esa ECOSPHERE

Decomposition of terrestrial resource subsidies in headwater streams: Does consumer diversity matter?

David Stoker,[1,†] Amber J. Falkner,[1] Kelly M. Murray,[2] Ashley K. Lang,[1,4] Thomas R. Barnum,[1,5] Jeffrey Hepinstall-Cymerman,[3] Michael J. Conroy,[3] Robert J. Cooper,[3] and Catherine M. Pringle[1]

[1]Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA
[2]Department of Entomology, University of Georgia, Athens, Georgia 30602 USA
[3]Warnell School of Forestry and Natural Resources, University of Georgia, Athens, Georgia 30602 USA

Citation: Stoker, D., A. J. Falkner, K. M. Murray, A. K. Lang, T. R. Barnum, J. Hepinstall-Cymerman, M. J. Conroy, R. J. Cooper, and C. M. Pringle. 2017. Decomposition of terrestrial resource subsidies in headwater streams: Does consumer diversity matter? Ecosphere 8(6):e01868. 10.1002/ecs2.1868

Abstract. Resource subsidies and biodiversity are essential for maintaining community structure and ecosystem functioning, but the relative importance of consumer diversity and resource characteristics to decomposition remains unclear. Forested headwater streams are detritus-based systems, dependent on leaf litter inputs from adjacent riparian ecosystems, and decomposition of these resources is an important ecosystem function. Here, we examined the effects of consumer community diversity on leaf decomposition in a reciprocal transplant experiment. We asked (1) whether stream consumer communities are adapted to local resources and (2) how functional trait diversity among communities affects the leaf decomposition process. We did not find evidence that communities were adapted to locally derived resource subsidies. Instead, we found that consumer biomass and functional trait diversity as well as resource characteristics were the primary biotic drivers of decomposition. Consumer biomass was stimulated by specific resource subsidies, leading to direct and indirect effects of resource subsidies on ecosystem functioning. Contrary to current theory, we show that decomposition was higher with decreased detritivore functional diversity, suggesting dominant traits encompassing a specific niche increased decomposition. We also show that top-down, consumer diversity effects can be equal in magnitude to the bottom-up effects of resource characteristics during the decomposition process. Our research illustrates the importance of considering multiple biotic and abiotic drivers interacting via multiple pathways to affect a crucial ecosystem function.

Key words: aquatic ecology; biodiversity and ecosystem functioning; Coweeta Hydrologic Laboratory, North Carolina, USA; detritus; functional diversity; structural equation modeling; terrestrial–aquatic linkage.

Received 25 April 2017; accepted 5 May 2017. Corresponding Editor: Debra P. C. Peters.

[4] Present address: Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA.
[5] Present address: Smithsonian Environmental Research Center, Edgewater, Maryland 21037 USA.
† **E-mail:** dstoker92@gmail.com

INTRODUCTION

Resource subsidies are pervasive across aquatic and terrestrial ecosystems (Polis et al. 1997, Marcarelli et al. 2011). These fluxes of energy and nutrients can structure food webs, shape species interactions (Richardson and Sato 2015), and affect ecosystem functioning, such as primary production and energy flow between trophic levels (Marcarelli et al. 2011). An important ecosystem function in many systems is the decomposition of detrital resources. Detritus is frequently transferred between terrestrial ecosystems and between terrestrial and aquatic ecosystems (Polis et al. 1997), forming the base of many food webs (Cebrian 1999). Detritus is also important for maintaining community stability and biodiversity (Moore et al. 2004), which can have cascading effects as biodiversity is essential for maintaining ecosystem processes (Hooper et al. 2005). Extensive biodiversity and ecosystem functioning research notwithstanding, the relative importance of different components of biodiversity for decomposition remains unclear.

Decomposition is often more predictably affected by consumer diversity than detrital diversity (Srivastava et al. 2009, Gessner et al. 2010). One measure of consumer diversity is intraspecific variation within communities. Intraspecific variation can arise due to spatial variation in environmental context and interspecific interactions (Thompson 2005), whereby consumers adapt to local environmental conditions and energy sources. For example, resource subsidies can differ in composition and characteristics, which can result in consumers receiving and adapting to different resources depending on spatial location (Kominoski et al. 2011, Jackrel and Wootton 2015*b*, Jackrel et al. 2016). Adaptation can occur through phenotypic or genotypic shifts within populations and through changes in community composition (Jackrel and Wootton 2014). Evidence from terrestrial and aquatic systems suggests that consumers have adapted to local environments and resource subsidies, resulting in increased decomposition of locally derived detritus by soil microbial communities (Ayres et al. 2009, Strickland et al. 2009) and by stream microbial and invertebrate communities (Kominoski et al. 2011, Jackrel and Wootton 2014); however, evidence regarding the contribution of local adaptation to the decomposition process compared to other biotic and abiotic drivers is limited.

Another measure of consumer diversity is interspecific variation among communities. Interspecific variation can arise from biotic and abiotic filters acting on community assembly (Poff 1997, Wisz et al. 2013). These filters can result in communities differing in composition (Villéger et al. 2010, Hough-Snee et al. 2015) and in the presence and distribution of functional traits (Villéger et al. 2010, Mouillot et al. 2013). Functional traits affect organismal performance in relation to habitat and resource use and can be used to link community functional diversity to ecosystem processes (Hooper et al. 2005, Petchey and Gaston 2006). Understanding how species and associated functional traits are distributed among communities is important because ecosystem functioning can depend on trait richness and dissimilarity. Increased ecosystem functioning can occur when the most productive species and traits (e.g., consumption rate, foraging habit) are also the most abundant (Dangles and Malmqvist 2004, McKie et al. 2008, Creed et al. 2009). Additionally, communities comprised of species with dissimilar traits, such as habitat preference and dietary breadth, can increase ecosystem functioning through facilitation and niche complementarity (McKie et al. 2008, Frainer et al. 2014).

