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PRIMARY RESEARCH PAPER

The effects of top-down and bottom-up controls on macroinvertebrate assemblages in headwater streams

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Abstract Headwater stream macroinvertebrates play an important role in processing allochthonous leaf litter, which suggests that bottom-up forces control macroinvertebrates. However, because larvae of stream-breeding salamanders are predators of macroinvertebrates and are abundant consumers in these ecosystems, macroinvertebrates in fishless headwater streams might also be controlled by top-down forces through predation by salamander larvae. The aim of this study was to test if and to what degree taxa richness, abundance, and biomass of macroinvertebrates are affected by bottom-up and top-down forces. We selected headwater streams with high abundances of fire salamander larvae (1.2–2.6 individuals per 1 m of shore length) and manipulated bottom-up and top-down forces on macroinvertebrates by leaf litter addition and by the exclusion of salamander larvae. The amphipod *Gammarus fossarum* Koch, 1836 was the dominant taxon and responded positively to litter addition. Linear models showed that neither predator exclusion nor leaf litter addition affected richness. However, variation in biomass and density were both explained by the individual and joint effects of bottom-up and top-down forces. These findings suggest that macroinvertebrates in these streams are strongly dependent on the organic matter input and salamander larvae, and headwater streams interact strongly with their adjacent terrestrial areas.

Keywords Headwater streams · Leaf litter · Fire salamander · Macroinvertebrates · Predation

Introduction

Forested headwater streams have strong interactions with their adjacent terrestrial areas. Small channel size and closed canopy cover create a physical habitat template of reduced light input, high input of organic matter (leaf litter), and low primary production (Clarke et al., 2008). Thus, the structure and composition of riparian forests are crucial to the functioning of headwater streams (Cummins, 2002; Wallace et al., 1997) in as much as these aquatic ecosystems highly depend on the input of organic matter as the principal carbon source.

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A wide variety of macroinvertebrate taxa colonize leaf litter in these forested streams (Dobson et al., 1992) and use this organic matter both as food and substrate (Richardson, 1992). Additionally, because a large portion of the allochthonous leaf litter is colonized, decomposed, and consumed mainly by shredders (Cummins, 1973), macroinvertebrates are thought to play an important role in leaf litter processing (Cummins, 2002; Gessner et al., 1999). According to Wallace et al. (1997), the exclusion of terrestrial leaf litter input to headwaters can result in a strong bottom-up effect, suggesting macroinvertebrates are controlled by bottom-up forces (via limitation of leaf litter) in these aquatic ecosystems.

Top-down forces should also be considered in the study of trophic interactions, since most ecosystems in nature are tritrophic, meaning they are formed by detritus (or a plant), a detritivore (or a consumer), and a predator (Power et al., 1992). Although field experiments indicate that fishes have a negative and taxon specific effect on macroinvertebrate abundance (Dahl, 1998; Williams et al., 2003; Meissner & Muotka, 2006), information on how top-down forces structure macroinvertebrates in fishless headwater streams is limited (but see Ruff & Maier, 2000; Keitzer & Goforth, 2013).

Larvae of stream-breeding salamanders are predators of stream invertebrates and are abundant consumers in many stream ecosystems, particularly in small, fishless headwater streams (Keitzer & Goforth, 2013; Reinhardt et al., 2013). Although the biomass and tropic position of these larvae suggest that they may influence macroinvertebrates through top-down effects, salamander larvae are often overlooked as top predators in headwater stream ecosystems and there is only a limited understanding of their role (Davic & Welsh, 2004; Keitzer & Goforth, 2013).

Only a small number of studies have examined how bottom-up and top-down forces combine to structure macroinvertebrate communities. While coastal stream predatory insects were only impacted by top-down forces (Sircom & Walde, 2009), lake macroinvertebrates and stream detritivores have been found to be impacted both by bottom-up and top-down forces (Liboriussen et al., 2005; Jabiol et al., 2014). We predicted that if salamanders are present in fishless forested headwater streams, then macroinvertebrate assemblages may also be structured both by bottom-up (via limitation of leaf litter) and top-down (via predation by salamander larvae and other predatory invertebrates) forces. To test this hypothesis, we examined a leaf litter macroinvertebrates fire salamander tritrophic food chain. In our system, the fire salamander (*Salamandra salamandra* (Linnaeus, 1758)), a widely distributed species in central Europe, served as predator. Adult fire salamanders inhabit old broadleaf forests and typically deposit their larvae into first order streams. In these fishless habitats, larvae of salamanders are the top vertebrate predators (Thiesmeier, 2004; Reinhardt et al., 2013).

