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Impacts of stream riparian buffer land use on water temperature and food availability for fish

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ABSTRACT

Restoration of degraded freshwater ecosystems has gained considerable attention in the USA over the past decades. However, most projects focus almost entirely on the restoration of physical habitat or specific water quality parameters, while ignoring critical ecological processes related to food web re-establishment. In this study, we investigate the impact of riparian habitat in different stages of restoration on food availability for fish in four streams in Pennsylvania, USA. The riparian buffer habitats ranged from open meadow to mature forest and included new to long-term restoration sites. We quantified abundance and community composition of aquatic macroinvertebrates and riparian arthropods with aerial and ground-dwelling life history strategies. We found that riparian habitat and water temperature exert a strong influence over potential food resources for fish, with the open meadow habitat having highest abundance of terrestrial and aquatic insects, lowest taxa richness, and possible multivoltine aquatic insect life-history. Our results provide insight into the importance of riparian buffer habitat and water temperature on the composition of food availability for fish species of concern such as brook trout. The significant differences emphasize the need to include food web dynamics into riparian habitat restoration design to guide future rehabilitation projects focusing on fish conservation.

Introduction

Freshwater ecosystems are experiencing a variety of threats, and as a result, the USA has seen a dramatic increase in funding for river and stream restoration (Sweeney et al. 2004; Bernhardt et al. 2005; Booth 2005). The typical restoration approach assumes that rehabilitation of physical habitat ensures the rehabilitation of ecological functions (Beechie et al. 2008; Wipfli and Baxter 2010). However, the restoration of physical habitats (realigning channels, building instream structures, etc.) has so far yielded ambiguous evidence that such efforts increase subsequent fish biomass (Reeves et al. 1995; Stewart et al. 2009). These disappointing restoration outcomes may derive from inadequate consideration of trophic deficiencies in systems targeted by restoration. For example, food production to support fish is often an absent or secondary goal compared to improving physical habitat complexity and composition in restoration projects (Humphries and Winemiller 2009; Booth et al. 2016), yet food availability at basal levels (quantity and diversity of biofilm and macroinvertebrates) may be just as important in predicting the successful outcome of restoration projects focused on fish

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population rehabilitation (Lipsey and Child 2007; Naiman et al. 2012). Because food supply is such a critical component of understanding consumption, behavior, and ultimately production of fish, the lack of understanding of fish food composition and availability in restoration sites is a potential bottleneck that may prevent river restoration projects from accomplishing their goals.

In the Northeastern and Mid-Atlantic United States, brook trout (*Salvelinus fontinalis*) are a popular native sport fish that have experienced declines due to deforestation (Hudy et al. 2008), pollution (Haines and Johnson 1982), interspecific competition (Wagner et al. 2013), and thermal regime shifts (Flebbe et al. 2006). Like many fish species, abundance and survival of brook trout are regulated by a combination of biotic and abiotic factors, among which water temperature plays a dominant role (Wehrly et al. 2007; Stranko et al. 2012). Past research suggests that, when 80% or more of the stream bank is covered by forest ≥30 m wide, stream water temperature is maintained at or below lethal temperatures for cold water fish species (Sweeney and Newbold 2014). Many projects have attempted to restore degraded instream habitat and temperature regimes for trout by restructuring channel morphology, planting riparian forests, and reducing fine sediment inputs (Blann et al. 2002), but few studies have investigated the consequences of these efforts for food web structure (Lipsey and Child 2007; Naiman et al. 2012).

Along with shifting temperature regimes, changes to brook trout food supply may be an important driver of abundance and survival (Nislow and Lowe 2006; Courtwright and May 2013). Food supply may be especially important for young-of-the-year (YOY), a life stage where the correlation of timing between hatching and food availability drives survival probability (Hayward and Margraf 1987; Cushing 1990; Biktashev et al. 2003). Trout feed predominantly on terrestrial subsidies and benthic macroinvertebrates that are drifting, and the importance of macroinvertebrate production in supporting aquatic food webs is well established (Wallace and Webster 1996; Baxter et al. 2005; Benke and Huryn 2006). Many aquatic macroinvertebrates have terrestrial adult life stages in which they emerge from the water into the riparian habitat to mate in the spring and summer (Merritt et al. 2008). The factors that control macroinvertebrate growth in their larval stages and the initiation of pupation and emergence are related to temperature, discharge, and disturbance (Ward and Stanford 1982; Lytle and Poff 2004). Water temperature is predicted to be particularly important in driving emergence timing for macroinvertebrates (Sweeney et al. 1991; Harper and Peckarsky 2006). Thus, changes to the magnitude, timing, and temperature of spring and summer flows that have been documented across the United States with changes to land use and to climate may have important implications for shifts in the density, body size, and timing of macroinvertebrate emergence events (Yarnell et al. 2010). Maximizing food consumption without increasing energy expenditure (e.g. foraging cost) is an important strategy of YOY fish since they need to maximize their growth rate to maximize competitive fitness (Van Leeuwen et al. 2016). Therefore, if YOY trout and macroinvertebrates experience changes to temperature regimes differently, then the feeding behavior of trout on particular species or body sizes of macroinvertebrates may also be affected.

Trout also consume a substantial portion of their diet from terrestrial invertebrates (Kawaguchi et al. 2003; Wipfli and Baxter 2010; Courtwright and May 2013), and energy flow between streams and nearby riparian habitats can be significant (Nakano and Murakami 2001; Baxter et al. 2005). Land use has impacted many streams in Pennsylvania, where our study took place, with close to 30% of streams being classified as being in poor condition (EPA 2015). Anthropogenic perturbations that modify land use in the vicinity of streams (agriculture, wood cutting, etc.), as well as climate warming (Rice and Jastram 2015) and the timing of flooding events (Nilsson 2000), have been known to affect the seasonality of different abiotic and biotic factors. This mismatch can potentially result in a lack of synchronicity between ecological processes and the phenology of many organisms that are so tightly bound to fluctuations in water temperature, day light, and other factors (McCluney et al. 2014). In addition, the composition of riparian vegetation species influenced by human activity, such as the introduction of non-native plants, can alter terrestrial insect composition and abundance with important consequences for fish that eat terrestrial insect subsidies (Roon et al. 2016).

