 (0.0) a	0.5 (0.0) c
Evenness	0.6 (0.0) a	0.6 (0.0) a	0.6 (0.0) a	0.4 (0.0) b	0.7 (0.0) a	0.6 (0.0) a	0.7 (0.0) a	0.4 (0.0) b
Filterer	2.8 (0.3) a	3.5 (0.4) a	2.4 (0.3) b	0.8 (0.1) c	5.6 (0.6) a	3.9 (0.6) a	3.4 (0.4) a	2.2 (0.3) a
Gatherer	3.7 (0.5) a	4.1 (0.5) a	1.9 (0.2) b	4.2 (0.7) ab	5.2 (0.6) a	3.1 (0.5) b	7.1 (0.7) a	1.0 (0.1) c
Collector	6.4 (0.6) a	7.6 (0.8) a	4.4 (0.4) b	5.1 (0.8) b	10.8 (1.0) a	7.0 (1.0) b	10.4 (1.0) a	3.2 (0.4) b
Grazer	3.0 (0.4) a	2.9 (0.4) b	1.8 (0.2) b	1.0 (0.2) c	5.6 (0.7) a	1.9 (0.2) b	5.6 (0.7) a	1.0 (0.1) b
Total	9.5 (0.9) a	10.5 (1.0) a	6.2 (0.5) b	6.1 (0.9) b	16.5 (1.6) a	9.0 (1.1) b	16.0 (1.5) a	4.2 (0.5) b
b. Surber								
Ephemerellidae	2.3 (0.6) a	0.7 (0.1) a	0.2 (0.1) b	1.3 (0.3) ab	2.7 (0.7) a	0.1 (0.0) b	3.7 (0.7) a	0.1 (0.0) b
Chironomidae	0.8 (0.2) a	0.6 (0.1) a	0.1 (0.1) a	1.7 (0.3) a	0.3 (0.1) a	0.0 (0.0) b	1.7 (0.3) a	0.1 (0.0) b
Ameletidae	0.4 (0.1) a	0.4 (0.1) a	0.1 (0.1) a	0.9 (0.2) a	0.2 (0.1) a	0.0 (0.0) a	1.0 (0.2) a	0.0 (0.0) a
Leptophlebiidae	0.4 (0.1) a	0.4 (0.1) a	0.1 (0.0) b	0.4 (0.1) a	0.6 (0.2) a	0.5 (0.2) a	0.4 (0.1) a	0.3 (0.1) a
Siphlonuridae	0.2 (0.1) a	0.1 (0.1) a	0.1 (0.1) a	0.3 (0.1) a	0.1 (0.1) a	0.1 (0.0) a	0.4 (0.1) a	0.0 (0.0) a
Baetidae	0.2 (0.1) a	0.1 (0.0) a	0.0 (0.0) a	0.1 (0.0) a	0.3 (0.1) a	0.0 (0.0) b	0.3 (0.1) a	0.0 (0.0) b
Hydropsychidae	1.8 (0.3) a	1.9 (0.3) a	1.9 (0.4) b	0.2 (0.1) c	3.2 (0.4) a	2.3 (0.5) a	2.4 (0.4) a	0.9 (0.2) a
Simuliidae	0.5 (0.1) a	0.5 (0.3) a	0.2 (0.1) a	0.4 (0.1) a	0.8 (0.4) a	0.0 (0.0) b	1.2 (0.4) a	0.1 (0.0) b
Polycentropodidae	0.4 (0.1) a	0.4 (0.1) a	0.2 (0.1) b	0.1 (0.0) b	0.8 (0.2) a	0.4 (0.1) a	0.7 (0.2) a	0.0 (0.0) a