To study bottom-up and top-down forces under natural conditions, we selected forested headwater streams with high abundance of fire salamander larvae and manipulated bottom-up and top-down forces on macroinvertebrates by leaf litter addition and exclusion of salamander larvae through six, one-week experimental periods from June through September 2013. The general aim of this study was to test if and to what degree taxa richness, abundance, and biomass of macroinvertebrates are affected by the individual and joint effects of leaf litter addition (bottom-up force) and salamander exclusion (top-down force) through summer and early fall, when salamander larvae are present in high density in these systems.

Materials and methods

Site selection

Three fishless headwater streams with fire salamanders were selected for this study: Buechholdenbächli (7° 46′17.79″ E, 47° 27′35.02″ N), Talbächli (7° 47′07.59″ E, 47 °27′19.88″ N), and Teufelgrabenbach (7° 37′38.32″ E, 47° 31′13.32″ N). These streams, in the Rhine River basin, are near Basel, northwestern Switzerland and range in elevation from 300 to 600 m above sea level. They are representative of natural forested streams in Central Europe, are fishless, and have a high density of salamander larvae (1.2–2.6 individuals per one m of shore length). The forest around the streams is mainly composed of beech (*Fagus sylvatica* Linnaeus, 1753) and oak (*Quercus robur* Linnaeus, 1753). The mean annual temperature of the region is 9.6°C, and the mean annual precipitation is 778 mm (MeteoSwiss, 2013).

Experimental design

Historical records of the three selected headwater streams suggested that salamander larvae would be present in these streams. To confirm this prediction, the streams were surveyed for 5 min along a 10-m stream section at three different sites to ensure that salamander densities were sufficient for further experimentation.

Within each stream, four pools containing salamander larva were then selected to test the effects of bottom-up and top-down forces on macroinvertebrate communities. Four plastic trays (10 cm × 10 cm × 2 cm deep) were filled with 3–4 equal-sized pieces of stone from the stream. The first tray contained only pieces of stone in order to mimic the natural stream bottom (Control). A second tray was prepared as for the control then covered also with 5 mm polyester mesh, which excluded not only some large-sized, predatory macroinvertebrate taxa but also early-stage salamander larvae. This was the predator-free treatment (Salamander exclusion, abbreviated as SaEx). The third tray was prepared as for the control and then 1 g of leaf litter was added to it (Litter addition, abbreviated as LiAd). Leaf litter was prepared by collecting leaves from a single beech tree in November 2012 immediately after senescence. The leaves were dried in the lab, kept at air temperature until use, and measured on a Sartorius balance (0.1 mg precision). In the fourth tray both the SaEx and the LiAd were applied (Both). In sum, the experimental design allowed us to test the effects of top-down (SaEx), bottom-up (LiAd) and the joint effects of bottom-up and top-down controls (Both) influences on macroinvertebrate communities.

We installed 48 experimental trays (4 treatments × 4 sites [replicates] × 3 streams), which were then sampled at 1 week intervals over a 6-week period (dates). Although macroinvertebrates can colonize hard substrate in a day (Koetsier, 2002), leaf decay experiments suggest leaf litter needs conditioning to be labile for stream macroinvertebrates, so we sampled trays after 1 week (Gessner & Chauvet, 2002). Sampling of more than 1 week was considered undesirable because of the risk of spates and also a longer conditioning exposure would increase the chance of the trays being removed by passers by.

Field work and identification

Female of the fire salamanders in Central Europe deposit larvae from March until June mostly into headwater streams (Thiesmeier, 2004). To use a period with a high density of larvae (1.2–2.6 individuals per 1 m of shore length), our experiment started on 18 June 2013. Although the winter of 2012/2013 was relatively long in Switzerland, fire salamander larvae density was high in the study streams when the experiment began. Because salamander larvae were never counted in the SaEx treatment, we conclude that the mesh efficiently excluded these predators.

