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Spatial and seasonal variation in the ecological significance of nutrient recycling by larval salamanders in Appalachian headwater streams

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Abstract. Salamanders are abundant consumers in many temperate streams and may be important recyclers of biologically essential nutrients, but their ecological role is poorly understood. The ecological significance of nutrient recycling by salamanders may vary spatially and seasonally because of their potentially patchy distribution in streams and the dynamic nature of stream hydrology and other nutrient fluxes. We examined the spatial and seasonal variation of salamander-driven nutrient recycling in 3 headwater streams in the southern Appalachian Mountains. We quantified the aggregate areal excretion rates of N (NH_4^+-N) for the larvae of the 2 most abundant salamander species in these steams before and after leaf fall to examine spatial and seasonal variation in the supply of nutrients from salamanders. We used short-term nutrient additions in each stream to examine temporal heterogeneity in the ecosystem demand for NH_4^+-N. Before leaf fall, salamanders were capable of meeting ~10% of the ecosystem demand for NH_4^+-N and could turn over the ambient nutrient pool in ~3 km. The significance of this contribution declined to ~3% after leaf fall and the turnover length increased 7×. The ecological significance of salamander nutrient excretion varied by as much as 17× within streams and was as high as 30% of the nutrient demand in some stream sections, a result suggesting that salamanders may create biogeochemical hotspots in these nutrient-limited ecosystems. Thus, salamanders appear to be capable of contributing substantially to stream nutrient cycles through the excretion of limiting nutrients and may be underappreciated members of headwater stream ecosystems, particularly at small spatial scales. However, this contribution varied substantially seasonally and spatially.

Key words: consumer-driven nutrient recycling, amphibian ecological roles, headwater stream, salamander, *Desmognathus quadramaculatus*, *Eurycea wilderae*.

Amphibian populations are declining globally (Stuart et al. 2004, Wake and Vredenburg 2008), and this decline could have substantial consequences for terrestrial and aquatic ecosystems (Whiles et al. 2006). However, the ecological roles of many amphibians are poorly understood, so the ecosystem-level consequences of these population declines are difficult to estimate. For example, the catastrophic decline of anurans in tropical streams of Central America has had substantial effects on these ecosystems (Ranvestel et al. 2004, Connelly et al. 2008, Colon-Gaud et al. 2009, 2010, Rugenski et al. 2012), but the importance of these species was largely unknown until many were in the process of local extirpation by disease (Lips et al. 1996). Larval salamanders are the most abundant amphibians in many North American streams, where their biomass can be >10 g/m^2 (Davic and Welsh 2004). They are environmentally sensitive species, whose abundance and diversity are expected to change in response to multiple interacting factors (Milanovich et al. 2010, Blaustein et al. 2011). However, the ecological implications of their potential decline or loss from stream ecosystems are largely unknown (Davic and Welsh 2004).

Larval salamanders of stream-breeding species are generalist consumers of aquatic insects and reach their highest abundance and diversity in small, fishless streams (Petranka 1998). Salamanders may affect stream ecosystems by recycling biologically important nutrients, such as N and P, a key ecosystem process performed by many freshwater consumers (Vanni 2002). By consuming biologically unavailable organic nutrients and releasing them in dissolved inorganic forms, freshwater consumers can supply nutrients to primary producers and heterotrophic

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microbes that form the base of aquatic food webs (Vanni 2002). Despite their high biomass in temperate forests (Burton and Likens 1975b), salamanders may play a minor role as nutrient sinks in forest nutrient cycles (Burton and Likens 1975a, but see Milanovich 2010, J. R. Milanovich and M. E. Hopton, US Environmental Protection Agency, unpublished data), but their role as nutrient recyclers in streams is poorly understood.

Larval salamanders are patchily distributed within streams as the result of abiotic factors, such as flow rate and stream substratum composition (Davic and Orr 1987, Tumlison et al. 1990, Baumgartner et al. 1999, Barr and Babbitt 2002, Bruce 2003, Smith and Grossman 2003), and biotic factors that include competition and predation (Resetarits 1991, 1995, Wiltenmuth 1997, Barr and Babbitt 2002, 2007, Lowe and Bolger 2002). Temporal patterns in larval salamander communities also can be influenced by species-specific life-history attributes because species vary in the timing of hatching, length of larval period, size at metamorphosis, and subsequent timing of stream emergence (Petranka 1998). This heterogeneity in salamander distribution would increase variability in the rate they supply nutrients to stream ecosystems both temporally and spatially with potentially important implications for stream nutrient cycling. For example, the spatial distribution of consumers can create biogeochemical hotspots and moments, which are areas and periods of high nutrient cycling and biological activity (McClain et al. 2003). Some evidence exists for spatial variation in stream consumer nutrient recycling (e.g., McIntyre et al. 2008, Benstead et al. 2010, Moslemi et al. 2012). Temporal variation has been less well documented (Benstead et al. 2010), but may also be important in determining the ecosystem-level significance of nutrient recycling by salamanders.

