



Nutrient recycling by insect and fish communities in high-elevation tropical streams

Carla L. Atkinson · Alexander V. Alexiades · Keeley L. MacNeill ·
Andrea C. Encalada · Steve A. Thomas · Alexander S. Flecker

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Abstract High- to mid-elevation streams are often oligotrophic, but harbor diverse groups of aquatic animals that can satisfy a substantial proportion of nutrient demand. Therefore, we tested the proportion of nutrient demand met by two dominant guilds of animal consumers in the Andes to ask: (1) Do excretion rates vary between insects and fish in montane tropical stream ecosystems? (2) What consumer guild dominates areal nutrient regeneration? (3) What is the nutrient demand and what proportion are

consumer taxa regenerating? We combined aquatic insect and fish biomass estimates with measured excretion rates of two fish species (one native, one introduced) and six aquatic insects and estimated nutrient demand in streams by conducting nutrient uptake measurements. Insect taxa had higher per-capita excretion rates than fish and had higher excretion N:P. Aquatic insect biomass tended to be higher than fish biomass and consequently total areal excretion rates by insects were higher. Collectively, communities contributed up to 15–24% of $\text{NH}_4\text{-N}$ demand and 1–19% of SRP demand. The additive effect of these groups on nutrient availability is likely an important function in low-nutrient tropical streams. Further work needs to be conducted to examine the interactions within entire communities and consequential impacts on nutrient cycling.

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C. L. Atkinson (✉)
Department of Biological Sciences, University of
Alabama, 300 Hackberry Lane, Tuscaloosa, AL 35487,
USA
e-mail: clatkinson@ua.edu

A. V. Alexiades
Department of Environmental Science, Heritage
University, Toppenish, WA 98948, USA

K. L. MacNeill · A. S. Flecker
Department of Ecology and Evolutionary Biology,
Cornell University, Ithaca, NY 14853, USA

A. C. Encalada
Instituto BIOSFERA, Laboratorio de Ecología Acuática,
Universidad San Francisco de Quito, Quito, Ecuador

S. A. Thomas
School of Natural Resources, University of Nebraska,
Lincoln, NE 68583, USA

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Introduction

Nutrient availability in ecosystems is often a major driver of community and ecosystem processes such as community assembly, trophic interactions, and food chain length (Post, 2002), organic matter decomposition (Elwood et al., 1981), and resource production

(Davis et al., 2010). While nutrient availability is often set by geologic, riparian, and climatic templates that bound ecosystem processes (Kaspari & Yanoviak, 2009; Small & Pringle, 2010), nutrient cycling by organisms can support a substantial proportion of nutrient demand in aquatic ecosystems (Vanni et al., 2006; Small et al., 2011; Atkinson et al., 2017; Williamson et al., 2018). Studies of biogeochemical processing have typically focused on the activities of microbial communities, but several recent studies have shown that animal consumers are essential for nutrient regeneration and material fluxes across multiple systems (Karberg & Lilleskov, 2009; Kohler et al., 2011; Subalusky et al., 2017). In marine systems, whales, sea birds, and fish have been shown to be important in the cycling and movement of nutrients such as nitrogen (N) and phosphorus (P) (Meyer et al., 1983; Roman & McCarthy, 2010; Allgeier et al., 2013; Layman et al., 2013). In freshwater aquatic systems, nutrient regeneration by aquatic animals can satisfy a large fraction of ecosystem nutrient demand (Grimm, 1988a; Childress et al., 2014).

Animal consumers can have strong top-down effects through the consumption of resources (Power, 1990; Rosemond et al., 1993; Vanni & Layne, 1997) and bottom-up effects through excretion and egestion of nutrients (Attayde & Hansson, 1999; Small et al., 2011; Subalusky et al., 2015; Halvorson et al., 2017; Atkinson et al., 2018b). Ecological stoichiometry theory (see Sterner & Elser, 2002) provides a useful framework for assessing the impacts of various taxonomic groups on freshwater ecosystem processes as the nutrients regenerated by an animal consumer's waste products are predicted to be related to their elemental composition and their diet. Animals are important sources (i.e., nutrient excretion), and potentially sinks (i.e., through tissue storage) for nutrients in aquatic ecosystems (Vanni et al., 2013), and animal excretion can be an important flux of nutrients that strongly alters biogeochemical dynamics in freshwater systems (Benstead et al., 2010; Atkinson et al., 2013). Several studies have highlighted the effect of animals on nutrient recycling and consequential increases in primary producer and consumer biomass (Spooner & Vaughn, 2006; Atkinson et al., 2013), alterations in primary producer community structure (Knapp et al., 1999; Allen et al., 2012; Atkinson et al., 2013), changes in organic matter decomposition rates