One week after installation, invertebrates were collected from each of the four trays and preserved in 80% ethanol. Material was replaced in each tray after each sampling event. Any trays filled by sediment or displaced from their initial position were eliminated from the experiment. In the laboratory, macroinvertebrates were counted and identified to the lowest practical taxonomic level under a dissecting microscope (Leica MZ-8) using the dichotomous keys of Wolfgang (1989), Lechthaler (2009), and Tachet et al. (2010). The wet weight of each taxon per sample was measured to the nearest 0.1 mg using a Sartorius balance. To reduce the influence of the conservation fluid on the wet weight, each sample was put into water for 1 min prior to weighing and then dried on paper towel for 1 min. External materials like caddisfly cases were removed before weighing (shells of molluscs were included) following Wirth et al. (2010). Biomass was determined as weight per m^2.

To examine the seasonal changes in the macroinvertebrate communities, the experiment was carried out on six dates (from June to September 2013). Because metamorphosed salamander larvae leave streams from July to October (Thiesmeier, 2004), the experiment was terminated in the Buechholdenbächli and Teufelgrabenbach streams on 19 September 2013. As the Talbächli stream dried out in late August, the experiment was prematurely terminated in this stream. Although the planned experiment was predicted to result in 288 experimental units (4 treatment × 3 streams × 4 sites [replicates] × 6 dates), the drying of Talbächli (loss of 64 experimental units) and the loss or damage of 16 additional trays resulted in 208 experimental units for analysis.

Statistical analyses

We examined how taxa richness, macroinvertebrate abundance, and biomass were affected by the individual and joint effects of SaEx and LiAd as well as by sampling date and stream identity using linear models (Crawley, 2007). As taxa richness showed only integer values, we applied a generalized linear model with Poisson distribution, while macroinvertebrate abundance and biomass were modeled with linear models using normal distribution and double square-root transformed values for invertebrate biomass and abundance. A minimal adequate model was selected using corrected Akaike Information Criterion corrected for small sample size (AICc). Statistical models were compared using the difference in AICc values between the best model and competing models (ΔAICc), using the probability that a particular model is the best fit to the data relative to the other models (AICc weight) and using evidence ratio which indicates the level of support for two or more competing models based on AICc weight (see Zeug et al., 2011).

In order to determine the taxa benefited from SaEx and LiAd, we used the indicator species approach proposed by Dufrene & Legendre (1997) rather than usual statistical tests such as ANOVA following Mouilot et al. (2008). All statistical analyses were performed in the R environment (R Core team, 2013).

Results

A total of 4,943 individual macroinvertebrates from seven orders and 14 families were collected during the study (Table 1). The macroinvertebrate community was dominated by Amphipoda: *Gammarus fossarum* (2,316 individuals/m^2, 97.47% of all individuals, mean population biomass 23.46 g/m^2) followed by Ephemeroptera: Baetidae (29 individuals/m^2, 1.23% of total individuals, 0.09 g/m^2 biomass) and Diptera *Simulium* (9 individuals/m^2, 0.004% of total individuals, 0.04 g/m^2 biomass). Other taxa were represented by less than 10 individuals/m^2 (Table 1). Indicator species analysis identified *Gammarus fossarum* as a single indicator taxon of LiAd (indicator value = 0.626, $P = 0.001$). Indicator species analysis did not find any other indicator taxa.

The comparison of alternative statistical models explaining taxa richness showed that the model without any predictor (null model) explains best the observed pattern of taxa richness (Table 2). This model showed that taxonomic richness did not vary enough for differences to be detectable across treatments, and there was no statistical evidence that SaEx, LiAd, or the sampling date changed the taxa richness of macroinvertebrate communities in the experimental trays. However, the low ΔAICc values, small changes in AICc weight values, and moderately increasing evidence ratio suggest that there is no strong evidence for one model over the others (Table 2). The second best model, where the value of ΔAICc < 2, predicts that only LiAd had an effect on macroinvertebrate taxa richness (Table 2).

We also compared the performance of different statistical models predicting macroinvertebrate abundance (Fig. 1) and found that the best-fit model includes the effects of SaEx, LiAd, date, as well as the interaction of SaEx and LiAd (Table 3). This model showed that SaEx and LiAd had a positive effect on macroinvertebrate abundance while sample date and the interaction of SaEx and LiAd had a negative effect (Table 4). The decreases in the mean density of macroinvertebrates over the six sampling dates were as follows: 269.2, 186.4, 123.8, 95.0, 95.0, and 100 individuals/m^2. The second best model indicates that LiAd and sample date had an effect on macroinvertebrate abundance, while the other alternative models showed ΔAICc values higher than 2 (Table 3).