The ecological significance of nutrient recycling by salamander communities will be mediated by spatial and temporal heterogeneity in other components of stream nutrient cycles, which can be considerable (Mulholland et al. 1985, Martí and Sabater 1996, Simon et al. 2005, Hoellein et al. 2007, Valett et al. 2008). Headwater streams in deciduous forests are heterotrophic ecosystems supported by seasonal leaf-litter inputs (Wallace et al. 1997) that drive temporal patterns in nutrient dynamics (Mulholland et al. 1985, Valett et al. 2008). Nutrient demand increases following leaf fall because higher standing stocks of organic matter in streams support and stimulate biological activity (Valett et al. 2008). These ecosystems also are characterized by very low ambient nutrient concentrations that limit productivity (Gulis and Suberkropp 2003, Cross et al. 2006, Greenwood et al. 2007, Rosemond et al. 2008). Thus, salamanders may contribute substantially to headwater stream nutrient cycling, but the significance of this contribution may vary both seasonally and spatially.

We investigated nutrient recycling by larval salamanders in southern Appalachian headwater streams to examine: 1) the ecosystem-level significance of nutrient recycling by larval salamanders and 2) spatial and temporal variation in the significance of this contribution. We predicted that larval salamanders would contribute substantially to nutrient cycles because their high densities would result in a large supply of nutrients to heterotrophic bacteria and fungi that form the base of detritus-based food webs. We expected that strong spatial variation in this contribution would result from the patchy distribution of salamanders and that seasonal changes in other nutrient fluxes would mediate the ecosystem-level significance of this contribution.

Methods

Study site

We conducted this study in 3 unnamed headwater streams (hereafter, Streams A, B, and C) in the Nantahala National Forest, a large forested tract of land in the Appalachian Mountains of southwestern North Carolina, USA (lat 35°1′N, long 83°W). In each stream, we established a 50-m study reach >20 m upstream from the nearest road crossing. Stream reaches were predominantly riffle habitat with an occasional pool and had mixed gravel, cobble, and sand substrata. Streams were similar in size (mean ± SE, wetted width = 1.66 ± 0.09 m, depth = 8.02 ± 0.67 cm, discharge = 3.89 ± 1.02 L/s) and had low ambient nutrient concentrations (NH_4^+-N = 6 ± 0.92 μg/L, soluble reactive P [SRP] = 6 ± 1.46 μg/L). Streams were heavily shaded by a dense canopy (~85%) of predominantly red maple (*Acer rubrum*), poplar (*Liriodendron* spp.), and oak (*Quercus* spp.) with a thick understory of rhododendron (*Rhododendron* spp.).

Study organisms

Southern Appalachian stream-breeding salamanders (family: Plethodontidae) include up to 7 species that potentially occur in the study streams. We observed 5 of these species, including *Eurycea wilderae*, *Desmognathus quadramaculatus*, *Desmognathus ocoee*, *Desmognathus monticola*, and *Gyrinophilus porphyriticus*. However, *E. wilderae* and *D. quadramaculatus* accounted for >90% of the observed salamanders

and were the only species that occurred in sufficient numbers to estimate densities. *Eurycea wilderae* are generally smaller than *D. quadramaculatus*, and reported densities for *E. wilderae* range from 1 to >90 larvae/m^2 (Johnson and Wallace 2005, Peterman and Truslow 2008, Nowakowski and Maerz 2009). *Desmognathus quadramaculatus* densities are highest in small streams (Bruce 1985), but density estimates are rare and range from 2 to 29 larvae/m^2 (Davic and Welsh 2004, Milanovich 2010).

Density estimation

We used a nondestructive sampling technique to estimate larval abundance based on spatially replicated counts. We placed leaf-litter baskets every 5 m along each study reach and sampled from 1 September to 4 September 2010 (before leaf fall), 18 October to 21 October 2010 (during leaf fall), and 20 November to 23 November 2010 (after leaf fall). We constructed litter baskets from plastic plant pallets (56 × 23 × 6 cm) covered in 1.75-cm mesh netting (Peterman and Truslow 2008, Nowakowski and Maerz 2009). We filled litter baskets 1 wk before surveys with dry leaf litter collected from the surrounding riparian area, placed them in the stream, and secured them with 1 large cobble. We checked litter baskets for larvae as described by Keitzer and Goforth (2012). We identified larvae, counted and measured them for snout-to-vent length (SVL; mm) before releasing them at the upstream end of the litter basket. This passive sampling method produces density estimates similar to those found with active salamander sampling methods (Peterman and Truslow 2008, Nowakowski and Maerz 2009).

We used an open-population binomial mixture model (Kery and Schaub 2012) to estimate the abundance of *E. wilderae* and *D. quadramaculatus* larvae separately. We assessed goodness-of-fit for the models with posterior predictive checks using the χ^2 test statistic as our measure of discrepancy (Kery and Schaub 2012). We fit models with JAGS (Plummer 2003) in R (version 0.99; R Project for Statistical Computing, Vienna, Austria) using the *rjags* package (Plummer 2011). We calculated densities by dividing the mean estimates of abundance by the area of the litter basket (0.13 m^2). Extrapolating these estimates to the whole stream may have resulted in overestimates of salamander densities, but our results are within the range reported in several other studies from this area (see Results and Discussion).