In this study, we evaluate stream riparian land-use habitat restoration strategies aimed at reforestation of the riparian zone by investigating the impact of different riparian forest restoration stages on food availability for fish. To achieve this objective, we survey the availability of food (total biomass, taxa composition, and per capita size of the most abundant taxon) across four streams in the eastern United States that have contrasting riparian habitat characteristics. The differences in riparian habitats in our study are based on different forest restoration stages including: open meadow (no restoration), recently restored (4 years old trees), long-term restoration (30–40 years old trees), and mature forest as a historic reference (>115 years old trees). We quantify food resources with respect to the life history of brook trout, a primary target species of many stream restoration efforts throughout the Northeast and Mid-Atlantic United States. We predicted that terrestrial food availability would be greatest in forested sites compared to sites with less forested area or open meadow. We also predicted that maximum and mean water temperatures would be lower, aquatic macroinvertebrate density and taxa richness would be higher, and aquatic macroinvertebrate body size would be smaller in forested sites, since forested streams tend, in general, to have lower gross primary production (Mulholland et al. 2001; Bernot et al. 2010; Lamberti and Steinman 1997). Our study provides insight into the potential drivers of food availability for trout that can guide the development of strategies that address restoration of both the physical habitat and the trophic structure of the stream ecosystem.

Methodology

Study sites

We compared temperature and food availability across four streams in the Brandywine watershed (Figure 1) in southeastern Pennsylvania. The four streams we selected for the study have similar channel morphologies, gravel sizes, and widths (Table 1) but vary substantially in their shade cover and riparian buffer widths, thereby representing the common range of riparian habitats in the region across a spectrum from treeless pasture fields to mature closed deciduous forest. We classified four different riparian habitats: (1) Taylor Run, an unrestored site where the riparian vegetation consists of treeless hay fields corresponding to a herbaceous riparian habitat characterized by a low vertical vegetation structure; (2) Sharitz Run, a recently restored site (4 years) where the riparian vegetation consists of a discontinuous single-tree forest and hay fields corresponding to a forested-herbaceous riparian habitat characterized by a diverse vertical vegetation structure; (3) White Clay Creek (hereafter WCC) with a 35–40-year-old restored riparian forest habitat of 15 to 30 m width and bordered by hay fields characterized by a diverse vertical vegetation structure; and (4) an unnamed tributary to the West Branch Brandywine Creek (hereafter called ChesLen) with a >115 years old mature forest riparian habitat dominated by trees with only few lower vegetation forms such as shrubs and characterized by a low diversity of vertical habitat structure. All four streams are designated as Trout Stocking Fishery-Migratory Fishery by the Pennsylvania Fish and Boat Commission and historically supported trout populations, but only ChesLen currently supports a reproductive brook trout population. Brown trout are currently found in WCC. While it would be ideal to have replicate streams within each riparian habitat category to statistically account for naturally occurring variation among streams, it was impossible to find replicate streams in the same basin with identical land-use histories. Thus, the riparian land cover at the four stream sites we selected best represents the restoration/land management gradient resulting from the massive local effort to plant approximately 1450 new km of riparian forest buffer per year through 2036 to achieve the goal of 70% forested riparian area (ACB 2015).

All biotic sampling (terrestrial and aquatic invertebrates) was conducted every two weeks from April to July 2015 at four riffle locations not further than 0.3 km apart within each of the four streams. We sampled the same four riffles within each stream on each of the seven dates. Stream physical characteristics and water temperature measurements were conducted at the most upstream
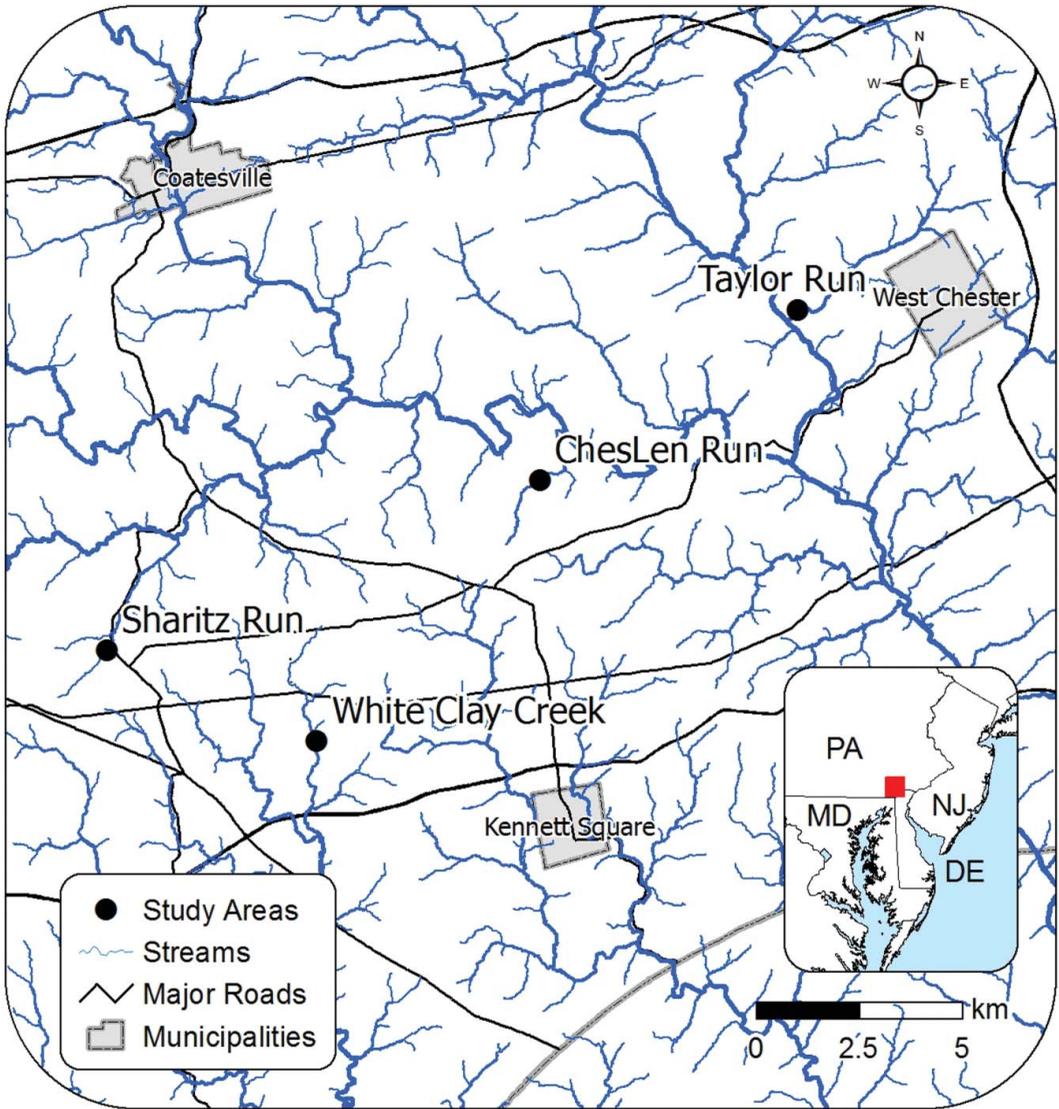
Figure 1. Map of study sites in the Brandywine watershed, Pennsylvania.