The linear model using salamander exclusion, litter addition, sample date, and the interaction of salamander exclusion and litter addition explains best the biomass of macroinvertebrates (Table 5). This model showed that salamander exclusion and litter addition had a positive effect on macroinvertebrate biomass, while the interaction of these terms had a marginally significant negative effect (Table 6, Fig. 2). This model also indicated that the biomass of the macroinvertebrates decreased with time (Table 6). Other alternative statistical models also explained well the observed patterns in biomass (Table 5). Three of these had an evidence ratio smaller than 2, all of them indicated an effect of litter addition and sample date, two of them the effect of salamander exclusion, and only one the effect of stream identity and the interaction of salamander exclusion and litter addition (Table 5).

Table 1 Mean density of taxa (individuals/m^2/sampling occasion) in the different treatments

Order	Family	Taxon	Treatment			
			Control	Salamander exclusion	Litter addition	Both
Tricladida	Dugesiidae	*Dugesia gonocephala* (Duges, 1830)	9.62	0	5.77	15.38
Amphipoda	Gammaridae	*Gammarus fossarum* Koch, 1836	1546.15	1921.15	3023.08	2775.00
Diptera	Dixidae	*Dixa* sp.	1.92	0	0	0
	Simuliidae	*Simulium* sp.	5.77	13.46	11.54	5.77
	Stratiomyidae		0	0	1.92	0
	Pediciidae	*Dicranota* sp.	0	1.92	3.85	5.77
	Tipulidae	*Tipula* sp.	1.92	0	0	0
Ephemeroptera	Baetidae	*Baetis* sp.	23.08	21.15	42.31	30.77
	Ephemeridae		1.92	0	0	0
	Heptageniidae	*Heptagenia* sp.	1.92	0	5.77	1.92
	Leptophlebiidae		1.92	5.77	3.85	3.85
Plecoptera	Perlodidae		1.92	0	0	3.85
Trichoptera	Polycentropodidae	Plectrocnemia	0	1.92	1.92	0

Table 2 The best five statistical models explaining taxa richness of macroinvertebrates

Model	AICc	ΔAICc	AICc weight	Evidence ratio
	503.80	0.00	0.23	1.00
Litter addition	504.27	0.47	0.19	1.26
Salamander exclusion	505.83	2.04	0.08	2.77
Date	505.84	2.04	0.08	2.77
Salamander exclusion + Litter addition	506.32	2.52	0.07	3.53

Models are arranged from the best to worst based on evidence ratios. *AICc* Akaike's Information Criterion corrected for small sample size, *ΔAICc* the difference in AICc values between the best model and competing models, *AICc weight* the relative likelihoods of a model given the data, *evidence ratio* relative likelihood of each model versus the best model

Discussion

Our results show for the first time that macroinvertebrate assemblages in fishless headwater streams are structured both by bottom-up and top-down forces, if larvae of fire salamander are present. These findings suggest that macroinvertebrates in these streams are strongly dependent on the bottom-up organic input and the larvae of salamanders that have a top-down effect on macroinvertebrates in these systems.

The communities we examined were dominated by a single species and only three taxa were represented by more than 10 individuals. Although the use of the one-week experimental period was necessary to avoid the risk of spates, our experimental design indicate only early colonization events of macroinvertebrates, where leaves might provide both substrate and food for macroinvertebrates (Richardson, 1992; Gessner & Chauvet, 2002). The observed significant differences among treatments indicate that stream macroinvertebrates colonize the substrate very quickly (Townsend & Hildrew, 1976). Compared to other studies (Heino et al., 2003; Schmera & Erős, 2004), the recorded number of macroinvertebrate taxa was low. A possible explanation for this is that small headwater streams have low taxa richness (Heino et al., 2005; Clarke et al., 2008; Schmera et al., 2012). Another explanation is that the colonization of the trays used in our