Nutrient excretion

We captured larvae for measurements of nutrient excretion with a dip net from streams at Coweeta Hydrological Laboratory, Macon County, North Carolina, USA from 1 June to 1 August 2009 and from streams in the Nantahala National Forest from 15 August to 1 December 2010. We put larvae of the same species in Whirl-Pak® bags (Nasco, Fort Atkinson, Wisconsin) with 300 mL of filtered (Type A/E; Pall-Gelman, Ann Arbor, Michigan) stream water for 60-min incubations. Bags contained 1 to 16 similarly sized individuals, and we placed them in shallow areas of the stream during incubations to reduce stress and maintain a constant water temperature.

We filtered water samples in the field and placed them on ice in the dark until analysis that day for NH_4^+-N. We froze water samples for quantifying SRP for later analysis according to Murphy and Riley (1962). However, the amounts of excreted SRP were generally below our detection limits, and therefore, we focused on NH_4^+-N dynamics. We used fluorometry (10-AU; Turner Designs, Sunnyvale, California) and a standard additions procedure to quantify NH_4^+-N (Holmes et al. 1999, Taylor et al. 2007). The difference in the amount of NH_4^+-N in larval incubation bags compared to in a control bag that was treated the same but did not contain larvae was divided by the number of individuals in the bag to calculate per capita N excretion rates (μg NH_4^+-N/h). We used analysis of covariance (ANCOVA) including species, average size (SVL), and number of individuals present in an incubation bag as covariates to examine the potential for crowding in incubation bags to increase salamander stress levels, which can influence excretion rates (Whiles et al. 2009).

We used a model-selection procedure based on Akaike's Information Criterion adjusted for small sample size (AIC_c) to assess models describing per capita excretion rates. The variables used in these models were species, the stream where measurements were made, the month from which samples were taken, and the average SVL of the salamanders used in the incubation. Species and stream were included because each can influence excretion rates for other aquatic organisms (Vanni 2002, Vanni et al. 2002, Small and Pringle 2010, El-Sabaawi et al. 2012a, b, Lauridsen et al. 2012). The month in which a sample was taken was treated as a categorical factor and was included as a surrogate for seasonal changes in water temperature, which may influence excretion rates (Schaus et al. 1997, Devine and Vanni 2002, Vanni 2002). The mean size of salamanders used in an incubation bag was included as an interaction term with all covariates in each model because size has a large influence on excretion rates for other aquatic organisms (Vanni 2002, Vanni et al. 2002). AIC_c values were used to rank models and select those that best

described per capita excretion rates, which were models with the lowest AIC_c value and ≤ 7 AIC_c units of this model (Burnham and Anderson 2002).

Stream nutrient dynamics

Seasonal variation in nutrient cycles was assessed with short-term additions (<3 h) of NH_4^+-N and SRP done twice in each stream, once before (31 August, 13 September, and 14 September 2010) and again after leaf fall (12 November, 13 November, and 17 November 2010). We dripped nutrients (QBG; Fluid Metering, Inc., Syosset, New York) continually to increase levels ~5× above ambient concentrations and added Cl^- (NaCl) as a conservative tracer to account for dilution and to calculate discharge (Webster and Valett 2006). We collected water samples every 10 to 15 m once a plateau in dissolved NaCl, measured as conductivity, had been reached. We filtered water samples in the field and kept them on ice until NH_4^+-N could be quantified the same day using the methods described previously. We used the decline in background-corrected NH_4^+-N concentration with distance from addition point to calculate nutrient uptake length, uptake velocity, and areal uptake rates (Stream Solute Workshop 1990). Seasonal changes in these parameters were compared with 1-sided paired *t*-tests with degrees of freedom adjusted according to Welch's approximation (Welch 1947) to determine if uptake velocity and areal uptake rates increased and uptake length decreased after leaf fall. We used a 2-sided paired *t*-test with the degrees of freedom adjusted according to Welch's approximation to examine a potential seasonal change in discharge.

Community-level nutrient recycling

We used the model-averaged estimates for the best set of models describing per capita excretion rates and a randomization procedure to estimate the size of individuals at a site (litter basket) to estimate community-level nutrient recycling. The randomization procedure consisted of randomly sampling the size of individuals at a site based on the known species-specific size distribution at that site. We based the size distribution on the mean and standard deviation of the size (SVL) of individuals actually captured and measured at a site. We used this size distribution to assign sizes randomly to individuals based on the estimated density for that species, site, and month. When individuals were assigned values lower than the minimum or greater than the maximum sizes observed for all individuals measured during the study, we replaced the size with either the minimum or maximum size as needed. We estimated the excretion rate of an individual from the model-averaged estimates. We calculated species-specific total areal excretion rates at a site by summing these estimated excretion rates. We repeated this procedure 500× at each site and for each season (before and after leaf fall) to calculate the mean estimated areal excretion rate at a site. We calculated aggregate areal excretion rates for the larval community by summing the mean values for both species. We used the proportion of ecosystem demand, measured as the areal uptake rate, supplied by the areal excretion rates to examine the ecosystem-level significance of nutrient recycling by larvae (McIntyre et al. 2008).