Headwater streams are a model system for evaluating how consumer diversity affects decomposition of resources subsidies. Streams are linked to adjacent riparian ecosystems through leaf litter subsidies (Wallace et al. 1997), which support stream communities across trophic levels from bacteria and fungi to invertebrate detritivores and predators. Leaf decomposition is an important ecosystem function that is influenced by both biotic and abiotic variables: Stream characteristics (e.g., water temperature, nutrients, and pH) can be important abiotic factors (Leroy and Marks 2006), while detrital quality (e.g., carbon (C), nitrogen (N), and phosphorous (P) content), microbial conditioning, and detritivore local adaptation, biomass, and functional diversity can be important biotic factors (Hieber and Gessner 2002, Kominoski et al. 2011, Frainer et al. 2014, Jackrel and Wootton 2014).

Here, we addressed two objectives to determine the drivers of leaf decomposition in detritus-based streams using a reciprocal transplant experiment. First, we evaluated the relative importance of local adaptation of invertebrate detritivore communities and detrital subsidy characteristics to decomposition. We hypothesized that detritivore communities would be adapted to subsidies representative of their adjacent riparian ecosystems, and we predicted that leaf decomposition would increase when communities were provided locally derived leaf subsidies. Second, we investigated how detritivore functional trait diversity and other biotic and abiotic factors affect leaf decomposition. We predicted that (1) detritivore biomass would be the primary driver of decomposition, (2) decomposition would increase when communities were composed of dominant traits or complementary traits, and (3) higher quality subsidies (i.e., higher N and P content) would increase decomposition due to increased consumption by detritivores.

METHODS

Site description

This experiment was conducted in two low-elevation and two high-elevation forested headwater streams at the Coweeta Hydrologic Laboratory Long-Term Ecological Research site in Otto, North Carolina, USA. The two low-elevation focal streams (Low-Elevation Stream 1 [LE_1] and Low-Elevation Stream 2 [LE_2]) were ~700 m above sea level, and the two high-elevation focal streams (High-Elevation Stream 1 [HE_1] and High-Elevation Stream 2 [HE_2]) were ~1400 m above sea level; the low- and high-elevation focal streams were separated by a linear distance of 4.75 km. The low- and high-elevation streams drained into separate larger streams: LE_1 and LE_2 drained into Coweeta Creek, and HE_1 and HE_2 drained into the Nantahala River. Streams in Coweeta are characterized by low water nutrient concentrations (nitrate (NO_3^- mg/L) = mean ± SE = 0.174 ± 0.002, ammonium (NH_4^+ mg/L) = 0.117 ± 0.003, phosphate (PO_4^{3-} mg/L) = 0.0056 ± 0.0004, Swank and Crossley 1988). Forest composition changes along an elevational gradient (Swank and Crossley 1988): Low-elevation forests are typically dominated by white oak (*Quercus alba*), while high-elevation forests are typically dominated by red maple (*Acer rubrum*), red oak (*Quercus rubra*), and tulip poplar (*Liriodendron tulipifera*). There was extensive loss of Eastern hemlock (*Tsuga canadensis*) throughout the forests surrounding the high-elevation focal streams due to the hemlock woolly adelgid (*Adelges tsugae*). All four focal streams were heavily shaded by a dense understory of *Rhododendron maximum.*

Stream survey

Environmental characteristics were measured for each of the four focal streams. A 50-m study reach was delineated and marked for each focal stream, with six transects spaced 10 m apart along the study reach. At each transect, we measured wetted-width, depth, and canopy cover. Canopy cover was estimated using a spherical densiometer. HOBO data loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) were deployed at the upstream end of each study reach to record mean daily water temperature for each stream. Flow velocity was estimated twice for each study reach at base flow. The focal streams were too shallow to permit use of a flow meter, so flow velocity was estimated using a neutrally buoyant, plastic ball and dividing the distance travelled by the time interval (Hauer and Lamberti 2007). Five replicate trials following this method were taken and averaged for each flow velocity estimate.

Leaf litter collection

We quantified leaf litter inputs for the low- and high-elevation focal streams to construct leaf packs representative of the riparian ecosystem for each elevation. Leaf litter was collected from the forest floor of the riparian zone of each focal stream at three transects (10, 30, and 50 m) along the 50-m study reach in mid-May 2014 (~6 months post-senescence). For each transect, a 1-m^2 square quadrat was placed 2 m up the stream bank; samples were collected from both sides of the stream at each transect. All leaf litter within the quadrat was collected and sorted by species; litter was only collected if it was likely to have fallen the previous autumn (i.e., leaf litter was visually inspected for relative degree of decomposition). Collected litter was oven-dried (60°C for 48 h) and weighed to determine relative input by mass for each tree species. The four species of highest relative input by mass were identified for each elevation (Appendix S1: Table S1) and then standardized to make a low-elevation leaf pack (LEP) and a high-elevation leaf pack (HEP). Inputs were standardized by dividing the relative proportion of each of the four dominant species by the sum of the relative proportions of the four dominant tree species for each elevation (Swan et al. 2009; Appendix S1: Table S1). White oak and red maple were present at each elevation but were not included in the HEPs and LEPs, respectively, because the species were not considerable inputs by mass at both elevations.