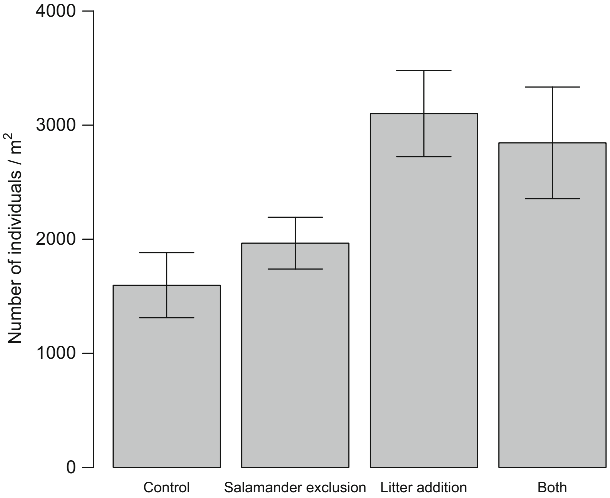

Fig. 1 Distribution of macroinvertebrate abundance (individuals/m^2) among different treatments. Bars show mean values while *vertical lines* standard errors

Table 3 The best five statistical models explaining abundance of macroinvertebrates

Model	AICc	ΔAICc	AICc weight	Evidence ratio
SaEx + LiAd + Date + SaEx:LiAd	268.46	0.00	0.41	1.00
LiAd + Date	269.82	1.36	0.21	1.98
SaEx + LiAd + Date + Stream + SaEx:LiAd	270.50	2.04	0.15	2.77
SaEx + LiAd + Date	271.03	2.57	0.11	3.62
LiAd + Stream + Date	271.82	3.36	0.08	5.36

Models are arranged from the best to worst based on evidence ratios. *AICc* Akaike's Information Criterion corrected for small sample size, *ΔAICc* the difference in AICc values between the best model and competing models, *AICc weight* the relative likelihoods of a model given the data, *evidence ratio* relative likelihood of each model versus the best model

SaEx salamander exclusion, *LiAd* litter addition, *SaEx:LiAd* interaction of salamander exclusion and litter addition

Table 4 The summary table of the minimal adequate model explaining macroinvertebrate abundance using different predictors

Predictors	Estimate	SE	*t*-value	*P*
Salamander exclusion (SaEx)	0.195	0.089	2.188	<0.001
Litter addition (LiAd)	0.418	0.089	2.188	0.029
Date	−0.026	0.006	−4.253	<0.001
SaEx:LiAd	−0.271	0.126	−2.152	0.033

SaEx:LiAd interaction of salamander exclusion and litter addition

experimental design was only through the water column, and not the substratum. Therefore, only a highly mobile fauna living close to the surface was sampled (Weigelhofer & Waringer, 2003).

The macroinvertebrate communities examined were dominated by the amphipod *Gammarus fossarum,* and this species responded positively to litter addition. This species is a shredder (see Cummins, 1973) and is widespread in Central Europe (Meijering, 1972). *Gammarus fossarum* is the main food source for the larvae of fire salamander in headwater habitats (Thiesmeier, 1982; Ruff & Maier, 2000).

Litter input from riparian vegetation has been identified as a major energy component of stream food

Table 5 The best five statistical models explaining biomass of macroinvertebrates

Model	AICc	ΔAICc	AICc weight	Evidence ratio
SaEx + LiAd + Date + SaEx:LiAd	−159.8	0.00	0.27	1.00
LiAd + Date	−159.4	0.37	0.22	1.20
SaEx + LiAd + Date + Stream + SaEx:LiAd	−158.6	1.16	0.15	1.79
SaEx + LiAd + Date	−158.6	1.19	0.15	1.82
LiAd + Stream + Date	−158.2	1.51	0.13	2.13

Models are arranged from the best to worst based on evidence ratios. *AICc* Akaike's Information Criterion corrected for small sample size, *ΔAICc* the difference in AICc values between the best model and competing models, *AICc weight* the relative likelihoods of a model given the data, *evidence ratio* relative likelihood of each model versus the best model

SaEx salamander exclusion, *LiAd* litter addition, *SaEx:LiAd* interaction of salamander exclusion and litter addition

Table 6 The summary table of the minimal adequate model explaining macroinvertebrate biomass

Predictors	Value	SE	*t*-value	*P*
Salamander exclusion (SaEx)	0.066	0.032	2.072	0.039
Litter addition (LiAd)	0.148	0.032	4.654	<0.001
Date	−0.011	0.002	−5.038	<0.001
SaEx:LiAd	−0.081	0.044	−1.808	0.072