(Rugenski et al., 2012), and strong effects on food webs (Atkinson et al., 2014). Most studies have focused on large stream consumers such as fish, mussels, and shrimp (McIntyre et al., 2008; Benstead et al., 2010; Atkinson & Vaughn, 2015) and have often only considered one of these taxonomic groups at a time. Few have examined the role of multiple consumer communities that span multiple trophic levels in nutrient regeneration (but see, Boers et al., 1991; Carpenter et al., 1992; Hopper et al., 2018), especially in streams, despite the additive and likely interactive roles among multiple consumer groups. Thus, studying the roles of multiple groups is needed to better understand the significance of animals in nutrient cycling.

Fish are large, mobile consumers that have been shown in previous studies to form biogeochemical hotspots of nutrient regeneration through aggregating behaviors (McIntyre et al., 2008; Capps & Flecker, 2013b). Fish influence nutrient availability and primary production in freshwater ecosystems through nutrient sequestration in body tissues and nutrient remineralization via excretion and egestion (Vanni & Findlay, 1990; Kraft, 1992; Schaus et al., 2010; Vanni et al., 2013). Fish are highly mobile (Matthews, 1998; Albanese et al., 2009), and therefore the subsidy provided by their biomass can periodically enhance productivity in stream ecosystems through carcass decomposition, gametic deposition, and nutrient excretion (Naiman et al., 2002; Schindler & Parker, 2002; Wilson & Xenopoulos, 2011; Childress et al., 2014; Childress & McIntyre, 2015). However, these effects are species- and system-specific (Atkinson et al., 2017). Previous studies have shown that native and introduced fish can have varying effects on nutrient availability (Capps & Flecker, 2013a; Capps et al., 2015a; Alexiades et al., 2017).

In contrast to fish, little work has investigated the role of aquatic insect communities in nutrient regeneration in freshwater ecosystems despite their high biomass and importance to food web structure within streams (Benke, 1998; Power et al., 2009; Benke & Huryn, 2010). Many studies have examined tissue stoichiometry of aquatic insects (Cross et al., 2003; Frost et al., 2003; Evans-White et al., 2005; Liess & Hillebrand, 2005), but the regeneration of nutrients relative to ecosystem demand by this group has largely been ignored (but see, Alves et al., 2010; Halvorson et al., 2015; Balik et al., 2018). Further, these

organisms span a variety of functional feeding groups in streams (e.g., leaf shredders, algal grazers, predators), which may have important implications for nutrient regeneration (Halvorson et al., 2015; Atkinson et al., 2017) and growth (Anderson & Cummins, 1979), because faster growth requires higher P demand (i.e., growth rate hypothesis; Elser et al., 2000). While fish are highly mobile consumers within streams, aquatic insects tend to be less mobile and can be dislodged and lost more easily from systems during high-flow events (Piniewski et al., 2017). Thus, these organisms may also vary in their contributions as nutrient regeneration hotspots depending on their spatial distribution, feeding mode, and flow conditions.

Recent meta-analyses of ectothermic aquatic animals showed that fish excrete N and P at higher mass-specific rates than invertebrates (Allgeier et al., 2015; Vanni & McIntyre, 2016). Vanni & McIntyre (2016) reported dramatic variation in excretion rates and suggest that more field measurements are needed, especially for tropical areas. Few studies have empirically measured nutrient regeneration by both invertebrates and vertebrates in the same system (but see, Carpenter et al., 1992; Attayde & Hansson, 1999; McManamay et al., 2010) and have not integrated measurements of ecosystem nutrient demand. Previous work have shown that vertebrates (Vanni et al., 2002; McIntyre et al., 2008) and benthic macroinvertebrates (Grimm, 1988b; Hall et al., 2003; Atkinson & Vaughn, 2015) can provide > 50% of ecosystem ammonium ($\text{NH}_4\text{-N}$) demand in small streams. Because consumer biomass is an essential determinant affecting nutrient flux, both the rates and the biomass of the animals must be considered along with ecosystem demand. Our previous work indicates that the nutrient content of basal food resources varies across elevation, with resources tending to be of lower quality at higher elevations, with aquatic insect diet responding to diet quality (Atkinson et al., 2018a), and thus nutrient regeneration may also vary as a result of elevation in these systems. Our goal was to investigate the role of two contrasting guilds of stream organisms, fish and benthic aquatic insects, on nutrient regeneration in nutrient-poor tropical highland Andean streams. Here we asked: (1) How do excretion rates vary across two consumer guilds, insects and fish, in montane tropical stream ecosystems? (2) What taxonomic groups dominate areal nutrient regeneration

across sites varying in elevation? (3) How do summed areal excretion rates compare to nutrient uptake estimates in these stream ecosystems?