Table 1. Characteristics of the four streams used in this study. All values are means for $N = 2$ riffles (most upstream and downstream of the sampled stream reach).

Characteristic	Taylor Run	Sharitz Run	White Clay Creek	ChesLen
Discharge (m³/s)	0.3	0.1	0.4	0.2
D_{50} (mm)	27.0 ± 4.0	26.5 ± 4.7	33.9 + 5.1	42.2 + 8.6
DO (%)	107.7 + 1.3	99.5 + 0.6	97.6 + 0.5	98.5 + 0.0
pH	7.9 + 0.1	7.9 + 0.1	7.7 + 0.0	7.8 + 0.1
Conductivity (μS)	697.5 +3.5	151.3 + 0.7	232.3 + 1.4	225.8 + 0.3
Embeddedness (N)	41.0 + 4.0	22.3 + 8.3	11.7 + 0.7	12.1 + 1.2
Riffle width (m)	5.5 + 1.0	3.0 + 0.1	5.4 + 1.1	6.0 + 0.2
Total suspended solids (mg/L)	40.1 + 8.7	107.3 + 1.1	109.8 + 72.4	107.2 + 20.5
Shade cover (%)	0.0 + 0.0	10.0 + 0.0	50.0 + 0.0	80.0 + 10.0
Forested riparian habitat width (m)	0.0	13.0–20.0	200.0–800.0	>800.0

and downstream riffles of each stream to ensure conditions were comparable through each stream reach.

Water temperature time series

We used HOBO ProV2 loggers (ONSET Corporation) to characterize the water temperature regime in each stream (accuracy: ±0.21 °C, resolution: 0.02 °C). Each logger was placed into white PVC tubing for protection from direct solar radiation. Prior to deployment, all loggers were checked for potential discrepancy in readings by comparing their measurements after placing them for 48 hours in a bucket with water and ice. During this period, ice melted and the water in the bucket slowly warmed, allowing for comparison of temperature measurements under different thermal conditions (from close to the freezing point to room temperature at 23 °C). We deployed the water temperature loggers in the most upstream and downstream riffle at each stream to ensure water temperature measurements were representative of the study reach conditions and attached to a rebar in the middle of the stream channel. Water temperature was recorded in 15-minute intervals from mid-April to mid-July 2015, and we calculated the following thermal metrics for each stream: maximum, minimum, median, mean, and daily variation calculated as the difference between maximum and minimum values.

The incubation time for trout eggs depends on the egg's development, which is primarily controlled by water temperature (e.g. Marten 1992), but in our study area (Brandywine watershed, PA) hatching typically occurs when the stream temperature reaches 15 °C (Stroud Water Research Center field observations, unpublished data).

Terrestrial invertebrate sampling

At each of four riffle locations along each of the four stream reaches, we deployed a single sticky and a single pitfall trap for 72 hours during each sampling date to describe terrestrial invertebrate communities ($n = 4$ for each stream × seven dates) (Henderson and Southwood 2016). To capture aerial arthropods, we used sticky traps comprised of clear, single, compact-disc (CD) cases covered in Tanglefoot[TM]. CD cases were secured to stakes at a height of 1 m above the ground on the stream bank with the sticky side faced toward the riparian habitat and away from the stream. After 72 hours, the sticky trap CD cases were carefully closed, wrapped in plastic, and transported to the laboratory where the entire sample was enumerated and identified to family. Because individuals were attached to the Tanglefoot[TM] material, biomass was not estimated for aerial arthropods. To capture ground-dwelling arthropods, we used pitfall traps consisting of plastic cups containing 95% ethanol buried flush with the ground surface on the stream bank. After being 72 hours, the contents of the pitfall traps were collected in a plastic bag, preserved in 95% ethanol, and transported to the laboratory where the full sample was enumerated and identified to family using a dissecting microscope at 5× magnification. We estimated the total biomass of ground-dwelling arthropods by drying all individuals of each taxon at 60 °C for 48 hours and then pooling all the biomass across all taxa. Hereafter, we refer to abundances and biomasses sampled from the sticky and pitfall traps as terrestrial abundance or biomass but recognize that other types of sampling schemes such as sweeping riparian vegetation with nets may also represent riparian arthropod activity and that our abundance values likely represent relative rather than true abundance.

Aquatic invertebrate sampling

We sampled benthic aquatic macroinvertebrates using a 500-μm mesh Surber net covering 0.093 m^2 of benthic area in each of four riffles per stream (one sample/riffle × seven dates) by disturbing the substrate for 30 seconds by hand (Hauer and Lamberti 2007). Samples were preserved in 95% ethanol and processed in the laboratory by counting invertebrates in X subsamples until a minimum of

100 individuals were enumerated and identified to family using a compound microscope at $10\times$ magnification (Merritt et al. 2008). When 100 individuals were enumerated, the subsample was completed so that all individuals within that subsample were counted, and the total abundance A_i of each taxon i per m^2 was calculated as $A_i/(X {}^*Y)$ where Y is the area of each subsample. The weight of each taxon was measured after being dried for 48 hours at 60 °C to calculate the biomass per m^2. To calculate a total biomass per m^2, all taxa were pooled. To estimate biomass of individuals from the most abundant taxon, Hydropsychidae, we divided the total hydropsychid biomass per sampling date by the number of hydropsychid individuals enumerated, resulting in a per capita mass. We sampled drift using submerged nets (0.47 W $\times$ 0.28 H) with 500-μm mesh in two riffles (most upstream and downstream) of each stream reach for $\sim$30–90 minutes a dusk. Length of sample time was used to standardize each sample to account for variation among samples according to standard methods (Hauer and Lamberti 2007) that are used to estimate drift density (No. per 100 m^3). Samples were preserved in 95% ethanol in the field and processed in the laboratory by counting all arthropods (aquatic and terrestrial) and calculating drift density.