Table 2. *Cont.*

	Vegetation		Location			Season		
	Deciduous	**Hemlock**	**Kentucky Ridge**	**Robinson Forest**	**Red River Gorge**	**Fall**	**Spring**	**Summer**
Heptageniidae	4.9 (1.3) a	2.2 (0.5) a	1.3 (0.2) a	1.5 (0.5) a	7.1 (1.7) a	0.7 (0.2) b	8.7 (1.7) a	0.2 (0.0) b
Elmidae	0.4 (0.1) a	0.3 (0.1) a	0.1 (0.0) a	0.3 (0.1) a	0.6 (0.1) a	0.2 (0.1) a	0.4 (0.1) a	0.4 (0.1) a
Simpson	0.4 (0.0) a	0.5 (0.0) a	0.4 (0.0) b	0.5 (0.0) b	0.6 (0.0) a	0.4 (0.0) b	0.7 (0.0) a	0.3 (0.0) b
Shannon	0.6 (0.0) a	0.7 (0.1) a	0.5 (0.1) b	0.7 (0.1) b	0.9 (0.1) a	0.6 (0.1) b	1.1 (0.1) a	0.4 (0.0) b
Evenness	0.5 (0.0) a	0.6 (0.0) a	0.5 (0.0) b	0.5 (0.0) b	0.6 (0.0) a	0.5 (0.1) b	0.7 (0.0) a	0.4 (0.0) b
Filterer	2.8 (0.4) a	2.8 (0.5) a	2.3 (0.5) b	0.8 (0.2) c	4.9 (0.7) a	2.8 (0.5) b	4.5 (0.7) a	1.1 (0.2) b
Gatherer	4.5 (0.8) a	2.4 (0.3) a	0.8 (0.2) b	4.8 (0.7) a	4.4 (0.9) a	1.0 (0.2) b	7.6 (1.0) a	0.8 (0.2) b
Collector	7.3 (1.1) a	5.2 (0.7) a	3.1 (0.5) b	5.7 (0.8) b	9.2 (1.4) a	3.8 (0.6) b	12.0 (1.4) a	1.9 (0.3) c
Grazer	5.8 (1.4) a	3.1 (0.5) b	1.5 (0.2) b	1.9 (0.5) b	8.9 (1.8) a	1.5 (0.2) b	9.9 (1.8) a	0.9 (0.2) b
Total	13.2 (2.3) a	8.4 (1.1) a	4.6 (0.7) b	7.6 (1.0) b	18.2 (3.1) a	5.3 (0.8) b	21.9 (3.0) a	2.8 (0.3) b
c. Hester-Dendy								
Chironomidae	0.5 (0.1) a	0.4 (0.1) a	0.2 (0.1) b	0.8 (0.2) a	0.5 (0.1) ab	0.2 (0.1) b	0.2 (0.2) a	0.2 (0.1) b
Ephemerellidae	0.3 (0.1) a	0.4 (0.1) a	0.2 (0.1) a	0.4 (0.1) a	0.4 (0.1) a	0.6 (0.2) a	0.1 (0.1) a	0.1 (0.0) a
Hydropsychidae	0.2 (0.0) a	0.2 (0.1) a	0.2 (0.1) ab	0.1 (0.0) b	0.3 (0.1) a	0.1 (0.1) b	0.1 (0.1) a	0.1 (0.0) b
Heptageniidae	0.2 (0.0) a	0.2 (0.0) b	0.2 (0.1) b	0.1 (0.0) c	0.4 (0.1) a	0.3 (0.1) a	0.1 (0.1) a	0.1 (0.0) b
Simpson	0.2 (0.0) a	0.2 (0.0) a	0.2 (0.0) a	0.1 (0.0) a	0.2 (0.0) a	0.2 (0.0) a	0.1 (0.0) a	0.1 (0.0) b
Shannon	0.2 (0.0) a	0.2 (0.0) a	0.2 (0.0) b	0.2 (0.0) b	0.3 (0.0) a	0.3 (0.0)	0.1 (0.0)	0.1 (0.0)
Evenness	0.2 (0.0) a	0.2 (0.0) a	0.2 (0.0) ab	0.2 (0.0) b	0.3 (0.0) a	0.3 (0.1) a	0.1 (0.0) a	0.1 (0.0) b
Filterer	0.3 (0.1) a	0.5 (0.1) a	0.2 (0.1) b	0.2 (0.1) b	0.8 (0.2) a	0.5 (0.2) a	0.1 (0.2) a	0.1 (0.0) b
Gatherer	1.3 (0.2) a	1.2 (0.2) a	0.7 (0.1) b	1.5 (0.3) a	1.5 (0.3) a	1.4 (0.2) a	0.6 (0.3) a	0.6 (0.1) b
Collector	1.6 (0.2) a	1.7 (0.3) a	0.9 (0.1) b	1.7 (0.3) ab	2.3 (0.4) a	1.8 (0.3) a	0.7 (0.4) a	0.7 (0.1) b
Grazer	0.3 (0.1) a	0.4 (0.1) a	0.3 (0.1) b	0.1 (0.0) c	0.6 (0.1) a	0.4 (0.1) a	0.3 (0.1) a	0.3 (0.1) a
Total	1.9 (0.3) a	2.0 (0.3) a	1.2 (0.2) b	1.9 (0.3) b	2.9 (0.4) a	2.3 (0.3) a	1.0 (0.4) a	1.0 (0.1) b