Methods

Study area

We studied three tributary streams within the Papalacta sub-basin that are on the eastern slope of the Andes and are part of the Napo drainage of the Amazon basin (Fig. 1). Our streams were small mountainous streams at 1727, 2115, and 2880 meters in elevation. We sampled insect assemblages and fish within a 125-m stream reach at all of our sites. Each site contained only one fish taxon, with native Andean climbing catfish, *Astroblepus vaillanti* (Regan, 1904) occurring at our two lowest elevation sites (1727 m and 2115 m) and introduced rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), occurring at the high-elevation site (2880 m), which is typical for streams in the region (Alexiades and Encalada, 2017). Average water temperatures varied between 10.4 and 14.5°C across the three sites during the study (Atkinson et al., 2018a). Dissolved oxygen concentrations were high across sites and there were low concentrations of both $\text{NH}_4\text{-N}$ and SRP across all sampling periods (Table 1).

Insect and fish areal biomass

Insect density and biomass were determined at all sites using 0.093 m² Surber samplers in February and March of 2014. We took five Surber samples per site that were equally spaced along a 125-m transect. Briefly, the area of the Surber sampler was placed on the stream bottom and we disturbed the stream bottom for 2 min, and then fixed the samples in 75% ethanol. Samples were then sorted in the lab and insects were enumerated and identified to genus. Additional insects were also collected with a D-Frame net for collection for length–dry mass relationships (Atkinson, unpublished). Insects were measured under a stereoscope and length–mass relationships were multiplied by the population density to estimate areal biomass of focal taxa ($\text{g}^{-1} \text{m}^{-2}$) (Table 2).

Fish density was estimated via three-pass electrofishing (FEG 1500; EFKO-Elektrofischfängergeräte,