Reciprocal transplant experiment

We used a full reciprocal transplant design in which representative leaf packs for each elevation were deployed in home sites (e.g., LEPs deployed in low-elevation streams) and away sites (e.g., LEPs deployed in high-elevation streams). The leaf decomposition experiment was conducted during mid-summer (8 June–3 July 2014) to parallel previous studies (Kominoski et al. 2011, Jackrel and Wootton 2014). Leaf packs were incubated in LE_1 and LE_2 from 8 June to 2 July 2014, and leaf packs were incubated in HE_1 and HE_2 from 9 June to 3 July 2014. Representative leaf packs comprised ~6 g of mixed-species leaf litter derived from the adjacent riparian forest for each elevation immediately prior to the experiment (e.g., Kominoski et al. 2011), with four species represented in standardized proportions by mass (Table 1); only leaves with minimal or no visible damage were used. Leaf litter was placed into plastic 2.5-mm mesh bags (30 × 15 cm) after determining initial dry mass. An additional 3 × 3-cm opening was cut in the center of each mesh bag to allow for colonization by larger invertebrates (e.g., large caddisflies, crayfish).

Sixteen leaf packs, eight LEPs and eight HEPs, were incubated in each of the four focal streams, for a total of 64 packs. In each focal stream, leaf packs were incubated across four run habitats along a 75-m reach, with two LEPs and two HEPs incubated within each run. Similar flow velocities for run habitats were selected among all four focal streams to minimize the effects of abrasion on leaf decomposition. Eight additional leaf packs per stream (four LEPs and four HEPs) were transported back to the laboratory on the same day to measure handling loss (Hauer and Lamberti 2007). Leaf packs were incubated in each focal stream for a total of 24 days. After retrieval, leaf packs were placed into sealed bags on ice and processed in the laboratory within 24 h. Leaves from each leaf pack were rinsed over nested sieves (1 mm and 250 μm) to remove inorganic material and invertebrates and then oven-dried (60°C for 48 h). Leaf decomposition was calculated as the percentage of mass lost, after correction for handling loss. Leaf decomposition was calculated for the whole leaf pack because we were unable to identify all remaining leaf material to species with reasonable confidence.

Table 1. Standardized proportions of the four dominant tree species placed into each leaf pack type, low-elevation leaf pack (LEP) and high-elevation leaf pack (HEP).

	Standardized proportion	
Species	LEP	HEP
Quercus alba	0.455	N/A
Quercus rubra	0.209	0.317
Rhododendron maximum	0.248	0.185
Fagus grandifolia	0.088	0.117
Acer rubrum	N/A	0.381

Note: N/A signifies a species not included in the respective leaf pack type.

Leaf nutrient analysis

Leaf packs were analyzed for total C, N, and P content to determine stoichiometric ratios (C:N and C:P). All leaf material from each pack was ground using a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, New Jersey, USA). Litter samples for total C and N content were analyzed with a Carlo Erba 1500N CHN Analyser (Carlo Erba, Milan, Italy). Litter samples for total P analysis were prepared using the ash/acid extraction method and analyzed with a spectrophotometer following the ascorbic acid method (Allen 1974). Nutrient analyses were completed at the Stable Isotope Ecology Laboratory at the University of Georgia (Athens, Georgia, USA).

Aquatic invertebrates

Invertebrates from all leaf packs were preserved in 70% ethanol and stained with Rose Bengal solution for sorting. Individuals from two size classes (250 μm–1 mm and >1 mm) were counted, identified to the lowest possible taxonomic level (primarily genus), and assigned to functional feeding groups (Merritt et al. 2008). Chironomidae (Order: Diptera) were identified as Tanypodinae or non-Tanypodinae. Biomass was determined using established length–mass regressions (Benke et al. 1999), and detritivore (shredders and collector–gatherers) biomass estimates and density were standardized by leaf mass remaining for later statistical analyses.

Statistical analysis

*Stream survey.—*For each environmental characteristic, we conducted a one-way analysis of variance (ANOVA) to compare differences across the four focal streams. Parameters were analyzed for normality using Shapiro-Wilks tests, and transformations were used when necessary. Wetted-width, flow velocity, and temperature were ln-transformed; untransformed values of all environmental characteristics are reported in the results. Model assumptions (e.g., homoscedasticity, normal error distribution) were inspected graphically. Significance for the stream survey was considered at $P < 0.01$ to account for multiple comparisons.

*Leaf decomposition and stoichiometry.—*We used a two-way ANOVA to compare leaf decomposition by leaf pack type (LEP and HEP) and deployment site (home and away). Leaf pack type and deployment were fitted as fixed effects, and stream was fitted as a random effect; model assumptions were inspected graphically. Leaf decomposition was ln-transformed to improve normality, and untransformed values are reported in the results. Comparing leaf decomposition between home and away deployment site provides a measure of local adaptation of stream communities: Higher decomposition in home deployment sites would suggest local adaptation to leaf litter subsidies derived from the adjacent riparian ecosystem. Two LEPs deployed in LE_1 were lost during the experiment, resulting in a slightly unbalanced design (30 LEP samples vs. 32 HEP samples). Stoichiometric ratios were compared between leaf pack types using two-tailed Welch *t* tests.