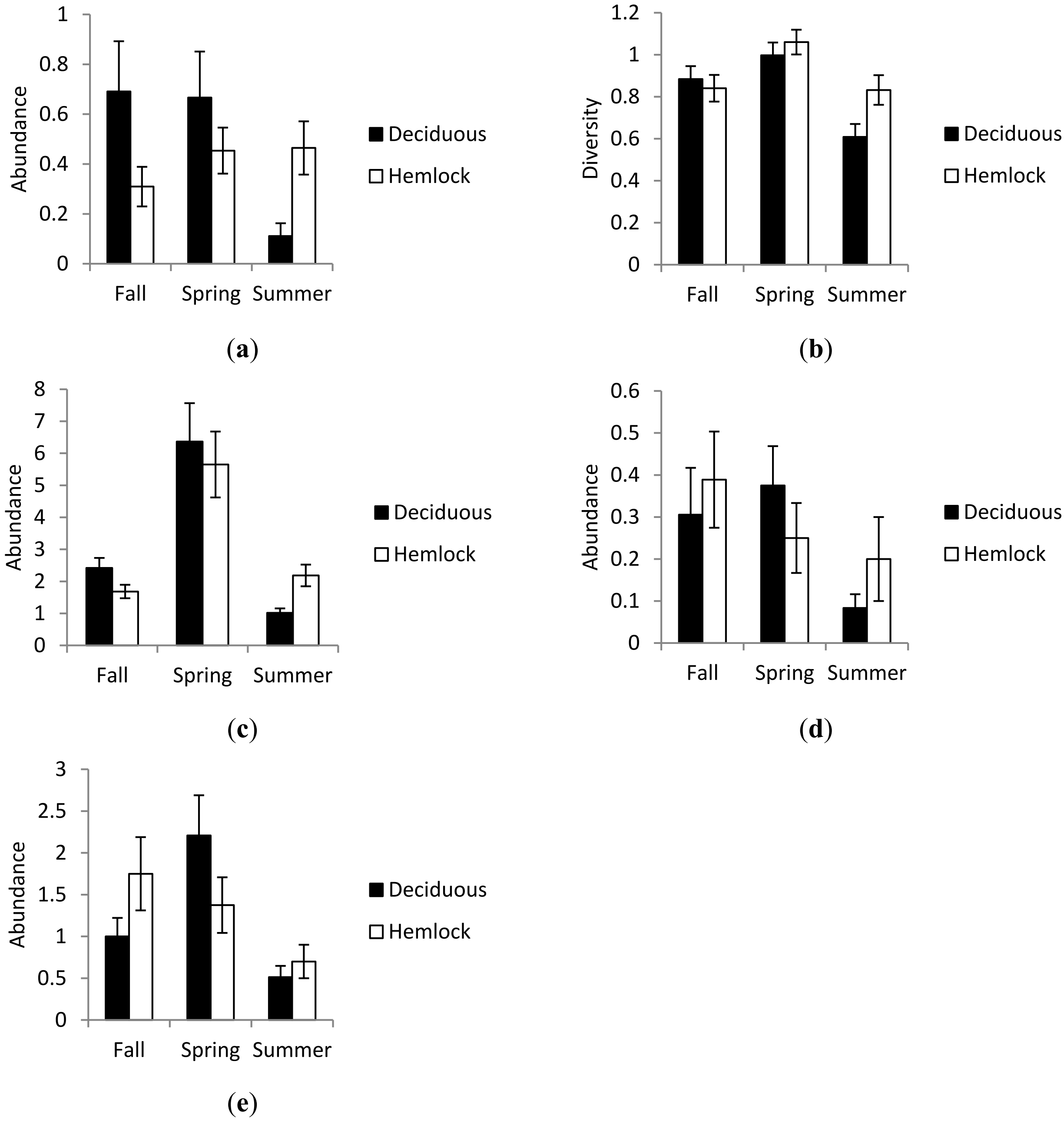

Figure 2. Interactions between riparian vegetation and season influences (**a**) abundance of Elmidae; (**b**) Shannon index of diversity; and (**c**) abundance of scrapers, sampled via kick nets, 2009–2010; and (**d**) Heptageniidae and (**e**) collector-gatherers, sampled via Hester-Dendy, fall 2009–summer 2010, from streams dominated by deciduous (■) and eastern hemlock (□) riparian vegetation.

The interacting effects of vegetation and location influenced the abundance of several taxa collected via kick net and Surbers, including the Chironomidae, Heptageniidae, Elmidae, Psephenidae, and Uenoidae (Table S1). This interaction was detected in grazers and total collectors (gatherers and filterers combined); in general these groups were more abundant in deciduous streams at Red River Gorge. The Chironomidae are an exception; the greatest abundance of chironomids was found at Robinson Forest in deciduous streams (Table 2).

2.3. Multivariate Ordination

The multivariate ordination indicated that headwater stream benthic invertebrate functional feeding group abundance was influenced by riparian vegetation and stream chemistry. The Monte Carlo test was significant ($p < 0.05$) for each ordination axis when all environmental variables (see Table S2) were incorporated into the CCA (Table 3), indicating linear relationships between feeding groups and the environmental data for each ordination axis [38].

Table 3. Canonical correspondence analysis of benthic invertebrates collected via kick net and environmental parameters from streams dominated by eastern hemlock and deciduous riparian vegetation.

	Ordination Axis		
	1	**2**	**3**
Monte Carlo Test—Taxa-Environment Correlations	$p = 0.04$	$p = 0.02$	$p = 0.02$
Eigenvalues	0.018	0.014	0.006
Pearson species-environment correlations	0.392	0.318	0.305
Cumulative percentage of variance of species data	4.6	8.2	9.8
Intraset correlation for environmental variables			