To examine the contribution of larval nutrient excretion to the ambient nutrient pool, we calculated volumetric excretion rates (E_v; μg NH_4^+-N/L) of channel units according to McIntyre et al. (2008), where $E_v = (E_A AT)/V$, E_A is the areal excretion rate (μg NH_4^+-N m^{-2} h^{-1}), A is the reach area (m^2), T is the travel time (h) through a channel unit, and V is the volume (m^3) of a channel unit. Channel units were defined as 5-m units between litter baskets in each 50-m reach. We used the average areal excretion rate, wetted width (m), water depth (m), and flow rate (m/s) of the upstream and downstream sites of a channel unit in these calculations. We predicted turnover length (m), the stream length required to turnover the ambient nutrient pool, from the cumulative volumetric excretion from upstream to downstream channel units.

Seasonal, spatial, and interspecific variation in the contribution of larval excretion to stream nutrient cycling

We examined seasonal and spatial variation in the density of larvae, aggregate excretion rates, ecosystem-level significance of excretion, and total volumetric excretion with linear mixed models that included month as a fixed effect and sites nested within streams as random intercepts to account for autocorrelation that may have resulted from repeated measures. We analyzed density estimates with a Poisson error distribution, whereas we used a Gaussian error distribution for other response variables. Likelihood ratio tests were used to assess the significance of month, with a significant effect interpreted as evidence for temporal variation. We examined small-scale spatial variation by calculating the coefficient of variation (CV) among sites within each stream for each month and by examining box plots. We used the channel unit as a random effect in our analysis of volumetric excretion to account for repeated measures and to examine small-scale spatial variation. We used a paired Wilcoxon signed rank test to compare the areal excretion rates among species

TABLE 1. Model selection results based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for models describing per capita N excretion rates. N was measured as NH_4^+-N. The snout-to-vent length (SVL) of individuals was included as a covariate in all models except the null model. The number of parameters (K), change in AICc value (ΔAIC_c), Akaike weight (ω_i), and cumulative Akaike weight (Cum. ω_i) are shown. Bold indicates supported models.

Model	K	AIC_c	ΔAIC_c	ω_i	Cum. ω_i
SVL	**3**	**99.54**	**0.00**	**0.66**	**0.66**
Species	**5**	**101.57**	**2.03**	**0.24**	**0.90**
Month	**13**	**103.68**	**4.13**	**0.08**	**0.98**
Month, species	15	106.70	7.16	0.02	1
Stream	17	110.77	11.23	0	1
Null	2	112.48	12.94	0	1
Species, stream	19	116.81	17.27	0	1
Month, stream	27	132.68	33.13	0	1
Full	29	138.54	38.99	0	1

because data failed to meet normality assumptions of a paired *t*-test, which we used to compare differences in log(*x*)-transformed volumetric excretion rates among species and to compare turnover distances before and after leaf fall. We ran statistical analyses in R with *lme4* (Bates et al. 2012), *AICcmodavg* (Mazerolle 2012), and *car* (Fox and Weisberg 2011) packages.

Results

Nutrient excretion rates

We examined 42 excretion samples for *D. quadramaculatus* ($n = 79$ individuals) and 30 for *E. wilderae* ($n = 290$ individuals). The mean number of individuals used in a single incubation bag was 2 for *D. quadramaculatus* (range = 1–6) and 10 for *E. wilderae* (range = 6–16). The number of individuals in incubation bags did not affect nutrient excretion ($F_{1,68} = 0.02$, $p = 0.9$) and did not interact with species identity to affect nutrient excretion ($F_{1,68} = 0.003$, $p = 0.91$).

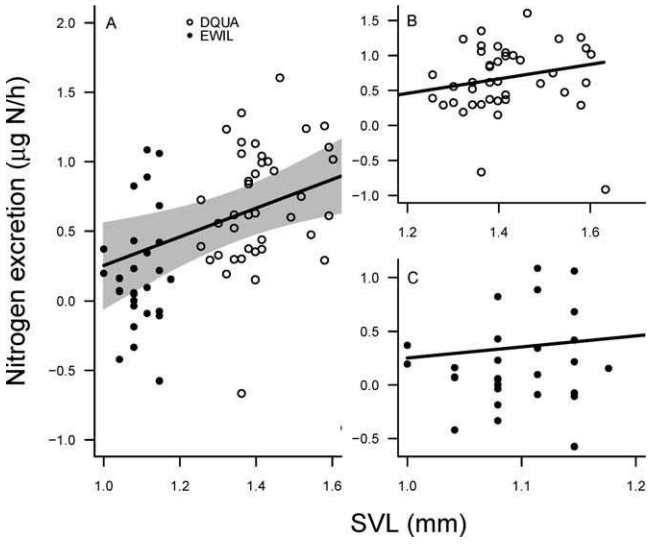

FIG. 1. Relationship between $\log_{10}$(N excretion rates) and $\log_{10}$(snout-to-vent length) (SVL) for all salamanders combined (A), *Desmognathus quadramaculatus* (DQUA) (B), and *Eurycea wilderae* (EWIL) (C). The solid black line shows the predicted model-averaged relationship and the gray shading is the predicted value ± 1 SE.