*Functional diversity.—*Functional trait diversity was calculated for the detritivore community. Four traits were selected to represent the capacity by which detritivores occupy available habitat and affect decomposition: (1) mean per capita biomass, (2) foraging habit (e.g., burrow, sprawl), (3) thermal preference (e.g., cold, warm, eurythermal), and (4) rheophily (e.g., erosional, depositional). Selected functional traits were chosen for the following reasons: First, detritivore biomass affects decomposition via metabolic requirements and feeding rates (Brown et al. 2004). Second, foraging habits can alter feeding efficiency as well as competitive or facilitative relationships and, in turn, affect detrital consumption (McKie et al. 2008, Patrick 2013). Lastly, thermal and rheophilic preferences reflect the ability for taxa to occupy and persist in available habitat and thereby affect ecosystem functioning. Mean per capita biomass for each taxon was calculated from the individuals collected during the experiment; all remaining trait values were modified from the Poff et al. (2006) trait matrix (Appendix S1: Table S2).

Detritivore community trait diversity was calculated using two trait diversity metrics: (1) functional richness (FRic) and (2) functional dispersion (FDis). Functional richness measures the amount of trait space occupied by taxa within the community (Villéger et al. 2008). Functional dispersion is the mean distance of individual taxa to the centroid of the community in trait space and simultaneously measures trait dissimilarity and evenness within the community (Laliberté and Legendre 2010). Communities with high FDis are composed of evenly distributed, dissimilar traits while communities with low FDis are composed of unevenly distributed, similar traits (i.e., FDis is a measure of trait complementarity). Functional dispersion is weighted by abundances while FRic is not (Villéger et al. 2008, Laliberté and Legendre 2010). Functional richness values were standardized to be constrained between 0 and 1 (Laliberté et al. 2014). Detritivores comprising >1.0% of macroinvertebrate biomass or abundance were included in the diversity analyses (Appendix S1: Table S3). This criterion excluded rare and small taxa but not rare and large taxa from the diversity analyses. Taxa included in the trait analyses comprised >70% and >75% of total invertebrate community biomass and abundance, respectively (Appendix S1: Table S3).

*Detritivore community.—*We further analyzed differences in detritivore diversity between leaf pack types and focal streams. To compare compositional differences between leaf pack types and among focal streams, we used site-abundance matrices to calculate Bray-Curtis dissimilarities. Bray-Curtis dissimilarities were compared using a permutational multivariate analysis of variance with 10,000 permutations (Oksanen et al. 2016), and results are illustrated using nonmetric multi-dimensional scaling. We compared FRic, FDis, and detritivore biomass and density by leaf pack type and focal stream using two-way ANOVAs, and model assumptions were inspected graphically. Significance for the detritivore community was considered at $P < 0.0125$ to account for multiple comparisons.

*Path analysis.—*Structural equation models (SEMs) were constructed to evaluate the causal pathways through which biotic and abiotic drivers affect leaf decomposition (Appendix S1: Fig. S1). The robustness of a SEM is determined by the fit to the data, rather than significant relationships within the SEM (Grace 2006). Model fit was assessed by comparing expected and observed covariance between predictor and response variables using chi-square tests (Grace 2006). Structural equation models were considered consistent with the data when expected and observed covariance was not significantly different. Plausible causal linkages between variables were added to candidate SEMs to improve model fit based on single degree of freedom chi-square criteria (Grace et al. 2010). Candidate SEMs were then compared using Akaike's information criterion and corrected for sample size (AIC_c; Burnham and Anderson 2002), with the SEM having the lowest AIC_c selected as the most parsimonious model.

We constructed four alternative SEMs (FRic and FDis for C:N and C:P, respectively) to examine how functional diversity and other biotic and abiotic variables affect decomposition (Appendix S1: Fig. S1). Alternative SEMs were constructed to test the importance of different nutrients (N vs. P) and trait diversity metrics (FRic vs. FDis). Each SEM had 62 samples (30 LEPs and 32 HEPs) with six explanatory variables (stream, leaf pack type, conditioned litter stoichiometry (C:N or C:P), and detritivore biomass, density, and functional diversity (FRic or FDis) and one response-only variable (leaf decomposition). Within each SEM, stream and leaf pack type (i.e., LEP or HEP) were the exogenous variables (independent variables that affect other variables but are not affected by other variables), while detritivore biomass, density, and functional diversity and litter stoichiometry were the four endogenous variables (variables affected by the exogenous variables and that can affect other endogenous variables). Leaf decomposition was fitted as a response-only endogenous variable that was affected by all exogenous and endogenous variables. Stream identity was fitted to account for extraneous sources of environmental variation, and leaf pack type was fitted to account for leaf litter characteristics not explained by litter stoichiometry (e.g., lignin, tannin, phenols). Both stream and leaf pack type were fitted as random exogenous variables with means, variances, and covariances set as free parameters. All SEMs were estimated by maximum likelihood with Satorra-Bentler scaled test statistics, which are robust to non-normality. Model results are reported as standardized path coefficients, which show the direction and magnitude of the causal relationship between variables and allow for the comparison of relationship strengths within the SEM (Grace 2006).

All above analyses were conducted using R (version 3.3.0, R Core Team 2016) and the FD (Laliberté et al. 2014), vegan (Oksanen et al. 2016), nlme (Pinheiro et al. 2016), and lavaan (Rosseel 2012) packages; significance was considered at $P < 0.05$. All data and R code are provided as supplements (Data S1).