Understory eastern hemlock stems	0.522	−0.122	−0.22
Understory deciduous stems	0.212	0.336	−0.233
Overstory eastern hemlock stems	0.005	−0.079	0.257
Overstory deciduous stems	0.058	−0.241	0.035
Sulfate	0.276	−0.812	−0.192
Nitrate	−0.513	−0.174	−0.334
Ammonia	−0.123	−0.067	0.351
Total Phosphorus	−0.023	−0.026	−0.292
Total Carbon	−0.214	0.113	0.142
Dissolved Organic Carbon	−0.068	0.197	0.121
pH	0.136	−0.072	0.222
Dissolved Oxygen	0.224	−0.086	0.141
Conductivity	0.147	−0.299	0.152
Functional feeding group weights			
Shredder	0.241	0.04	0.283
Scraper	−0.185	0.499	−0.258
Collector-Gatherer	0.484	−0.147	−0.092
Collector-Filterer	−0.272	0.194	0.648
Predator	−0.447	−0.475	−0.11

The CCA ordination accounted for 9.8% of the overall variation within the data (Table 3). The first ordination axis accounted for 4.6% of the variance; this axis was most strongly linked to understory hemlock stem count, and negatively associated with stream nitrate concentrations (Table 3, Figure 3). Collector-gatherers and shredders were positively associated with axis 1, while there was a negative association for scrapers, collector-filterers, and predators (Table 3). The second ordination axis accounted for 3.6% of the overall variation. The strongest positive association with this axis was understory deciduous stems, and sulfate concentrations generated the strongest negative association

(Table 3, Figure 3a). Scrapers had the strongest positive association to this ordination axis, and predators, followed by collector-gatherers, had the strongest negative association (Table 3). Finally, 1.6% of the overall variation was accounted for by the third ordination axis. The environmental variable most strongly tied to this axis was stream ammonia concentrations (Table 3, Figure 3b). Positive associations with axis 3 were found for shredders and collector-filterers, while scrapers, collector-filterers, and predators were negatively associated (Table 3).