The model containing the average SVL of individuals used in incubations had the lowest AIC_c value, whereas models containing either species identity or incubation month were ≤ 7 AIC_c units of the lowest model. Therefore, we retained the latter for model-averaged excretion estimates (Table 1). SVL had a positive effect on per capita excretion rates (Fig. 1A), so the larger species, *D. quadramaculatus*, had higher per capita excretion rates (Fig. 1B) than *E. wilderae* (Fig. 1C). Per capita excretion rates also appeared to decrease slightly in months that were later in the sampling period, but this effect was minimal compared to the influence of the average SVL of individuals (Fig. 2A–F).

Density estimates

The models used to estimate abundance provided an adequate fit for both species (Bayesian *p*, *E. wilderae* = 0.48, *D. quadramaculatus* = 0.47). Total larval density estimates declined significantly from September to November ($\chi^2_2 = 77.88$, $p < 0.001$), with a similar pattern occurring across streams for *D. quadramaculatus* ($\chi^2_2 = 51.39$, $p < 0.001$) and *E. wilderae* ($\chi^2_2 = 32.47$, $p < 0.001$). Considerable small-scale variation occurred in both species as indicated by the CV and box plots of within-stream densities (Fig. 3A–C).

Stream nutrient dynamics

We increased ambient NH_4^+-N levels 4× on average during short-term nutrient additions (range

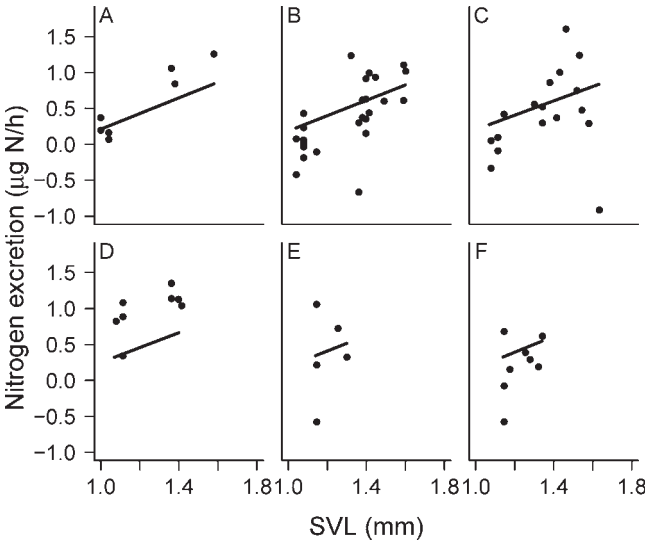

FIG. 2. The relationship between $\log_{10}$(N excretion rates) and $\log_{10}$(snout-to-vent length) (SVL) for measurements made in June (A), July (B), August (C), September (D), October (E), and November (F). The solid line shows the model-average predicted relationship.

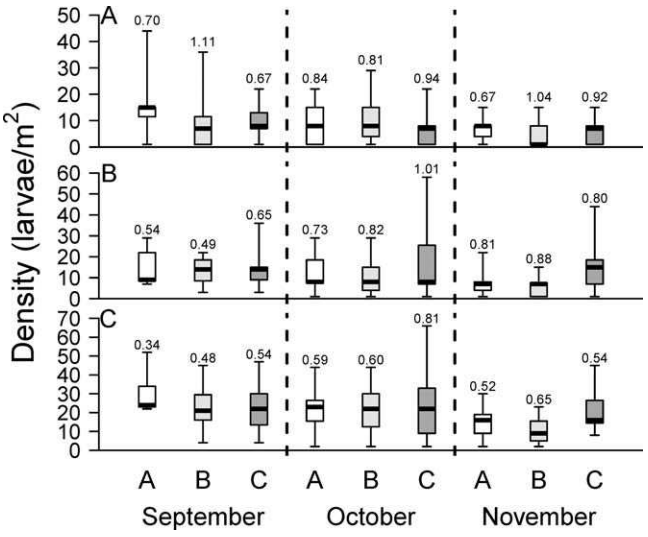

FIG. 3. Density estimates of *Desmognathus quadramaculatus* (A), *Eurycea wilderae* (B), and both combined (C) for each stream and season. Lines in boxes show medians, box ends show quartiles, and whiskers show the 10th and 90th percentiles of the density estimates. The coefficient of variation (CV) calculated for within stream variation is shown above the box plot.

= 2.5–6) and observed strong seasonal changes in nutrient dynamics and discharge in all streams (1-sided paired *t*-test, $t_2 = 3.60$, $p = 0.035$; Table 2). Nutrient uptake velocity was greater after than before leaf fall ($t_2 = 5.28$, $p = 0.017$), but discharge ($t_2 = 2.84$, $p = 0.10$) and uptake length ($t_2 = 0.75$, $p = 0.26$) did not differ before and after leaf fall.