Data analyses

We performed Kruskall–Wallis test on the hourly water temperature series to determine if all sites were derived from the same population. We also used a linear mixed effects model to compare daily mean, maximum, minimum, and variation among the different streams. All analyses were completed in R version 3.2.2 (R Development Core Team 2008).

We used linear mixed effects models using the lme package to compare benthic macroinvertebrate density, biomass, and taxa richness across the four streams. Models consisted of density, biomass, or richness as a function of the fixed effects of stream and the random effect of riffle nested within sampling date. Sampling date was used as a random effect because differences in density between sampling dates were expected as macroinvertebrates passed through their life cycles and our primary concern was to identify differences across streams with varying riparian habitat condition. *Post hoc* analyses of user-defined contrasts corrected for multiple comparisons were used to assess differences across streams. To investigate relationships between aquatic insects and water temperature, we used linear models to correlate invertebrate density and biomass with mean daily temperature and the coefficient of variation. Drift samples were analyzed by pooling all taxa across every sampling date to compare mean drift densities across the four streams. We used a linear mixed effects model consisting of density as a function of the fixed effects of stream and the random effect of riffle nested within sampling date to assess differences in drift density across streams.

To compare how much food could theoretically be available for brook trout, we used the biomass data from pitfall and Surber traps to calculate a mean potential daily food availability for fish in mg/m^2/d. Those values were converted to potential grams of trout produced per stream reach (m^2) per day by multiplying the drift input (potential terrestrial subsidy input and benthic input) by the food conversion factor of 0.2 (Waters 1988), and then the daily values were used to calculate the potential mean value over the study period (4 months). The proportion of trout diets that could be attributed to the terrestrial subsidy was estimated as the terrestrial component/total component $\times$ 100. We recognize that the calculated values may overestimate the overall potential for trout production, and do not intend for these values to be used in isolation to make management decisions. Instead, we use these data to offer a preliminary baseline with which to compare the differences in food availability in the studied streams in terms of potential for trout.

Results

Temperature

Taylor Run (meadow riparian habitat) had not only the warmest mean water temperatures of the four streams (Figure 2), but also the most variable, with mean daily fluctuation of 5.63 °C (Table 2).
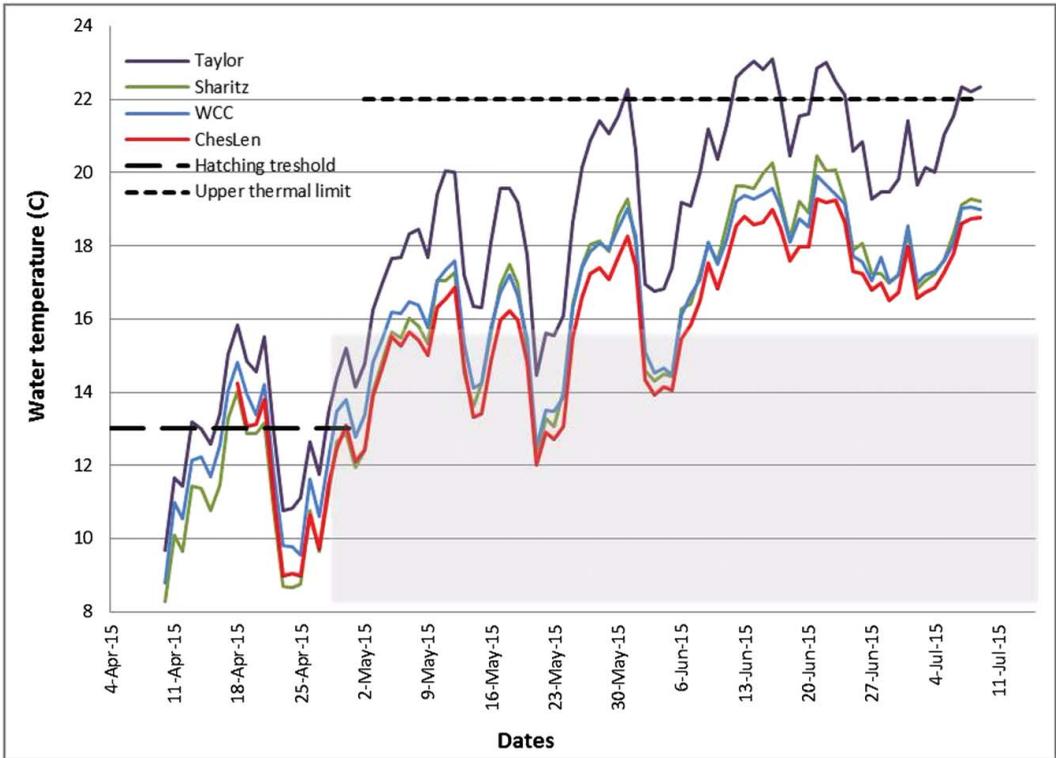
Figure 2. Daily mean water temperature at the four streams from April 11th to July 9th 2015. The horizontal black line indicates the threshold water temperature for brook trout hatching and then, once fish hatched, the upper thermal limit that usually initiates movement toward thermal refugia, as well as the optimal growth range indicated by the grey zone.

The maximum daily fluctuation often reached over 9.0 °C in Taylor Run. Sharitz Run (forest-herbaceous riparian habitat) was the second warmest stream (daily mean and daily variation value of 16.09 and 4.90 °C), but is not statistically different ($p > 0.05$) from WCC (restored forest riparian habitat) (daily mean and daily variation value of 16.26 and 4.19 °C). ChesLen (mature forest riparian habitat) was the coolest stream and the least variable. ChesLen's mean water temperature regime was also statically different from the three other streams ($p < 0.001$). The mean daily variation was 3.79 °C and the daily maximum did not exceed 6.04 °C.

The temperature threshold (Figure 2) for the brook trout egg hatching period was reached earlier in the spring in Taylor Run (April 13), followed three days later by Sharitz Run (April 16) and another later by WCC (April 17). The brook trout hatching period was reached on April 18 in ChesLen. The water temperature was colder for the four streams after this initial period of egg hatching temperatures, and the hatching threshold temperature was only reached again and maintained for the remaining duration of the spring for Taylor Run on April 28, on April 29 and 30 for Sharitz Run and WCC, and ChesLen on May 3. The hatching period in the warmest stream, Taylor

Table 2. Descriptive statistics for the water temperature (°C) for each stream (mean ± SE). DV stands for daily variation.