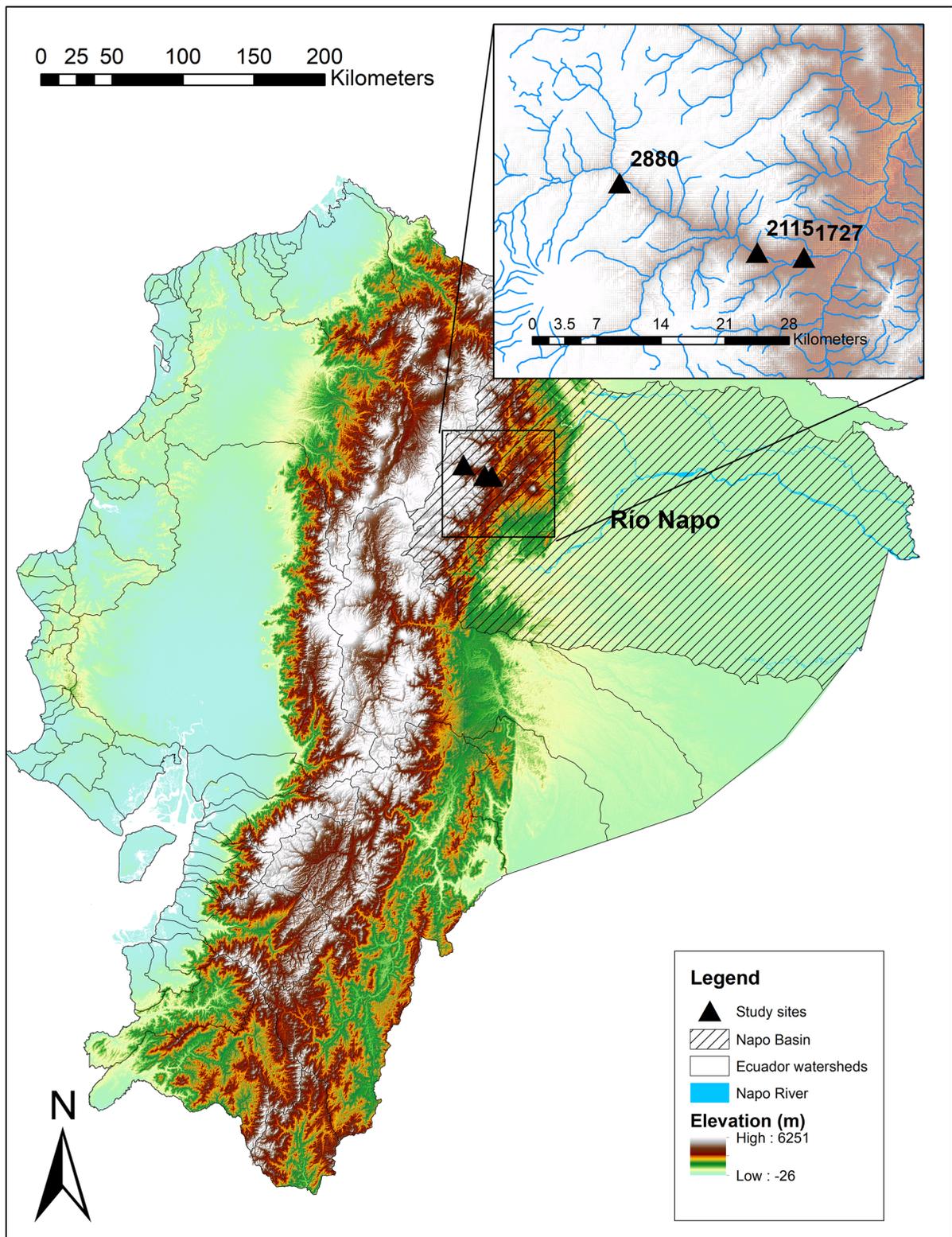


Fig. 1 Map of the study sites with their elevation indicated. All study sites were in small streams that empty into the Papallacta River

Table 1 Physicochemical parameters (mean \pm standard error) of our three study sites in the Napo basin, Ecuador

Elevation (m)	Temperature ($^{\circ}$ C)	Dissolved oxygen (mg/l)	% dissolved oxygen	NH ₄ -N (μ g/l)	SRP (μ g/l)
1727	14.5 \pm 0.66	8.1 \pm 0.12	99.5 \pm 0.46	3.2 \pm 0.11	12.7 \pm 0.28
2115	14.0 \pm 0.62	7.9 \pm 0.11	99.2 \pm 0.49	3.2 \pm 0.29	5.9 \pm 0.19
2880	10.4 \pm 0.69	7.8 \pm 0.14	97.9 \pm 0.48	3.7 \pm 0.09	22.6 \pm 0.31

Table 2 Taxa in this study ranged a variety of functional feeding groups (see Atkinson et al., 2018a, b)

Taxa	Functional feeding group	No. sampled for excretion at 1727 m	No. sampled for excretion at 2115 m	No. sampled for excretion at 2880 m	Biomass (g m^{-2}) at 1727 m	Biomass (g m^{-2}) at 2115 m	Biomass (g m^{-2}) at 2880 m
<i>Anacroneuria</i>	Predators and shredders	12	11	18	0.836	0.205	0.250
<i>Andesiops</i>	Collector-gatherers	12	11	11	0.027	0.072	0.070
<i>Baetodes</i>	Scrapers/collector-gatherers	15	7	13	0.042	0.064	0.051
<i>Leptohyphes</i>	Collector-gatherers	8	7	16	0.003	0.123	0.014
<i>Leptonema</i>	Collector-filterers	8	11	13	0.858	0.212	0.372
<i>Thraulodes</i>	Collector-gatherers	6	5	0	0.019	0.019	0.000
<i>Astroblepus</i>	Predators	12	9	0	0.800	0.220	0.000
<i>Oncorhynchus mykiss</i>	Predators	0	0	12	0.000	0.000	2.960

The number of replicate individuals used of each taxon used in our excretion assays is reported here for each taxon and site combination. The mean biomass data for each site are based on our Surber samples from 2014 for insects and from electrofishing surveys in 2015 for fish

Leutkirch, Germany), using a Leslie–DeLury binomial model (Leslie & Davis, 1939; DeLury, 1947) from fish captured using standard backpack electrofishing techniques (Beauchamp et al., 2009). Each 125-m stream section was isolated using blocking seines or natural features (shallow riffles) to survey a closed population compatible with depletion estimates. We weighed captured fish to the nearest gram and the estimated mean weight for each taxonomic family was multiplied by population density, yielding an estimate of areal biomass ($\text{g}^{-1} \text{m}^{-2}$) (Table 2). Fish sampling was conducted in February and March of 2015.

Excretion rates

We conducted excretion assays on aquatic insects at each site in January–February 2014 and in February

2015. We used D-nets (mesh = 500 μ m) to collect benthic insects and then sorted them to the lowest practical taxonomic unit in trays with stream water. The most common insects found across all sites were used in the excretion assays (*Anacroneuria* [$N = 41$], *Andesiops* [$N = 34$], *Baetodes* [$N = 35$], *Leptohyphes* [$N = 31$], *Leptonema* [$N = 32$], *Thraulodes* [$N = 11$; only collected at Sites 1727 and 2115]) given that would be the best representation of the community and their role in nutrient provisioning. At each site, we placed an individual insect into containers with 30 ml of filtered stream water (25 mm Whatman™ GFFs, 0.7 μ m pore size) and the vials were placed into the stream to maintain a temperature and were left undisturbed for 60 min before the insects were removed. At each site we incubated 4–5 vials that had filtered stream water without insects to act as a control. Following removal, insects were retained for

genus identification and for length–dry mass relationships.