RESULTS

Stream survey

Stream characteristics (Table 2) differed by individual stream, although these differences depended on the environmental characteristic. High-elevation streams were wider than the low-elevation streams ($F_{3,20} = 5.126$, $P = 0.009$). Depth and canopy cover did not differ among the focal streams (both $P > 0.32$). Flow velocity differed by stream ($F_{3,4} = 33.79$, $P = 0.003$), with highest velocity in HE_1, intermediate velocity in LE_1 and LE_2, and lowest velocity in HE_2 (Table 2). Mean daily water temperature differed among the focal streams ($F_{3,92} = 322.4$, $P < 0.001$), with warmer temperatures at low elevation and cooler temperatures at high elevation (Table 2).

Leaf decomposition and stoichiometry

Leaf decomposition differed by leaf pack type (Fig. 1A) but not deployment (Fig. 1B). Decomposition of HEPs (mean ± SE = 27.51% ± 1.61%) was higher than LEPs (19.80% ± 1.41%; $F_{1,56} = 14.533$, $P < 0.001$, Fig. 1A), irrespective of deployment site. Decomposition was not significantly higher in home sites (24.44% ± 1.40%) compared to away sites (22.87% ± 1.58%; $F_{1,56} = 1.547$, $P = 0.219$, Fig. 1B). Because deployment had no significant effect on leaf decomposition, it was removed from all later analyses. There were differences in stoichiometry between LEPs and HEPs, with HEPs having significantly lower C:N (LEP: 55.24 ± 0.86, HEP: 46.38 ± 0.88; $t = 7.170$,

Table 2. Measurements of latitude, longitude, width, depth, flow velocity mean daily water temperature, and canopy cover for each of the four focal streams in the experiment, where LE_1, low elevation stream 1, LE_2, low elevation stream 2, HE_1, high elevation stream 1, and HE_2, high elevation stream 2.

Variable	Unit	LE_1	LE_2	HE_1	HE_2
Latitude	35°N+	3.81	3.83	2.73	2.66
Longitude	83°W+	25.74	25.72	28.57	28.54
Width	cm	74.5 ± 17.5	76.3 ± 16.0	218.7 ± 71.0	86.8 ± 18.9
Depth	cm	3.0 ± 0.4	2.5 ± 0.4	3.1 ± 0.4	2.8 ± 0.1
Flow velocity	m/s	0.18 ± 0.01	0.18 ± 0.02	0.44 ± 0.02	0.09 ± 0.01
Temperature	°C	15.8 ± 0.2	15.3 ± 0.1	12.8 ± 0.1	11.8 ± 0.1
Cover	%	95.8 ± 0.5	92.1 ± 2.0	92.2 ± 2.7	91.5 ± 0.9

Note: Values represent mean ± SE.

$P < 0.001$) and C:P (LEP: 2194.15 ± 67.22, 1901.80 ± 67.15; $t = 3.077$, $P = 0.003$) ratios.

Detritivore community

Detritivore community composition did not vary between leaf pack types ($F_{1,57} = 1.245$, $P = 0.283$; Fig. 2A) but did vary among focal streams ($F_{3,57} = 3.351$, $P < 0.001$; Fig. 2B). Functional richness did not differ by leaf pack type (LEP: 0.49 ± 0.04, HEP: 0.58 ± 0.05; $F_{1,57} = 2.365$, $P = 0.123$; Fig. 3A), but FRic differed among focal streams ($F_{3,57} = 5.612$, $P = 0.002$; Fig. 3B). Similar to community composition and FRic, FDis also did not differ by leaf pack type (LEP: 2.07 ± 0.13, HEP: 2.33 ± 0.15; $F_{1,57} = 2.333$, $P = 0.132$; Fig. 3C) but differed among focal streams ($F_{3,57} = 5.315$, $P = 0.003$; Fig. 3D). Detritivore biomass varied by leaf pack type ($F_{1,57} = 9.339$, $P = 0.003$; Fig. 3E) but not by stream ($F_{3,57} = 3.248$, $P = 0.028$; Fig. 3F). Conversely, detritivore density did not vary by leaf pack type ($F_{1,57} = 5.785$, $P = 0.019$; Fig. 3G) but varied by stream ($F_{3,57} = 5.084$, $P = 0.003$; Fig. 3H).

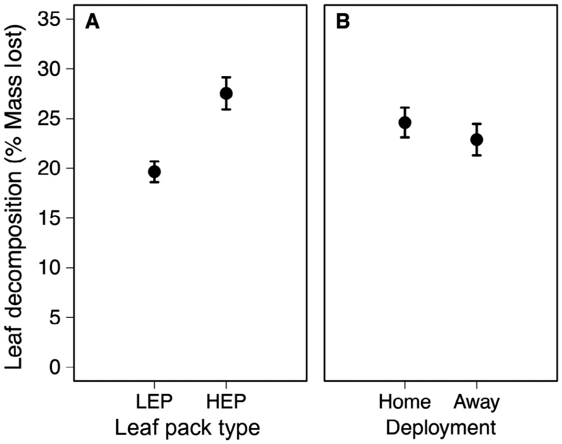

Fig. 1. Leaf decomposition by (A) leaf pack type, low-elevation leaf pack (LEP) and high-elevation leaf pack (HEP), and (B) deployment, home and away. Leaf decomposition was calculated as the percentage of mass lost at the end of the 24-day decomposition experiment. Points represent mean ± SE.