	Taylor Run	Sharitz Run	White Clay Creek	ChesLen Run
Mean	18.6 ± 0.4	16.1 ± 0.4	16.3 ± 0.3	15.6 ± 0.2
Median	19.3 ± 0.4	16.8 ± 0.3	16.9 ± 0.3	16.3 ± 0.2
Min	7.4 ± 0.4	5.3 ± 0.4	6.6 ± 0.4	5.7 ± 0.2
Max	26.4 ± 0.4	22.6 ± 0.3	21.5 ± 0.3	20.9 ± 0.3
Mean DV	5.6 ± 0.2	4.9 ± 0.2	4.2 ± 0.2	3.8 ± 0.1

Run (meadow riparian habitat), was consistently earlier compared to the coolest stream ChesLen, but was not consistently different from that in Sharitz Run or WCC ($p = 0.006$).

Terrestrial invertebrate subsidies

Terrestrial arthropod abundance was greatest for both the pitfall trap and sticky trap sampling methods in the least forested site Taylor Run (Table 3). For aerial arthropods, Sharitz and Taylor Runs, the two stream sites with the greatest abundances per sticky trap, were consistently similar ($z = -1.808$; $p = 0.27$), but all other sites had different abundances (Figure 3(A)). Richness was greatest at Taylor Run, lowest at ChesLen, but no consistent differences between Taylor Run, Sharitz Run, and WCC were detected (Figure 3(B)). In the pitfall traps, abundance was similar in Taylor and Sharitz Runs ($z = 0.25$, $p = 0.99$), and in WCC and ChesLen ($z = -0.62$, $p = 0.92$) (Figure 3(C)). Biomass was only statistically greatest in Sharitz Run (Figure 3(D)) compared to WCC ($z = -2.78$, $p = 0.03$), due to a higher abundance of relatively heavy Lumbricidae earthworms. Richness was higher in Sharitz Run compared to Taylor Run ($z = 3.51$, $p = 0.002$), WCC ($z = 4.03$, $p < 0.001$), and ChesLen ($z = -3.72$, $p = 0.001$) (Figure 3(E)).

Aquatic macroinvertebrates

Abundance of aquatic macroinvertebrate families varied across stream (Table 4), with Chironomidae being most abundant in Taylor Run, and Hydropsychidae being most abundant in Sharitz Run, WCC, and ChesLen. Macroinvertebrate density (Table 4) was greatest in Taylor Run, followed by WCC, ChesLen, and Sharitz Run (Figure 4(A)). Sharitz Run and ChesLen did not have significantly different densities ($z = -0.47$; $p = 0.97$). Biomass (Figure 4(B)) varied among streams, with ChesLen being significantly lower than WCC ($z = -3.83$; $p < 0.001$), marginally lower than Taylor Run ($z = -2.26$; $p = 0.11$) and having no detectable differences with Sharitz Run ($z = -0.46$; $p = 0.97$). Total biomass summed across all taxa peaked for all streams between May 15 and May 29 2015 except for the stream with the most variable temperature, Taylor Run, which had no discernable peak in biomass. Per capita biomass of Hydropsychidae, the most abundant family in three of the four streams, peaked on May 29 in WCC, ChesLen, and Sharitz, suggesting that these streams likely have a single cohort. However, little variation in hydropsychid biomass, and thus no peak, was detected in Taylor Run across the sampling dates, suggesting that overlapping cohorts may exist in this one stream (Figure 4(C)). Taxa richness was two times lower in Taylor Run compared to all other streams ($p < 0.001$) (Figure 4(D)), and was heavily influenced by a single taxon, Chironomidae, which comprised 65% of samples on average. We looked at the correlation between temperature and macroinvertebrate abundance and biomass to investigate potential relationships between water

Table 3. Abundance, biomass, or taxa richness averaged (mean ± 1 SE) across all seven sampling dates from April to July 2015 using terrestrial sticky traps, terrestrial pitfall traps, or aquatic surber samplers.