We conducted excretion assays on fish in February–March 2015 on both *Astroblepus* ($N = 22$; Sites 1727 and 2115) and *Oncorhynchus mykiss* ($N = 13$; Site 2880). In order to account for handling stress, we identified the initial peak in excretion rates due to handling stress and fasting effects, and calculated where the exponential decay curve flattened out (half-life) following methods outlined in Whiles et al. (2009). Based on these findings, fish were incubated in 1 to 5 l of stream water (depending on mass) for approximately 30 min to minimize handling stress response and to avoid oxygen stress and waste buildup (Whiles et al., 2009). We also used 4–5 containers with filtered stream water without fish as a control.

The resulting water samples from both the insect and fish excretion assays were immediately analyzed for ammonium ($\text{NH}_4\text{-N}$) the same day as collection using the fluorometric method (Holmes et al., 1999; Taylor et al., 2007) on a portable fluorometer (Aquafluor, Turner Designs, Inc, Sunnyvale, CA, U.S.A.). A remaining 10 ml of sample was frozen and run within 30 days for soluble reactive phosphorus (SRP) concentrations using the molybdate-blue colorimetric analysis (Murphy & Riley, 1962; Solorzano & Sharp, 1980) on a Cary 60 UV–Vis Spectrophotometer (Agilent, Santa Clara, CA).

Excretion rates were calculated based on the difference in dissolved ammonium ($\text{NH}_4\text{-N}$) and soluble reactive phosphorus (SRP) concentrations between identical containers with and without insects or fish. For each individual of each species, mass-specific nutrient excretion rates ($\mu\text{g nutrient g}^{-1} \text{h}^{-1}$) were calculated based on Vanni et al. (2002). Excretion N:P was calculated as molar ratios for each individual measured.

Areal excretion rates

We estimated insect areal excretion rates ($\mu\text{g nutrient m}^{-2} \text{h}^{-1}$) for each site. We calculated the areal excretion rate for each insect taxon as the product of the average biomass of the taxa and their taxon-specific biomass-corrected excretion rate. To test for outliers, we conducted a Bonferroni-adjusted outlier test using the R package car version 2.1-3. If outliers were detected (Bonferroni $P < 0.05$), we removed them from subsequent analyses. Outliers (6% of our

data points) from our biomass-corrected excretion rates were removed prior to calculating areal excretion rates. All insect taxon-specific values were summed to estimate the insect community areal excretion rate. Fish areal excretion estimates were calculated for each species as the product of the areal biomass estimates and the mass-based excretion rates (McIntyre et al., 2008).

Water chemistry and nutrient uptake dynamics

We measured nutrient uptake in January 2013 (Site 1727) and February 2014 (Sites 2115 and 2880; Fig. 1) during base flow conditions, using a pulse injection technique (Covino et al., 2010) where we dissolved reactive (NH_4Cl , KH_2PO_4 , and K_2HPO_4) and conservative tracers (NaCl), and added the mix to each stream in a pulse. Downstream from the addition point, we collected SRP and $\text{NH}_4\text{-N}$ samples every 30 s as the tracers passed through the stream, as monitored by a conductivity meter, until the stream returned to background concentrations. We calculated uptake length (S_w) for each sample collected using the following equation (Workshop, 1990):

$$S_w = \left| \left(\frac{\Delta L}{\ln(N : C_{\text{meas}} - N : C_{\text{inj}})} \right) \right|, \quad (1)$$

where ΔL is the reach length, $N:C_{\text{meas}}$ is the measured ratio of the nutrient of interest (N) to the conservative tracer (C), and $N:C_{\text{inj}}$ is the ratio of the concentrations of the solutes added to the stream. We chose the reach length of each stream based on targeting an average travel time of 15 min between the nutrient addition point and the sampling point. We estimated travel time during a pulse injection with only conservative tracer earlier on each injection day. We regressed the individual sample uptake lengths against their respective nutrient concentrations (the geometric mean of the measured nutrient and the predicted nutrient) to the ambient nutrient concentration to calculate ambient uptake length ($S_{w\text{-ambient}}$). Using $S_{w\text{-ambient}}$, we calculated ambient areal uptake, (U , $\mu\text{g m}^{-2} \text{h}^{-1}$), which is independent from stream size:

$$U = \frac{Q * [N_{\text{bkgd}}]}{w * S_{w\text{-ambient}}}, \quad (2)$$

where N_{bkgd} is the background concentration of the nutrient of interest (i.e., the in-stream concentration),