Path analysis

Of the four alternative SEMs, the FRic/C:P model best fit the available data (Fig. 4; $\Delta AIC_c = 34.2$, Appendix S1: Table S4). Greater detritivore biomass and lower FRic were linked to higher leaf decomposition. Leaf pack type had both direct and indirect effects on leaf decomposition: HEPs had higher decomposition (single pathway = 0.31) but also supported greater detritivore biomass (compound pathway = 0.31 × 0.47 = 0.15). Detritivore density and biomass were correlated, but density had no further significant effects on decomposition. Decomposition was lower in the high-elevation focal streams, and although C:P was lower in HEPs and in the high-elevation focal streams, C:P had no significant effect on decomposition.

DISCUSSION

Decomposition in detritus-based streams was mediated by consumer biomass and functional diversity as well as resource characteristics. We did not find evidence that adaptation by stream detritivore communities to local resources increased leaf decomposition (Fig. 1). Instead, we show that biomass was the strongest driver of decomposition, and we also found that

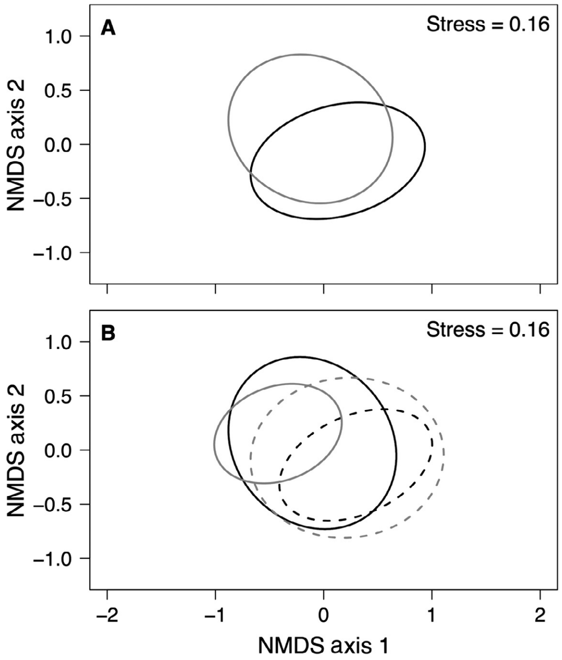

Fig. 2. Plots of detritivore community composition. (A) Nonmetric multi-dimensional scaling (NMDS) representation of the detritivore Bray-Curtis dissimilarity between leaf pack types, low-elevation leaf pack (LEP) and high-elevation leaf pack (HEP), with LEPs represented by a black line and HEPs represented by a gray line. (B) NMDS representation of the Bray-Curtis dissimilarity among focal streams, with low-elevation streams represented by black lines (LE_1 = solid line, LE_2 = dashed line) and high-elevation streams represented by gray lines (HE_1 = solid line, HE_2 = dashed line).

consumer functional diversity and resource characteristics had comparable effects on decomposition (Fig. 4). Of particular importance was our finding that decomposition was higher with lower detritivore functional diversity. Our results demonstrate the importance of considering multiple drivers when evaluating essential ecosystem functions.

Despite evidence for adaptation to locally abundant resources in streams (Kominoski et al. 2011, Jackrel and Wootton 2014, 2015*b*), our evidence suggests decomposition is not a result of local adaptation by stream consumers (Fig. 1). Consumers can exhibit preferences for specific resources, resulting in adaptation to a subset of all subsidies (Jackrel and Wootton 2015*b*). We used mixed-species packs without additional treatments looking at decomposition of all single- and mixed-species combinations, which could have obscured adaptation to specific resources. Additionally, previous experiments were conducted in systems that received subsidies primarily from one tree species (Jackrel and Wootton 2014, 2015*a*), or in streams where the riparian ecosystem was dominated by either deciduous or coniferous trees (Kominoski et al. 2011). Our focal streams received diverse leaf subsidies from riparian ecosystems that were not dominated by a single tree species (Appendix S1: Table S1), which could result in weaker selective pressures for consumers to adapt to a specific resource and instead adapt toward a more diffuse, generalist diet. Our results and those from previous studies suggest that local adaptation could be a stronger driver of decomposition in systems receiving less diverse resource subsidies.

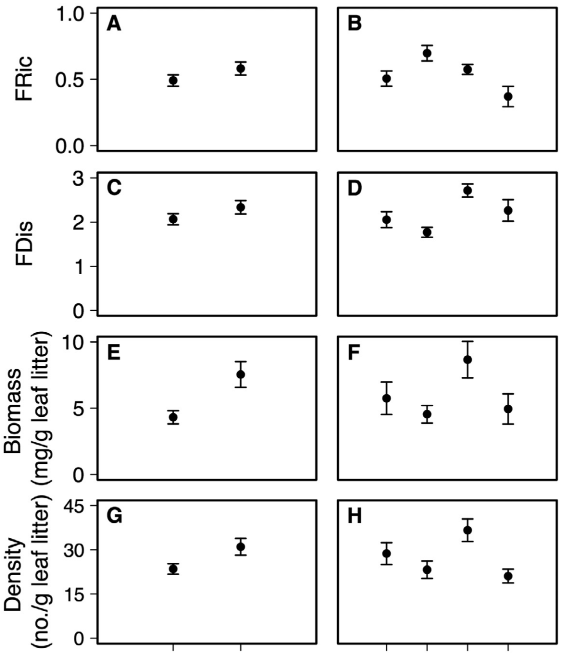

Fig. 3. Plots of detritivore functional diversity, biomass, and density by leaf pack type, low-elevation leaf pack (LEP) and high-elevation leaf pack (HEP), and focal stream. Detritivore functional diversity was quantified using two indices: functional richness (FRic; A, B) and functional dispersion (FDis; C, D). Detritivore biomass (E, F) and density (G, H) were standardized by remaining leaf mass. Points represent mean ± SE.