Ecosystem-level significance of nutrient excretion

Mean aggregate areal excretion rate was 73 ± 7 µg NH_4^+-N m^{-2} h^{-1} before leaf fall and declined significantly to 39 ± 4 µg NH_4^+-N m^{-2} h^{-1} after leaf fall ($\chi^2_1 = 19.23$, $p < 0.001$). Small-scale spatial variation was evident, and CVs for within stream variation ranged from 0.47 to 0.84 (Fig. 4A). The mean areal excretion rate of *D. quadramaculatus* was significantly higher (35 ± 4 µg NH_4^+-N m^{-2} h^{-1}) than that of *E. wilderae* (21 ± 2 µg NH_4^+-N m^{-2} h^{-1}) ($W = 693$, $p = 0.008$). *Desmognathus quadramaculatus* had higher mean areal excretion rates, but areal excretion by *E. wilderae* was greater than that of *D. quadramaculatus* in several areas (Fig. 5A–F).

The ecosystem-level significance of nutrient excretion by salamanders was significantly higher before than after leaf fall ($\chi^2_2 = 75.49$, $p < 0.001$) (Fig. 4B). The salamander assemblage was capable of contributing 10 ± 1% of the ecosystem demand before and 3 ± 0.3% after leaf fall. Seasonal differences in volumetric excretion were significant ($\chi^2_1 = 178.95$, $p < 0.001$), and considerable small-scale spatial variation was present within streams (Fig. 4C). This variation led to a significant increase in turnover distances ($t_2 = 4.67$, $p = 0.04$), which were 3.1 ± 1.2 km before and 20 ± 3.8 km after leaf fall. Total volumetric excretion by *D. quadramaculatus* (8 ± 2 ng NH_4^+-N/L) was higher than that by *E. wilderae* (5 ± 2 ng NH_4^+-N/L) ($t_{59} = 3.26$, $p = 0.002$).

Discussion

Seasonal patterns in the ecosystem-level significance of salamander-driven nutrient recycling

Salamanders clearly contributed to nutrient recycling in our study streams, and a distinct seasonal pattern was present in the ecosystem-level significance of salamander-driven nutrient recycling. Before leaf fall, salamanders were capable of meeting ~10% of the stream demand for NH_4^+-N, which is similar in magnitude to a number of other freshwater consumer assemblages from a variety of biomes (e.g., Grimm 1988, Small et al. 2009, Benstead et al. 2010, Wilson and Xenopoulos 2011, Moslemi et al. 2012, J. R. Milanovich and M. E. Hopton, unpublished data), but is significantly less than has been observed for some fish assemblages in tropical streams (e.g., McIntyre et al. 2008, Small et al. 2011) or invasive snails in temperate streams (Hall et al. 2003). This result is not surprising given the biomass and excretion rates of salamanders compared to organisms in studies in

TABLE 2. Seasonal variation in NH_4^+-N dynamics and hydrology showing discharge (Q), average ambient nutrient concentrations, uptake length (S_w), uptake velocity (V_f), and areal uptake rates (U). Values were obtained from short-term nutrient additions done once before (Sep = September) and once after (Nov = November) leaf fall. Parameters with significant seasonal differences are shown in bold. Significance was considered at the $\alpha = 0.05$ level.

Stream	Q (L/s)		Ambient (μg/L)		S_w (m)		V_f (mm/s)		U (μg m^{-2} h^{-1})	
	Sept	Nov	Sept	Nov	Sept	Nov	Sept	Nov	Sept	Nov
A	0.86	6.10	6.6	3.8	17.73	36.1	**0.029**	**0.103**	**692**	**1410**
B	1.92	3.72	9.8	8.3	56.68	21.37	**0.021**	**0.094**	**740**	**2799**
C	3.23	7.50	5.5	4.5	71.42	52.63	**0.036**	**0.075**	**703**	**1209**

which investigators have found exceptionally large contributions by consumers. For example, our biomass estimates of salamanders (~6 g wet mass/m^2) are significantly lower than estimates for fish or snails in those studies (>100 g/m^2, but see Small et al. 2011). Moreover, salamanders did not excrete nutrients at exceptionally high rates, which was the case for a single fish species in the Small et al. (2011) study.