Q is the stream discharge (Liters * second⁻¹), and w is the average stream width. Lastly, we calculated uptake velocity, or v_f , a stream size-independent measure of the demand for nutrients relative to concentration:

$$v_f = \frac{Q}{w * S_w} \text{ or } \frac{U}{[\text{nutrient}_{\text{bkgd}}]}$$

All water samples were filtered with 25 mm WhatmanTM GFFs (0.7 µm pore size) and stored in the dark and cold until analyzed. NH₄-N samples were filtered into 30-ml brown bottles and analyzed the same day as collection using the fluorometric method described above (Holmes et al., 1999, as modified by Taylor et al., 2007). SRP samples were analyzed using the same methods as above on the same day as collection when possible or frozen for later analysis when not.

Data analysis

We used a two-way ANOVA to determine if there were significant differences among species and sites in per-capita NH₄-N and SRP excretion rates. To conform to the assumption of normality required for parametric statistical analyses, we used the natural logarithm of our per-capita NH₄-N and SRP excretion rates. Significant differences between sites and/or species were further investigated using Tukey's HSD post hoc tests. We also used a two-way ANOVA to determine if there were differences among species and sites in areal NH₄-N and SRP excretion. We compared the relative supply (i.e., areal excretion rates) to demand (i.e., uptake) across our three study streams for each taxonomic group. This was calculated using the percent NH₄-N and SRP demand that these animals provided through excretion by dividing the NH₄-N and SRP areal excretion rates (E_a) by NH₄-N and SRP uptake rates (U).

Results

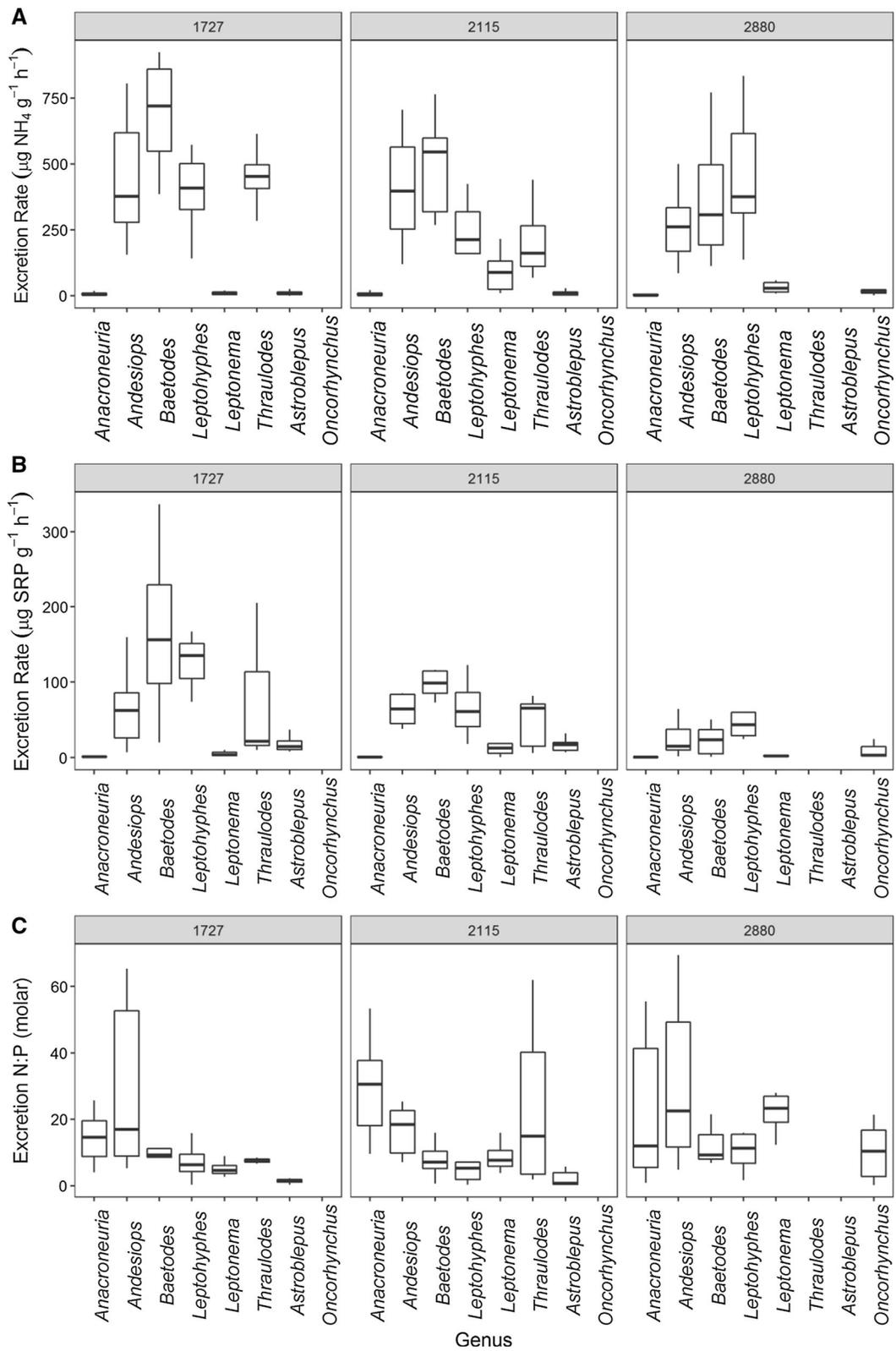
Taxon-specific–mass-specific excretion rates