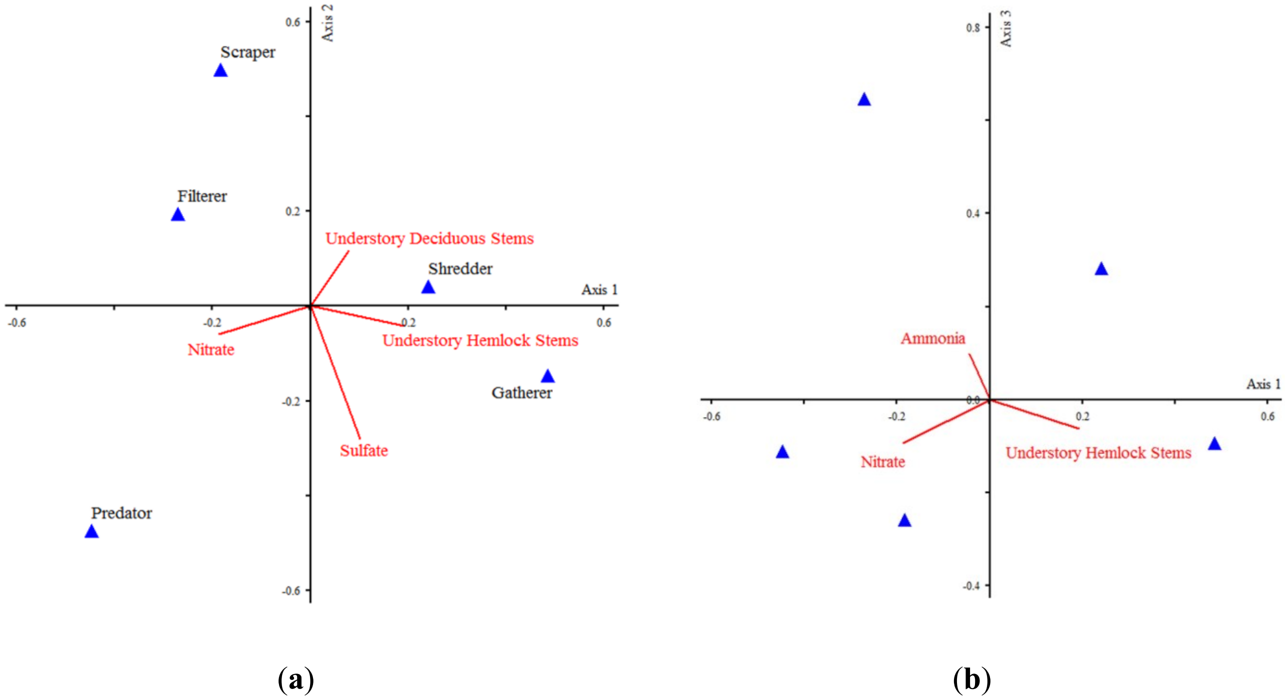

Figure 3. Canonical correspondence analysis showing (**a**) ordination axis 1 and 2; and (**b**) ordination axis 1 and 3 for benthic invertebrate functional feeding groups collected from headwater streams with riparian zones dominated by eastern hemlock and deciduous trees at the Robinson Forest site in 2010.

3. Discussion

We sought to understand the extent to which eastern hemlock riparian vegetation influences benthic invertebrate community composition in headwater streams. To this end we compared benthic collector and grazer community parameters in streams with eastern hemlock dominated riparian vegetation to those same parameters in streams with deciduous dominated riparian vegetation to evaluate the extent to which adelgid-induced hemlock loss could influence composition and abundance of these two functional feeding groups. This comparative approach has been used extensively to characterize the influence of eastern hemlock in structuring forest communities [1,3,15,16,20,38–40].