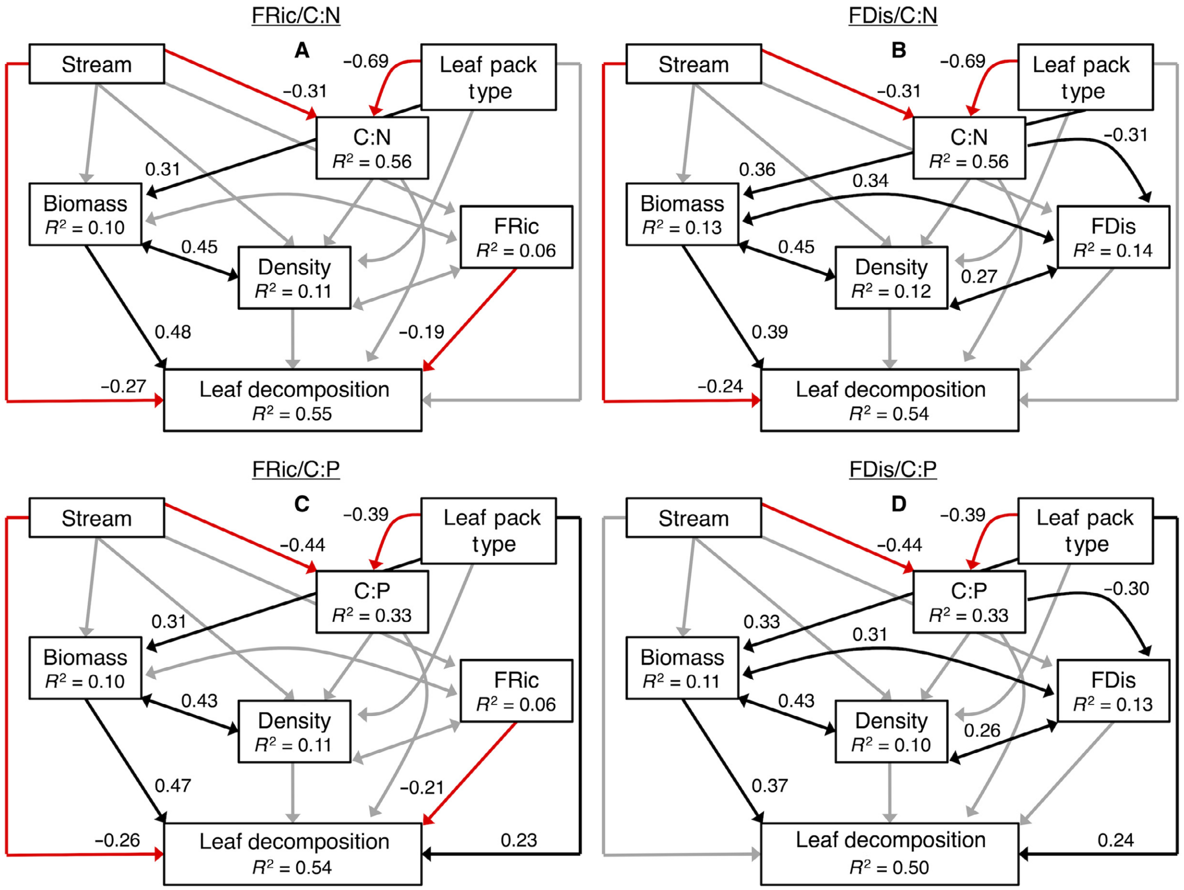

Fig. 4. Path diagrams showing the effects of detritivore biomass, density, and functional diversity (functional richness [FRic] and functional dispersion [FDis]), and abiotic variables on leaf decomposition. The top row of figures modeled the effects of conditioned litter C:N and FRic (χ^2 = 3.348, DF = 3, P = 0.341; A) and C:N and FDis (χ^2 = 1.046, DF = 2, P = 0.593; B). The bottom row of figures modeled the effects of conditioned litter C:P and FRic (χ^2 = 1.959, DF = 3, P = 0.581; C) and C:P and FDis (χ^2 = 0.326, DF = 2, P = 0.849; D). The FRic/C:P model best fit the available data (C). Black lines represent positive pathways, while red lines represent negative pathways; gray lines represent pathways included in the model that were not statistically significant. Standardized path coefficients, which show the direction and magnitude of the relationship between variables, are reported next to each line. Lines represent causal pathways included in the model, with single-headed arrows indicating a unidirectional pathway and double-headed arrows indicating correlation between variables. The R^2 is reported for each endogenous variable.

Detritivore functional diversity was linked to decomposition, but the strength and significance of the relationship depended on how functional trait diversity was quantified. There was no evidence to support the hypothesis of trait complementarity increasing leaf decomposition. Instead, leaf decomposition was higher with lower detritivore FRic (Fig. 4), suggesting that communities composed of abundant taxa and associated traits encompassing a specific niche increased decomposition (Dangles and Malmqvist 2004, McKie et al. 2008, Creed et al. 2009). We found that the family Chironomidae and the stoneflies *Tallaperla* and *Leuctra* were the most abundant detritivores. All three detritivores have the same rheophilic preferences but have differing thermal preferences: *Tallaperla* prefer cold to cool water while *Leuctra* and Chironomidae prefer cool to warm water. Additionally, *Leuctra* and *Tallaperla* have similar per capita biomass but differ in foraging habits. The differences in functional traits among these detritivores yielded a unique trait combination for each taxon that likely shaped the FRic of the detritivore communities and resulted in higher leaf decomposition. Controlled experiments manipulating the presence and abundance of these dominant taxa and associated traits would elucidate the mechanisms through which leaf decomposition was affected.