|	Taylor Run	Sharitz Run	White Clay Creek	ChesLen Run
Aerial arthropods				
Abundance (No./trap)	32.5 ± 3.0	27.3 ± 2.3	16.4 ± 1.5	9.9 ± 0.8
Richness (No./ trap)	5.9 ± 0.3	5.7 ± 0.4	5.3 ± 0.3	4.2 ± 0.2
Ground arthropods				
Abundance (No./trap)	47.6 ± 6.3	50.0 ± 6.4	32.7 ± 3.5	28.8 ± 5.5
Biomass (G./trap)	0.2 ± 0.0	0.3 ± 0.1	0.1 ± 0.0	0.2 ± 0.0
Richness (No./trap)	9.4 ± 0.7	12.9 ± 1.5	8.7 ± 0.7	9.1 ± 1.0
Aquatic macroinvertebrates				
Abundance (No./m^2)	17,350.0 ± 2,050.0	3260.0 ± 900.0	9570.0 ± 1360.0	3630.0 ± 1170.0
Biomass (G./m^2)	3.5 ± 0.5	2.2 ± 0.6	4.7 ± 0.6	1.8 ± 0.4
Richness (No./m^2)	5.3 ± 0.4	12.0 ± 0.5	13.1 ± 0.5	13.1 ± 0.4
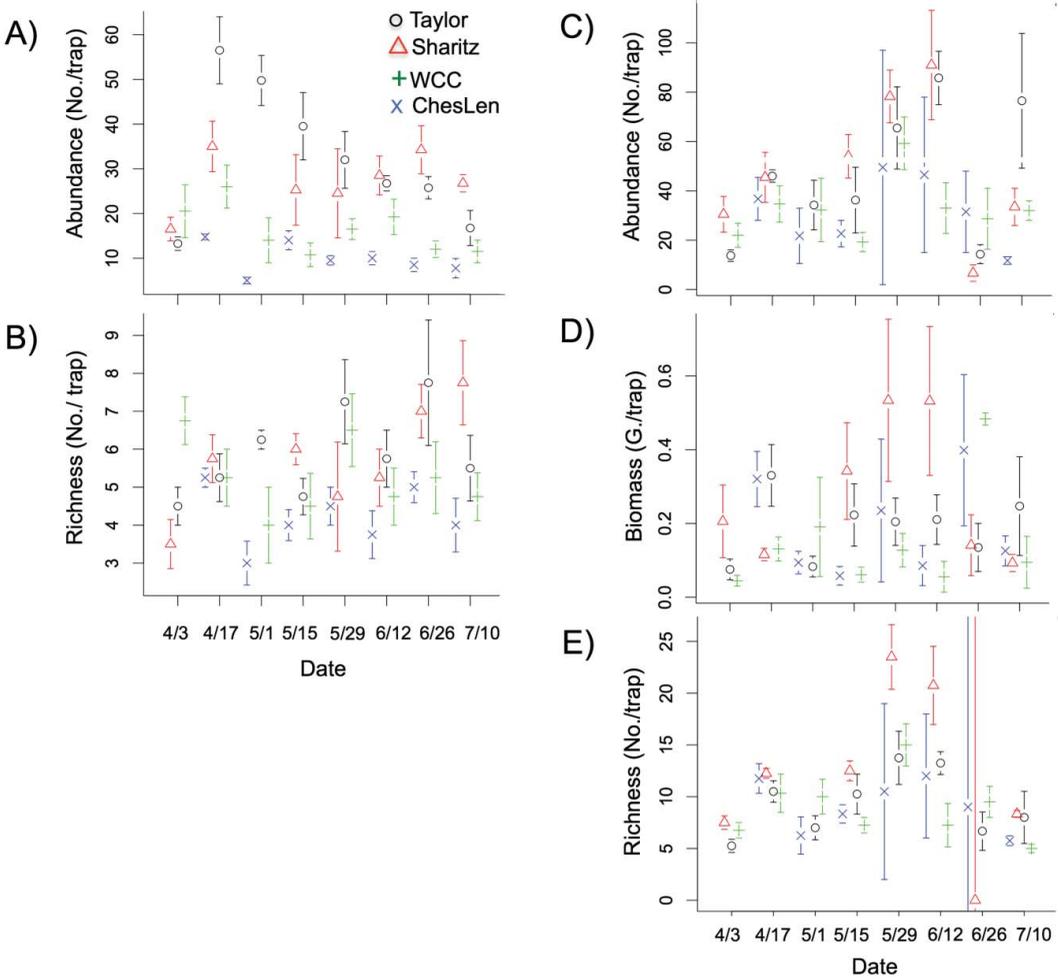
Figure 3. Terrestrial input of aerial insect (a) abundance and (b) taxon richness measured in sticky traps deployed in the riparian zone. Terrestrial input of ground-dwelling insect (c) abundance, (d) biomass, and (e) taxon richness measured from fall traps deployed in the riparian zone. Values are means ± 1 SE.

temperature and aquatic insect abundance and biomass (Figure 5). We found that only mean temperature showed a consistent relationship with macroinvertebrates, with abundance increasing as mean water temperature increases (Figure 5(A)) likely driven by high temperatures and high macroinvertebrate abundances that we observed in Taylor Run. No differences in drift density between streams were detected ($F = 1.8$; $p = 0.19$).

Table 4. Aquatic macroinvertebrate density (mean ± SE) for the five most abundant taxa (listed alphabetically) across all seven sampling dates from April to July 2015.

| Taxon	Taylor Run	Sharitz Run	White Clay Creek	ChesLen
Baetidae	820 ± 210	300 ± 60	300 ± 80	270 ± 80
Chironomidae	9830 ± 1,260	560 ± 180	2250 ± 310	840 ± 250
Ephemerellidae	10 ± 5	240 ± 70	1340 ± 190	150 ± 30
Hydropsychidae	3170 ± 910	1140 ± 400	2850 ± 710	890 ± 420
Philopotamiidae	0 ± 0	320 ± 120	240 ± 70	420 ± 160
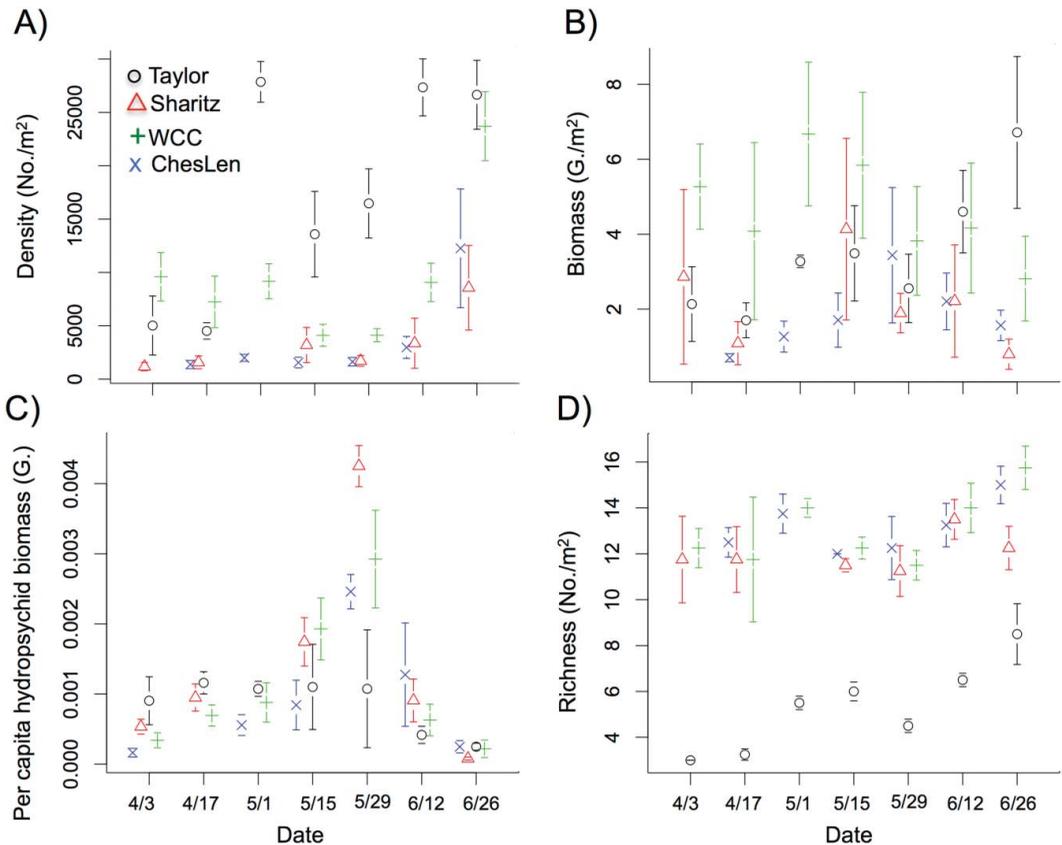
Figure 4. Aquatic macroinvertebrate (a) density and (b) biomass. The individual size of hydropsychids (c) showed one peak on 5/29 for all streams except Taylor. Taxon richness (d) was lowest in Taylor.