Eastern hemlock is prevalent in headwater riparian zones of central and southern Appalachia, and while there was some eastern hemlock present in our streams classified as deciduous dominated, eastern hemlock stem density was greater in streams that were categorized as eastern hemlock. We found distinct differences in associated benthic invertebrate communities throughout the year. We found only minor differences in stream chemistry between the two stream types ([41] and Table S2), corroborating studies that found similarities in temperature, discharge, pH, or nitrate between eastern hemlock and deciduous dominated streams [1,42]. The water chemistry parameters for our study streams approximate those reported in undisturbed Appalachian streams [43], and these streams are considered high quality via the Hilsenhoff Family Index of Biotic Integrity [42,44,45].

Riparian vegetation alone did not affect any measure of benthic collector or grazer evenness or family level diversity, in contrast to similar studies in the Northeastern US [1,15]. Snyder *et al.* [1] found that eastern hemlock headwater streams had greater invertebrate diversity (via Simpson's Index) than did streams with deciduous dominated riparian vegetation, whereas Willacker *et al.* [15] found greater richness, more unique taxa, and more overall taxa in deciduous dominated streams relative to hemlock dominated streams, but also found higher collector-gatherers in hemlock-dominated streams. Benthic invertebrate abundance and richness is likely linked to both litter quality and seasonal availability. We found that collector-gatherers and grazers were more abundant in eastern hemlock streams in the summer, a time of year when hemlock litter is readily available and deciduous tree litter is relatively sparse. Eastern hemlock litter enters streams more consistently, though in smaller amounts, than does litter from deciduous trees [16]. Conifer litter is considered low quality; hemlock litter is low in nitrogen [11] with low rates of microbial conditioning [46]. Shredders also comprise a sizeable portion of the benthic invertebrate communities in these streams, and show seasonal fluctuations in abundance that reflects seasonal fluctuations in hemlock litter inputs [16]. The consistent input and slow rate of microbial conditioning of eastern hemlock results in a constant and available resource for shredders, which generate FPOM through their feeding activities, thereby providing abundant resources that facilitate growth and development of collector-gatherers during summer months [31,47–50]. Shredder-collector-grazer processing chains have been demonstrated experimentally [49,51–53], and suggest that changes in leaf-litter contributions to streams can alter the abundance of benthic functional feeding groups [24], with repercussions for stream and riparian food webs and energy flow [54–57].

Our multivariate analysis provides insights into environmental factors that contribute to the observed patterns in invertebrate functional feeding group communities. The CCA explains 9.8% of the overall variation within our data, typical of the <10% variation commonly accounted for in ecological data using this approach [58]. Our CCA corroborates the significant findings of the generalized linear mixed model for functional feeding groups, and demonstrates that shredders and collector-gatherers are positively associated with understory eastern hemlock stem density, which occurs at greater densities in streams classified as eastern hemlock dominated [16,41]. Riparian eastern hemlock appears to exert considerable influence on benthic invertebrate functional feeding group composition in headwater stream communities, as expected with a foundation species. With the loss of eastern hemlock due to adelgid-induced mortality, we should expect to see alterations in spatial and temporal patterns of benthic invertebrate abundance and diversity.

4. Materials and Methods

4.1. Study Sites

Three protected areas in the Cumberland Plateau physiographic province of eastern Kentucky were selected (Figure 1). This region contains steep, mountainous terrain with underlying shale and sandstone and abundant coal seams [59]. The Red River Gorge Geological Area and Natural Bridge State Park State Nature Preserve is located in the Northern Forested Plateau Escarpment ecoregion. Robinson Forest is situated in the Dissected Appalachian Plateau ecoregion, and Kentucky Ridge State Forest is located further south in the Cumberland Mountain Thrust Block ecoregion [60]. Yearly precipitation ranges from 106 to 139 cm, and temperatures can range from −6.2 to 8.3 °C in January and from 16.6 to 31.6 °C in July [60]. Elevation ranges from 167 to 1261 m throughout this area of the state [60]. The dominant vegetation type is mixed mesophytic forest [61,62] and eastern hemlock is found throughout [63].