Mass-specific excretion rates varied significantly across taxonomic groups for both NH₄-N ($F_{7,204} = 179.45$, $P < 0.001$; Fig. 2A) and SRP ($F_{7,155} = 66.57$, $P < 0.001$; Fig. 2B) with mayflies

(*Andesiops*, *Baetodes*, *Leptohyphes*, and *Thraulodes*) tending to have the highest mass-specific NH₄-N and SRP excretion rates (Table 3). NH₄-N excretion varied significantly across sites ($F_{2,204} = 13.99$, $P < 0.001$) with taxa at the low-elevation site having the higher excretion rates than animals at the other two sites, but the middle- and high-elevation sites did not vary significantly in excretion rates. SRP excretion rates also varied as a function of site ($F_{2,155} = 23.12$, $P < 0.001$) with the high site having lower SRP excretion rates, but the two low-elevation sites did not vary between one another. The interaction between taxonomic group and site was significant for NH₄-N ($F_{10,204} = 3.87$, $P < 0.001$), but not SRP ($F_{10,155} = 1.10$, $P = 0.37$) excretion rates. Excretion stoichiometry (molar N:P) varied across sites ($F_{2,143} = 6.66$, $P = 0.002$) and taxa ($F_{7,143} = 17.19$, $P < 0.001$), but there was not a significant interaction ($F_{10,143} = 23.12$, $P < 0.001$). Two insect taxa, *Anacroneuria* and *Andesiops*, excreted at higher N:P than the native fish *Astroblepus* and another mayfly taxa, *Leptohyphes* (Fig. 2C; Table 3) and animals at the high-elevation site had higher N:P excretion than animals at the two low-elevation sites.

Community-level areal excretion

There were significant differences in mean areal NH₄-N excretion among taxa ($F_{7,204} = 15.46$, $P < 0.001$), but not across sites ($F_{2,159} = 1.70$, $P = 0.19$). Specifically, *Baetodes* and *Oncorhynchus* had the highest areal NH₄-N excretion rates, but did not vary from one another. Mean areal NH₄-N excretion by taxa ranged (mean ± standard deviation) between 1.6 ± 1.2 (*Leptohyphes*) and 48.2 ± 29.7 (*Baetodes*) µg NH₄-N m² h⁻¹ at the low-elevation site (1727 m), 1.4 ± 1.4 (*Anacroneuria*) and 31.5 ± 12.1 (*Baetodes*) µg NH₄-N m² h⁻¹ at the mid-elevation site (2115 m), and 1.4 ± 2.7 (*Anacroneuria*) and 36.4 ± 32.1 (*Oncorhynchus*) µg NH₄-N m² h⁻¹ at the high-elevation site (2880 m; Fig. 3A). Overall, *Baetodes* and *Oncorhynchus* exhibited the highest NH₄⁺-N areal excretion and *Anacroneuria* had the lowest NH₄-N areal rates. Mean areal SRP excretion was significantly different among our taxa ($F_{7,159} = 12.82$, $P < 0.001$) but did not vary across sites ($F_{2,159} = 2.77$, $P = 0.07$) and the interaction was not significant ($F_{10,159} = 15.46$, $P = 0.45$). Multiple comparisons across taxa indicated that the two fish