Potential for summer trout production

The terrestrial arthropod and aquatic macroinvertebrate potential contributions to drift biomass were converted into trout production values using methodology from Waters (1988). Except for WCC, the terrestrial subsidies contribute to, on average, 60% of the potential food available for trout to eat. In WCC, the aquatic macroinvertebrates were the main contributor to the potential food available. The stream that had the most potential for trout production over the sampling period based on food inputs was Sharitz Run (terrestrial = 8.5 ± 0.4; aquatic = 3.8 ± 0.9; total = 12.3 g/ m^2), followed by WCC (terrestrial = 1.7 ± 0.6; aquatic = 2.9 ± 0.9; total = 4.6 g/m^2). Both Sharitz Run and WCC had consistently higher values of potential trout production ($p < 0.006$) than Taylor Run (terrestrial = 2.0 ± 0.4; aquatic = 1.5 ± 0.3; total = 3.5 g/m^2) or ChesLen (terrestrial = 2.1 ± 0.6; aquatic = 1.4 ± 0.5; total = 3.5 g/m^2).

Discussion

Restoration of physical habitat for fish species, especially relating to salmonids (Booth et al. 2016), is on the rise, but most fish in young life stages are also sensitive to food resources, a component of streams that is also impacted by the same altered climate, land use, and hydrology that typically motivate physical restoration projects. Trophic mismatch, the disconnect in timing between periods of food availability and food acquisition, has been documented across many ecosystems, with extensive consequences for food webs, ecosystem productivity, and reproductive success (Cushing 1990;
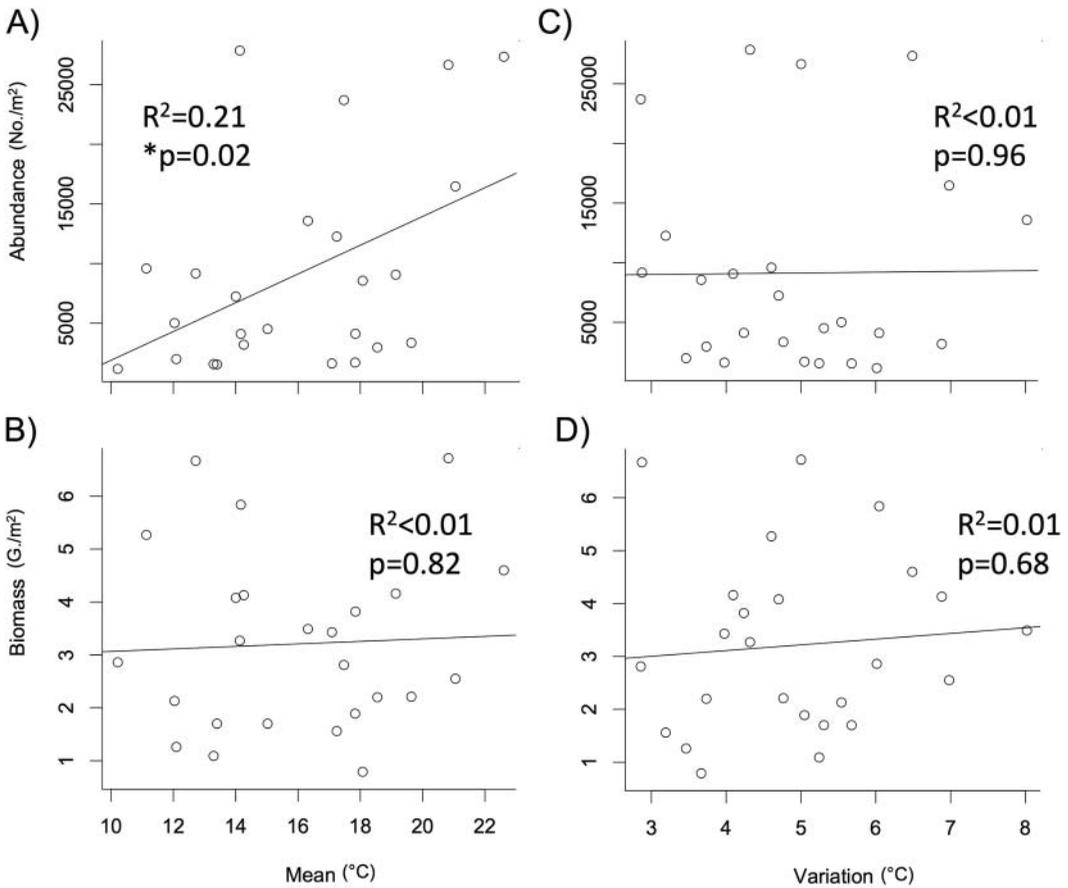
Figure 5. Temperature mean (a,c) and variation (b,d) relationships to aquatic insect abundance and biomass and linear regression R^2 values (asterisk indicates significant relationship).

Edwards and Richardson 2004; Post and Forchhammer 2008). Although it is recognized that (1) food size and composition is important for young-of-year trout and (2) that land use and climate warming may be altering phenology of these important traits of trout food, the impact of changing phenology, body size, and the implications for trout growth is relatively understudied. Moreover, stream and habitat restoration projects rarely assess the changes to food composition and how habitat improvement really translates into fish production. Our study indicates that potential food availability across riparian habitats ranging along a gradient in restoration stage varies in abundance, aquatic vs. potential terrestrial inputs, and taxa richness. We also found that water temperature may drive the abundance of aquatic food availability and that predicted trout production potential was greatest in the recently restored Sharitz Run and historically restored site WCC compared to degraded open meadow Taylor Run and pristine fully forested ChesLen sites. These findings may provide evidence that productivity and disturbance jointly influence species diversity in this watershed because abundance and calculated food availability was highest in the two streams (Sharitz and WCC) that represent intermediate disturbance (Huston 2014). Together, these findings indicate that restoration efforts may ultimately provide conditions that not only support physical habitat for trout but also for their food.