The contribution of salamander excretion to stream nutrient demand declined to <4% after leaf fall. Furthermore, volumetric excretion rates declined 94% and turnover distances increased >6× after leaf fall. This seasonal pattern probably was caused by the nearly 40% decline in salamander densities combined with a 2.5× increase in stream nutrient demand and changes in stream hydrology. The seasonal decline in salamander densities probably reflected emergence of transforming larvae (Petranka 1998), downstream drift (Bruce 1985, 1986), and low larval survivorship (Organ 1961, Bruce 1988). Seasonal patterns in stream nutrient cycles are well documented, and within-stream differences can be as great as differences among streams in very different biomes (Hoellein et al. 2007). Our study spanned periods of the lowest and highest leaf litter standing crops in southern Appalachian Mountain streams (Golladay et al. 1989), and the increased nutrient demand probably was driven by rapid colonization of leaf litter by and subsequent metabolic demands of heterotrophic microbes and fungi (Mulholland et al. 1985, Tank et al. 2000, Webster et al. 2003, Valett et al. 2008). Discharge increased in all streams after leaf fall, and increased discharge can lead to decreased volumetric excretion and increased turnover distance in streams (Benstead et al. 2010). The amount of nutrients supplied by salamanders declined from before to

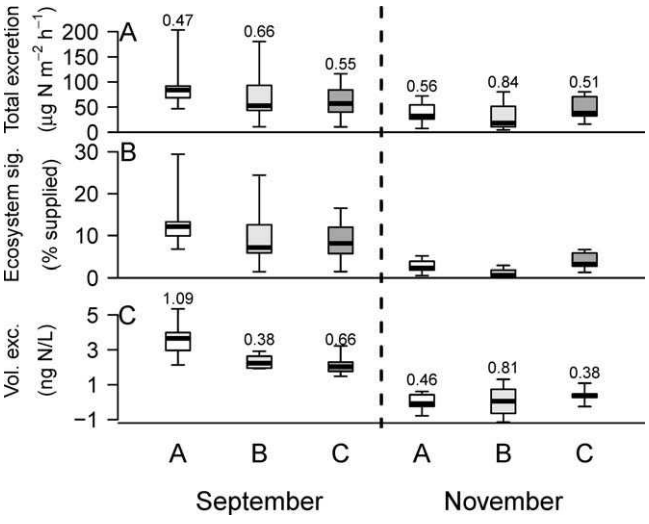

FIG. 4. Seasonal and spatial variation in the total areal excretion rates (A), ecosystem-level significance (sig.) of NH_4^+-N supplied by salamanders (B), and $\log_{10}$(volumetric excretion) (vol. exc.) (C). Lines in boxes show medians, box ends show quartiles, and whiskers show the 10th and 90th percentiles of the density estimates. The coefficient of variation (CV) for ecosystem significance is identical to the total excretion and is not shown.

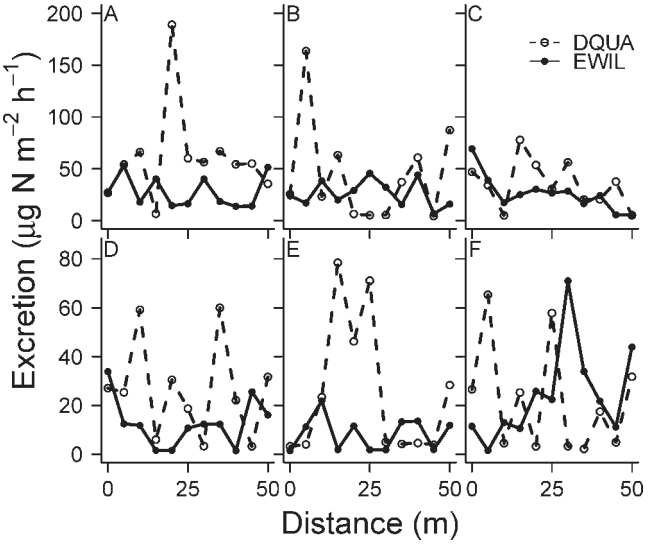

FIG. 5. The species-specific supply of N (*Desmognathus quadramaculatus* = DQUA, *Eurycea wilderae* = EWIL), measured as NH_4^+-N, along a stream study reach before (A–C) and after (D–F) leaf fall for Stream A (A, D), Stream B (B, E), and Stream C (C, F).

after leaf fall, but we think that the large seasonal change in the ecosystem-level significance of this supply was driven more by changes in stream nutrient demand and hydrology than by changes in salamander densities. These results emphasize the importance of considering temporal variation in consumer-driven nutrient recycling in streams that can be highly dynamic in both hydrology and nutrient cycling rates.

We think that life-history factors explain the seasonal decline in salamander larvae in the study streams, but this pattern could have been caused, at least in part, by potential bias in our sampling technique. Our passive leaf baskets provided a resource (i.e., detritus) that may have artificially attracted salamanders, thereby resulting in overestimation of salamander densities and associated contributions to nutrient recycling. Despite this potential bias, passive leaf baskets produce estimates similar to those from more active sampling techniques (e.g., dip netting), even during summer months when detritus may be limiting, as long as imperfect detection is taken into account (Peterman and Truslow 2008, Nowakowski and Maerz 2009). Our estimates based on passive sampling and adjusted for imperfect detection also appear reasonable when compared to estimates from other recent studies in this area (Peterman and Truslow 2008, Milanovich 2010). In addition, Davic and Welsh (2004) reported a similar decline (~40%) in larval salamander densities from June to October using an active sampling method, so passive leaf baskets do not appear to be more seasonally biased than other common sampling techniques. Therefore, we think that differences between our estimates and those of other studies in which estimates were lower (e.g., Johnson and Wallace 2005) may relate to the patchy distribution of larvae within and among streams rather than overestimation of densities with the passive sampling method.