Candidate streams were selected using GIS and remote sensing [42], and the presence of riparian eastern hemlock was determined using the vegetation database from the Kentucky GAP Analysis [64]. Boundaries of drainage basins were determined using surface hydrology modeling of 30 m resolution digital elevation models from the Kentucky Office of Geographic Information. Drainage basin areas were extracted from digital elevation models using the Hydrology toolkit of ArcGIS [65]. Streams with similar drainage areas and suitable eastern hemlock in the riparian zone were visited and evaluated for suitability. Ultimately, three streams with riparian zones dominated by eastern hemlock and three streams with deciduous dominated riparian zones were selected at each of the three sites for a total of eighteen streams. A 30 m reach was designated in each stream at least 150 m upstream of the confluence for vegetation and stream characterization and benthic invertebrate sampling [16].

We assessed vegetative composition and structure using two 0.04-ha fixed-radius whole plots randomly placed in accessible areas within each stream's riparian zone, one on each side of the stream [16,41]. Ten subplots, five 0.004-ha and five 0.0004-ha, were nested within each whole plot to enhance precision of the vegetation assessments. Whole plots were utilized to assess overstory and midstory vegetation, 0.004-ha subplots were used to assess saplings and shrubs (>137 cm height), and 0.0004-ha micro plots were used to assess seedlings, shrubs (<137 cm height), and vines. One of each subplot was positioned at the whole plot center and in each cardinal direction, 7.7 m from the plot center. Each surveyed reach contained two 0.04-ha whole plots, ten 0.004-ha subplots, and ten 0.0004-ha microplots [66]. 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 [67].

Watershed areas for the 18 streams were compared between dominant riparian vegetation type and across study locations using analysis of variance with a Tukey adjustment (PROC GLM, SAS Software v9.3). The number of stems and basal area of eastern hemlock and the six most commonly encountered overstory deciduous trees were calculated from riparian vegetation assessments and compared between eastern hemlock dominated and deciduous dominated riparian zones using the Kruskal-Wallis non-parametric procedure (PROC NPAR1WAY). High, median, and low temperature readings from each sample date were analyzed using analysis of variance between dominant riparian vegetation type and across locations. Comparison of least squares means was used as a post-hoc means separation procedure when appropriate. All analyses were performed using SAS v9.3 [68].

4.2. Benthic Invertebrate Collectors and Grazers

Three cross-stream transects were established across three riffles within each 30 m reach, and benthic invertebrates were sampled at 30 d intervals using a standard kick net (30 cm wide by 17 cm tall) with a 30-second kick interval and a 0.25 m^2 Surber sampler. Each of the three riffles per stream reach were sampled for a total six samples per stream (*n* = 54 for each sampling method). Artificial substrates (Hester-Dendy samplers, Forestry Suppliers; Jackson, MS, USA) consisting of five 2.5 × 5 cm^2 plates were used to passively monitor colonization by invertebrates; one sampler was deployed at each end of the designated 30 m reach (two per stream, *n* = 18 per riparian vegetation type). The use of multiple collection approaches allowed us to sample benthic invertebrates that utilize different microhabitats within the lotic environment, to provide a more complete picture of the benthic collector and grazer communities. Benthic invertebrate samples were preserved in the field using 70% ETOH and identified in the laboratory to the order or family level [69]. Each individual specimen was then assigned to a functional feeding group based on the most common feeding mode in each family (collector-gatherer, collector-filterer, grazer, shredder, or predator) [69]. Monthly sampling began in September 2008 and concluded in September 2010.