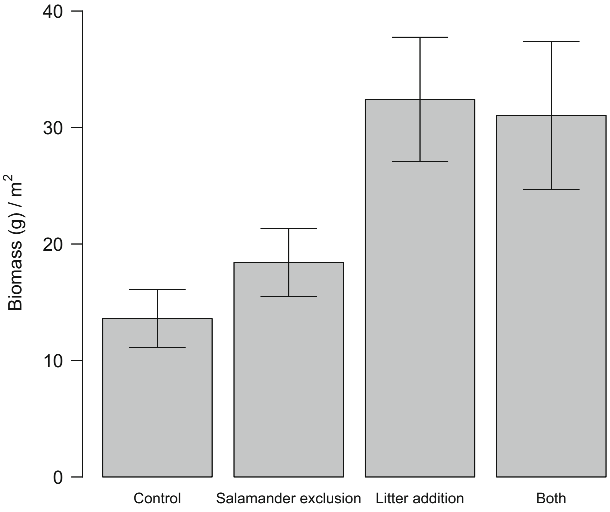

Fig. 2 Distribution of macroinvertebrate biomass (g/m^2) among different treatments. Bars show mean values while *vertical lines* standard errors

webs (Cummins, 1973; Wallace et al., 1997). Although the best-fit statistical model suggested that taxa richness did not respond to any treatment and indicator analyses showed that only *G. fossarum* responded to litter addition, the second best statistical model indicated that litter addition had an impact on taxa richness. Our results, which show that macroinvertebrate abundance and biomass increases in response to litter addition, are in agreement with other studies reporting that stream macroinvertebrates are under pressure from a strong bottom-up effect (Flory & Milner, 1999; Johnson & Wallace, 2005). These findings are in agreement with the observation that shredding macroinvertebrates show aggregated spatial distribution (Murphy et al., 1998) and mostly follow the patchy distribution of leaf packs on the stream bottom (Dobson & Hildrew, 1992; Schmera, 2004). The increasing abundance and biomass in response to the exclusion of salamanders suggests that macroinvertebrates are also under predatory pressure from salamanders. Although experimental studies have reported similar results (Huang & Sih, 1991; Keitzer & Goforth, 2013; Reinhardt et al., 2013), our study is the first to simultaneously examine the effects of leaf litter and salamander larvae on stream macroinvertebrates. The minimal adequate models examining macroinvertebrate abundance and biomass had an estimate value for litter addition that was always larger than the estimate value for salamander exclusion. Moreover, the alternative models more frequently included litter addition than salamander exclusion. Together, this suggests that bottom-up forces have a stronger impact on macroinvertebrate abundance and biomass than top-down forces. On the other hand, the negative interaction between leaf litter addition and salamander exclusion suggests that the combination of salamander exclusion and litter addition does not increase macroinvertebrate abundance and biomass in the way that would be assumed based on the additive effect of individual treatments. A possible explanation is that the mesh size used to exclude salamander larvae could easily have also excluded larger *Gammarus fossarum* individuals (length >8 mm), which was by far the most abundant macroinvertebrate species. The control trays are likely to have provided little protection from predation by the salamander larvae, and as expected, abundance/biomass was reduced in comparison to mesh-covered trays. In trays with leaves, abundance/biomass was always higher than in trays without leaves, as again expected. In these trays, it was thought that leaves provided cover and protection from predation, preventing the salamander larvae from reducing the *Gammarus* abundance so easily. All of these findings suggest that our systems can easily be modeled by a litter amphipod salamander larvae food chain with a stronger bottom-up and a weaker top-down control.

In conclusion, we demonstrated that macroinvertebrate abundance and biomass in fishless headwater streams were structured both by bottom-up and top-down forces. We found that headwater streams interact strongly with adjacent terrestrial areas and the riparian buffer zone is extremely important for these streams. This buffer zone provided food source for macroinvertebrates in the form of allochthonous leaf litter, and the top predators of these streams, the salamander larvae, come from this zone. In sum, our study emphasizes the importance of the riparian buffer zone in the structure of macroinvertebrate communities and also the function of headwater streams (Richardson & Danehy, 2007; Clipp & Anderson, 2014; Olson et al., 2014).

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