Spatial patterns in the ecosystem-level significance of salamander-driven nutrient recycling

Salamanders appeared to supply a modest amount of nutrients at larger spatial scales, but small-scale variation within streams was considerable, and in some areas, salamanders supplied up to 30 and 7% of stream nutrient demand before and after leaf fall, respectively. This small-scale spatial variation was driven by salamander distributions within streams and resulting patchy distributions in the amount of nutrients supplied. Thus, the ecosystem-level significance of salamander-generated NH_4^+-N varied as much as 16× within streams before leaf fall and 17× after leaf fall. Volumetric excretion showed even greater variability (as much as 25× within a stream), a result that probably was related to the patchy salamander distribution and small-scale differences in stream hydrology. This spatial variation in volumetric excretion is similar to that reported for nutrient recycling by patchily distributed stream fish (McIntyre et al. 2008) and invertebrate consumer communities (Benstead et al. 2010).

The spatial distribution of fish can create biogeochemical hotspots in tropical streams (McIntyre et al. 2008), and salamanders might create biogeochemical hotspots in Appalachian headwater streams. The patchy distribution of salamanders within streams led to considerable small-scale spatial heterogeneity in the ecosystem-level significance of salamander nutrient recycling. Salamanders never met >30% of the stream nutrient demand, but these patches may still represent areas of increased biogeochemical activity in these nutrient-limited ecosystems where elevated nutrient levels can dramatically increase biological activity (Gulis and Suberkropp 2003, Cross et al. 2006, Greenwood et al. 2007, Rosemond et al. 2008). The potential for salamanders to create biogeochemical hotspots may be even greater at the local scale of a leaf pack, where nutrient excretion by consumers can increase decomposition rates by increasing fungal biomass (Diaz et al. 2012), microbial activity (Rugenski et al. 2012), and the palatability of detritus (Iwai and Kagaya 2007, Iwai et al. 2009, Rugenski et al. 2012). Thus, we expect that salamander excretion within leaf packs may influence decomposition dynamics.

Relative contribution of each species to NH_4^+-N excretion

A few species can dominate nutrient cycling in even relatively diverse consumer communities as the result of either their high relative biomasses within consumer communities (McIntyre et al. 2007) or exceptionally high excretion rates (Small et al. 2011). *Desmognathus quadramaculatus* excreted NH_4^+-N at ~⅓ the size-specific rate of *E. wilderae*, although they excreted ~3× more NH_4^+-N h^{-1} because of their larger size. Thus, *D. quadramaculatus* contributed ~2× more to total areal NH_4^+-N excretion and also contributed more to volumetric excretion in 72% of channel units despite having lower mean densities than *E. wilderae*. However, we note that in 28% of the channel units, *E. wilderae* contributed more to volumetric excretion. Thus, differences in the distribution of these species within streams led to some spatial complementarity in salamander nutrient supply among species.

Salamanders appear to contribute significantly to stream nutrient recycling, but caution should be used when interpreting or generalizing these results. Use of the single-addition method for examining stream nutrient dynamics can lead to overestimation of nutrient uptake lengths (Mulholland et al. 2002). This method allows meaningful comparisons among streams and seasons, but we may have underestimated nutrient areal uptake rates. Therefore, we may have overestimated the significance of salamander nutrient recycling, although temporal and spatial patterns should still be valid. We attempted to keep addition levels low ($<5\times$ increase) as recommended by Mulholland et al. (2002), but we still probably overestimated uptake lengths. Consequently, our results may represent a minimum NH_4^+-N uptake and, thus, a maximum in the ecosystem-level significance of salamander-driven nutrient recycling by these 2 species.

Conclusions

Our results highlight the importance of considering spatial and temporal variation in the contribution of consumer-driven nutrient recycling in highly dynamic stream ecosystems, and we suspect the variability we observed is common in streams from a variety of biomes. Furthermore, we found that salamanders contributed substantially to N cycling and may create biogeochemical hotspots at small spatial scales as a result of their patchy distribution in streams. A substantial portion of N excretion by salamanders may occur as organic N (J. R. Milanovich and M. E. Hopton, unpublished data), and research investigating this contribution would improve our understanding of the role of salamanders in consumer-driven nutrient recycling. We also observed substantial differences in the contributions of different salamander species, with evidence for spatial complementarity among species, results suggesting they are not functionally redundant despite belonging to the same functional feeding guild (i.e., predators of aquatic insects). Thus, our results indicate that declines in salamander populations or changes in species composition have the potential to affect consumer-driven nutrient recycling in headwater streams, particularly at small spatial scales. Unfortunately, the ecological role of most amphibian species remains poorly understood despite existing evidence that they are important components of many ecosystems (Davic and Welsh 2004, Whiles et al. 2006). Research into the causes and consequences of amphibian declines is needed to improve conservation efforts and management decisions related to these potentially key members of terrestrial and aquatic ecosystems.

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