Three sampling intervals that represent spring, summer, and fall across two years were used to assess the influence of riparian eastern hemlock on benthic collectors and grazers from kick net and Hester-Dendy samples (see Supplemental Materials). Only one year's data are available for the Surber sampler, and only one set of fall data are available for the Hester-Dendy samples due to low stream flow. Shannon's and Simpson's diversity indices were calculated based on family level identifications [41]. Invertebrate abundances across the three sampling methods were calculated and compared by riparian vegetation type, study location, and season using a generalized linear mixed model with a split-plot design. Tukey's HSD ($\alpha = 0.1$) was used as a *post hoc* means separation procedure when appropriate. Only those taxa with abundances greater than 50 were considered for the analysis.

4.3. Multivariate Ordination

The influence of riparian overstory and understory vegetation and stream chemistry characteristics on benthic macroinvertebrate abundance was evaluated using canonical correspondence analysis (CCA), which allowed us to explore arthropod associations along environmental gradients [70] to provide insight as to which stream characteristics most influence benthic collector and grazer populations. CCA is widely used by ecologists to explore and relate patterns of taxa distribution or abundance to environmental variables [38,58,70,71]. This approach provides an indication of which of the environmental variables included in an analysis are important in structuring community composition [38,58]. Only invertebrates from the upstream and downstream-most sample riffles were used for this analysis, as they corresponded with the upstream and downstream vegetation assessment plots; the midstream riffle was disregarded. In streams with riparian zones classified as either hemlock or deciduous, we compared invertebrate abundance to overstory and understory eastern hemlock and deciduous stem counts, and incorporated stream physical and chemical variables including concentrations of sulfate, nitrate, ammonia, total phosphorus, calcium and magnesium ions, and dissolved oxygen, pH, and conductivity [42]. 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 [72]. This procedure was performed solely on the kick net dataset as it was the most robust.

Significant Monte Carlo tests ($p < 0.1$) indicate the formation of linear combinations of environmental variables that maximally separate the niches of the taxa that are present [58] between benthic invertebrate functional feeding groups and riparian vegetation for the ordination axes [38]. We present the strongest intraset correlation values, which indicate the environmental variables with the greatest correlation to functional feeding group abundances [71]. Weights demonstrate the association of invertebrate taxa with the ordination axes, and eigenvalues explain variance extracted in relation to environmental variables. We used biplots to present relationships of functional feeding groups to riparian vegetation [38,71,73]. Environmental gradients include stem density of riparian hemlocks or deciduous trees and stream chemical parameters, and are characterized as lines radiating from the center of the plot, the length and direction of which relate to the strength of the relationships between environmental variables [70].

5. Conclusions

We compared the spatial and temporal composition of benthic collector-gatherers, collector-filterers, and grazers in headwater streams with hemlock dominated riparian vegetation to those with deciduous riparian vegetation to evaluate the extent to which adelgid-induced hemlock loss could influence composition and abundance of these two functional feeding groups. Consistent with expectations, we found elevated family level diversity and abundance of collector-gatherers in Hester-Dendy samples from hemlock streams collected in summer, potentially attributable to the steady input of hemlock litter providing food resources for benthic shredders [16], which then create FPOM for use by collector-gathers [31]. Contrary to expectations we also found increased abundance of grazing heptageniids in hemlock streams during summer sampling; we had expected grazer abundance to be higher in deciduous streams during spring, before canopy formation impeded algal growth. Riparian vegetation provides linkages between streams, influences headwater stream conditions, serves to support food webs, and affects community structure of downstream habitats [32,46,47,50,51]. Changes in headwater benthic invertebrate communities should be expected as hemlock woolly adelgid continues to invade the range of eastern hemlock in North America.

Acknowledgments

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, Abraham Nielsen, Heather Spaulding, Melanie Sprinkle, Matt Thomas, and Sarah Wightman for field and laboratory assistance. Luke Dodd and Xia Yu provided statistical guidance, and Chris Barton, John Obrycki and Lee Townsend reviewed an earlier version of this manuscript. We appreciate the comments of three anonymous reviewers, whose suggestions greatly improved this work. 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 15-08-052 with the approval of the Director.

Author Contributions

Co-authors shared equally in the conceptualization, interpretation, and presentation of this work. Data collection and data analysis was performed by J.K. Adkins.

Conflicts of Interest

The authors declare no conflict of interest.

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