The timing of insect life cycle stages is tightly coupled with temperature and hydrologic regimes, and the size distribution of prey to ensure rapid growth just after trout hatch must not exceed trout gape size for proper feeding (Keeley and Grant 2001). We detected the potential for multi-voltinism

for the most abundant taxon, Hydropsychidae, in the warmest stream Taylor Run, which may impact ecosystem productivity on annual scales because multi-voltine systems generally have higher production rates (Downing 1984). Latitude, water temperature, and the subsequent length of growing season can determine the number of annual macroinvertebrate cohorts of some species (Sota 1988), and climate warming may alter macroinvertebrate response to water temperature and photoperiod (Bradshaw and Holzapfel 2006). Having many cohorts in one stream can be an advantage for fish, offering a diversity of size classes, especially for inferior competitors that grow slowly and need smaller food items later in the summer. Size of prey can also influence feeding behavior, successful captures, and growth (Persson 1988). Fish that grow faster will typically occupy better feeding and resting habitat, increasing their survival (Fausch and White 1981), an important factor particularly in streams where brook and brown trout compete (Carlson et al. 2007).

In the streams we studied, terrestrial subsidies represented a major portion (approximately 60%) of potential food and appeared to supplement instream food availability. We hypothesize that the terrestrial contribution may be especially important in streams having low benthic macroinvertebrate biomass, like ChesLen. These findings support previous work showing that terrestrial input of beetles for example can contribute a substantial amount (40%) for actual trout consumption in the northeast (Utz et al. 2011). In other salmonids, terrestrial subsidies are also known to be vital for growth (Wipfli 1997). Trout use of terrestrial invertebrate subsidies also declines with increasing benthic invertebrate biomass, suggesting that productivity in the aquatic environment influences the degree to which brook trout need to utilize terrestrial subsidies (Wilson et al. 2014). Because other factors besides terrestrial food availability, such as fish behavior and competition, may influence actual consumption, future work might investigate these connections. Our study shows that the greatest abundance of flying insects was observed for the stream that had only grass riparian habitat, potentially because there were fewer obstacles with less vegetation to navigate but still enough to act as a windbreaker (Whitaker et al. 2000), although riparian vegetation can increase microhabitat availability and thus insect abundance and diversity (Burke and Nol 1998; Briers and Gee 2004). The two streams having the most contrasting but homogenous riparian habitat condition, either completely open or completely forested, had lower terrestrial biomass, suggesting that high biomass in the intermediately disturbed sites may link terrestrial insect diversity to the legacy of disturbance condition in the riparian habitat (Connell 1978). For instance, Sharitz Run presents the greatest terrestrial biomass and abundance, offering a diverse array of habitats in the riparian buffer zone, with both widening-in-development and fully-open areas.

Trout production values were consistent with those reported in the literature, with the most productive of our sites, Sharitz Run, having values comparable to highly productive streams (Waters 1988). Both Sharitz Run and WCC historically hosted brook trout populations. Now Sharitz Run only has brown trout in the downstream section at the confluence with Doe Run during specific times of the year when the temperature regime is below the thermal tolerance threshold, and Doe Run acts as a brown trout source; during the end of July through August the water temperature regime is too warm to host a trout population in Sharitz (Ouellet and Daniels 2016). Parts of WCC host reproductive brown trout populations (unpublished data Stroud Water Research Center), and the maximum water temperatures are usually under 25 °C, with the presence of several thermal deep pool refugia where the water temperature stays near 18 °C (unpublished data Stroud Water Research Center). The trout production values we estimated for WCC were consistent with previous studies in the same stream (Weisinger 2010).

ChesLen and Taylor Run had the lowest estimates of potential trout production, but ChesLen was the only stream still supporting an actively reproductive wild brook trout population. ChesLen was also the stream that we documented as having the coolest and least variable thermal regime and the largest riparian buffer. Because ChesLen and Taylor Run were similar in trout production estimates, we hypothesize that there may be a tradeoff between food availability and thermal habitat suitability. Even if the food availability is high in Taylor Run, with potential for multiple cohorts and relatively high rates of secondary production, the thermal habitat is unsuitable (maximum values over 22 °C

and daily fluctuation reaching 9 °C), especially for extremely thermally sensitive brook trout (maximum thermal tolerance = 24 °C). Even though production for trout estimates were similar, chironomids like those that dominated in Taylor Run have relatively small body sizes, likely lower lipid content, typically hide in thick algal mats, and would require fish to use extra forging to achieve sufficient energy intake compared to the most abundant taxa in the other streams (Persson 1988; Jellyman and Harding 2016). In contrast, fish in ChesLen had access to thermally suitable habitats (under 20 °C). Food abundance was lower in ChesLen, which could potentially cause higher mortality rates of YOY (Hutchings 1991), yet electrofishing surveys conducted in this stream estimated juvenile biomass to be 4.3 kg/ha, which would qualify as class A by the PA Fish and Boat Commission (PFBC 2009). Therefore, it appears that food abundance is not limiting in ChesLen, even if the values were the lowest of the four studied streams. These results support previous findings showing that even if the food is abundant, if the thermal regime is not suitable, cold water species will be extirpated from historical habitats (Flebbe et al. 2006). We did not examine availability of low flow habitats in pools or behind large boulders or instream wood, and low flow areas are also important elements often created during restoration efforts that could be considered for future studies (Xu et al. 2010). Documenting mortality and growth rate, overall health condition and feeding behaviors of fish, and low-flow habitat in these different streams is an obvious next step.

Conclusion

Taken together, our findings show that terrestrial habitat type, water temperature, and restoration stage can influence food availability in streams. Food abundance is important but ultimately, fish populations may be sustainable if there is just enough food available to insure a positive growth rate. Water temperature may play a more limiting role in determining fish growth rates and restricting the accessibility to ideal habitats in restoration sites. Since riparian restoration is a practice often used to mitigate the impacts of climate change on stream water temperature and quality, we encourage future restoration projects to include thermal suitability thresholds specifically targeting aquatic organisms such as fish in project designs to meet goals of increasing fish production.

Acknowledgments

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

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Lindsey K. Albertson studies the interactions between freshwater organism ecology and physical stream geomorphology. Using experiments, field surveys, and theoretical models, she studies feedbacks between animals, sediment erosion, and flow regimes. She is also interested in the impacts of changing hydrology and species invasions on ecogeomorphic linkages. Her research aims to deepen the understanding of the biological and geomorphological

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