Functional traits and trait combinations may only have a significant effect on ecosystem functions if those traits are in sufficient abundance within the community. Realized community assemblages are shaped by environmental filters and species interactions (Poff 1997, Wisz et al. 2013), and variation among the focal streams in this experiment likely structured functional diversity of the detritivore communities (Fig. 3B, D). Larger-bodied detritivores, such as the caddisflies *Lepidostoma* and *Pycnopsyche*, were more abundant in the colder, high-elevation focal streams. The lower abundances of these larger taxa in the low-elevation focal streams plausibly resulted in reduced complementarity of biomass, foraging habit, and habitat preference, which could explain the decreased FDis in the low-elevation focal streams (Fig. 3D). Moreover, these taxa had lower abundances compared to other detritivores across all the focal streams, which further reduced the potential for trait complementarity (Laliberté and Legendre 2010).

Detritivore biomass was expected to have the strongest effect on leaf decomposition, given the relationship between biomass and metabolic rates (Brown et al. 2004) and evidence from previous studies (Hieber and Gessner 2002, Sanpera-Calbet et al. 2009, Frainer et al. 2014). Supporting this prediction, we found that detritivore biomass was the primary driver of leaf decomposition, ranging from ~1.8 to 2.2 times as strong as other biotic and abiotic drivers (Fig. 4). Detritivore biomass was affected by leaf pack type, with greater biomass supported on HEPs compared to LEPs (Fig. 3E), which could result from two mechanisms that are not mutually exclusive. First, HEPs had higher nutrient content, which could result in detritivores preferentially consuming these resources (Marcarelli et al. 2011, Jackrel and Wootton 2015*a*). Second, HEPs could have provided a more heterogeneous and preferred source of habitat for detritivores. High-elevation leaf packs were comprised of labile red maple and relatively recalcitrant rhododendron (*Rhododendron maximum*) and American beech (*Fagus grandifolia*, Table 1; Kominoski et al. 2007, Sanpera-Calbet et al. 2009). Litter serves as substrate for detritivores during foraging, and detritivore biomass is often increased when multiple leaf species contrasting in nutrient content and structural characteristics are present (Sanpera-Calbet et al. 2009, Jabiol et al. 2014).

We focused on invertebrate detritivores, but there are other important components of the decomposition process. Fungi and bacteria contribute to leaf decomposition directly by feeding on litter and indirectly by altering litter stoichiometry (Hieber and Gessner 2002). We did not quantify the microbial contribution to leaf decomposition, but invertebrate contributions to decomposition are often larger than microbial contributions in temperate streams (Hieber and Gessner 2002, Moore et al. 2004, Kominoski et al. 2011). Water temperature could accelerate decomposition by increasing the activity of invertebrates and microbes (Ferreira and Canhoto 2015, Griffiths and Tiegs 2016). In our study, decomposition was lower in the high-elevation focal streams (Fig. 4), likely due to the large differences in water temperature between the low- and high-elevation focal streams (Table 2). We did not find a relationship between litter nutrient content and decomposition, but other litter characteristics, such as micronutrients and secondary compounds, could be more useful predictors (García-Palacios et al. 2016, Jackrel et al. 2016).

Our results suggest that multiple drivers affect decomposition through direct and indirect pathways, and both consumer diversity and resource characteristics matter for decomposition. We found that the potential effects of local adaptation by stream consumers on decomposition were outweighed by other drivers, with detritivore biomass being the primary driver of decomposition. We also found that detritivore functional diversity was comparable in magnitude to the effects of detrital resource characteristics. Importantly, decomposition was higher with lower detritivore functional diversity, which contradicts current theory (Srivastava et al. 2009, Gessner et al. 2010). These results are particularly significant because anthropogenic stressors and increased disturbance could affect consumer community composition and functional diversity (Villéger et al. 2010, Mouillot et al. 2013). Moreover, changes in the composition and evenness of resource subsidies could have cascading effects on decomposition, as subsidies support consumer assemblages and possess structural and functional components that are related to the decomposition process (Swan et al. 2009, Kominoski et al. 2013). As environmental change progresses, it will be essential to evaluate how the relative importance of consumer diversity and resource characteristics is altered and how that, in turn, affects decomposition.

Acknowledgments

We thank James Hunt, Alex Fulmer, and Somer Rowe for assistance with fieldwork; Sarah Clement for laboratory assistance; Tom Maddox, Emmy Deng, and Mike Marshall at the University of Georgia Stable Isotope Ecology Laboratory for nutrient analyses; David. W. P. Manning and Christopher J. Patrick for advice on structural equation modeling; Pedro J. Torres, Irene Wyatt, and Samson Murray for stimulating conversations during data analysis and manuscript preparation; and Jarrett E. K. Byrnes for providing R script for calculating AIC_c. Comments from Chris J. Patrick, Maura P. Dudley, Carissa N. Ganong, Kelsey Solomon, Jessica Chappell, and two anonymous reviewers greatly improved the manuscript. This project was funded through a NASA Global Climate Change Grant (NNX10AB54A) and the NSF-funded Coweeta LTER (DEB-0823293, DEB-9632854, and DEB-0218001), with additional support at the University of Georgia from the Odum School of Ecology and the Center for Undergraduate Research Opportunities (Undergraduate Research Assistantship grant awarded to David Stoker).

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