◀ **Fig. 2** Average **A** $\text{NH}_4\text{-N}$ excretion rates, **B** SRP excretion rates, and **C** N:P excretion stoichiometry for each of the taxonomic groups at the three sites studied here. The first six taxa are insects and the last two are the fish species studied. *Oncorhynchus mykiss* was not collected at the low-elevation sites and *Astroblepus* and *Thraulodes* were not collected at the high-elevation sites

taxa, *Astroblepus* and *Oncorhynchus*, had significantly higher areal SRP excretion contributions from the insect taxa. Mean areal SRP excretion by taxa ranged between 1.1 ± 1.2 (*Anacroneturia*) and 15.3 ± 9.1 (*Astroblepus*) $\mu\text{g SRP m}^{-2} \text{ h}^{-1}$ at the low-elevation site (1727 m), 0.11 ± 0.1 (*Anacroneturia*) and 14.2 ± 6.9 (*Astroblepus*) $\mu\text{g SRP m}^{-2} \text{ h}^{-1}$ at the mid-elevation site (2115 m), and 0.13 ± 0.2 (*Anacroneturia*) and 13.3 ± 15.4 (*Oncorhynchus*) $\mu\text{g SRP m}^{-2} \text{ h}^{-1}$ at the high-elevation site (2880 m). Mean SRP areal excretion varied across taxa with *Astroblepus*, *Baetodes*, and *Oncorhynchus* exhibiting the highest areal rates across the sites (Fig. 3B; Table 3).

Uptake rates and excretion relative to demand

Uptake rates of $\text{NH}_4\text{-N}$ varied between 547 and 787 $\mu\text{g NH}_4\text{-N m}^{-2} \text{ h}^{-1}$ (uptake velocity (v_f) range 0.005–0.020 cm s^{-1}) and uptake of SRP ranged between 361 and 19,022 $\mu\text{g SRP m}^{-2} \text{ h}^{-1}$ (v_f range 0.001–0.018 cm s^{-1}) at our three sites. Uptake rates of $\text{NH}_4\text{-N}$ were greatest at our low-elevation sites and SRP uptake was greatest at our higher elevation site. At the low-elevation site, the insect community and

native fish excretion accounted for 15% of $\text{NH}_4\text{-N}$ and 3% of SRP demand with insects making up the majority of excreted nutrients supplying a larger proportion relative to fish (Fig. 4C; Fig. 4D). At the mid-elevation site, communities supplied a larger proportion of both $\text{NH}_4\text{-N}$ and SRP in relation to demand (22.5% and 20.6%, respectively; Fig. 4A; Fig. 4B) in comparison to the low-elevation site with insect excretion accounting for the majority of uptake (e.g., 21% of $\text{NH}_4\text{-N}$ and 17% of SRP uptake; Fig. 4B). Specifically, Baetidae mayflies (*Andesiops* and *Baetodes*) made up the majority of $\text{NH}_4\text{-N}$ supplied through excretion (Fig. 4A). *Astroblepus* supplied more $\text{NH}_4\text{-N}$ and SRP in relation to demand (1.5% and 4%, respectively; Fig. 4A; Fig. 4B) at the intermediate site in comparison to the low-elevation site, but this was still less than what was supplied from insect excretion. At the high-elevation site, introduced trout supplied the greatest amount of $\text{NH}_4\text{-N}$ (4.8%) relative to uptake followed by *Baetis* mayflies (Fig. 4A). Given the high SRP uptake rates at our high-elevation site, SRP excretion by insects and fish was small relative to demand, only accounting for 0.1% (Fig. 4D).

Discussion

By investigating two disparate, but co-occurring groups of consumers (fish and insects), we were able to show that insects and fish can satisfy a substantial proportion of nutrient demand in tropical montane

Table 3 Results from Tukey's HSD post hoc analysis comparing mass-specific and areal excretion rates of our insect and fish taxa

Genus	Mass-specific excretion			Areal excretion	
	$\text{NH}_4\text{-N}$	SRP	N:P (molar)	$\text{NH}_4\text{-N}$	SRP
<i>Anacroneturia</i>	c	f	ac	c	f
<i>Andesiops</i>	a	ab	ac	ab	ab
<i>Astroblepus</i>	bc	ac	d	ac	ac
<i>Baetodes</i>	a	bd	abc	d	bd
<i>Leptohyphes</i>	a	d	b	ac	d
<i>Leptonema</i>	d	e	abc	ab	e
<i>Oncorhynchus</i>	bd	ce	bc	bd	ce
<i>Thraulodes</i>	a	abd	abc	ac	abd

Non-overlapping letters between genus comparisons indicate significant differences in mass-specific excretion rates, excretion stoichiometry, or areal excretion rates

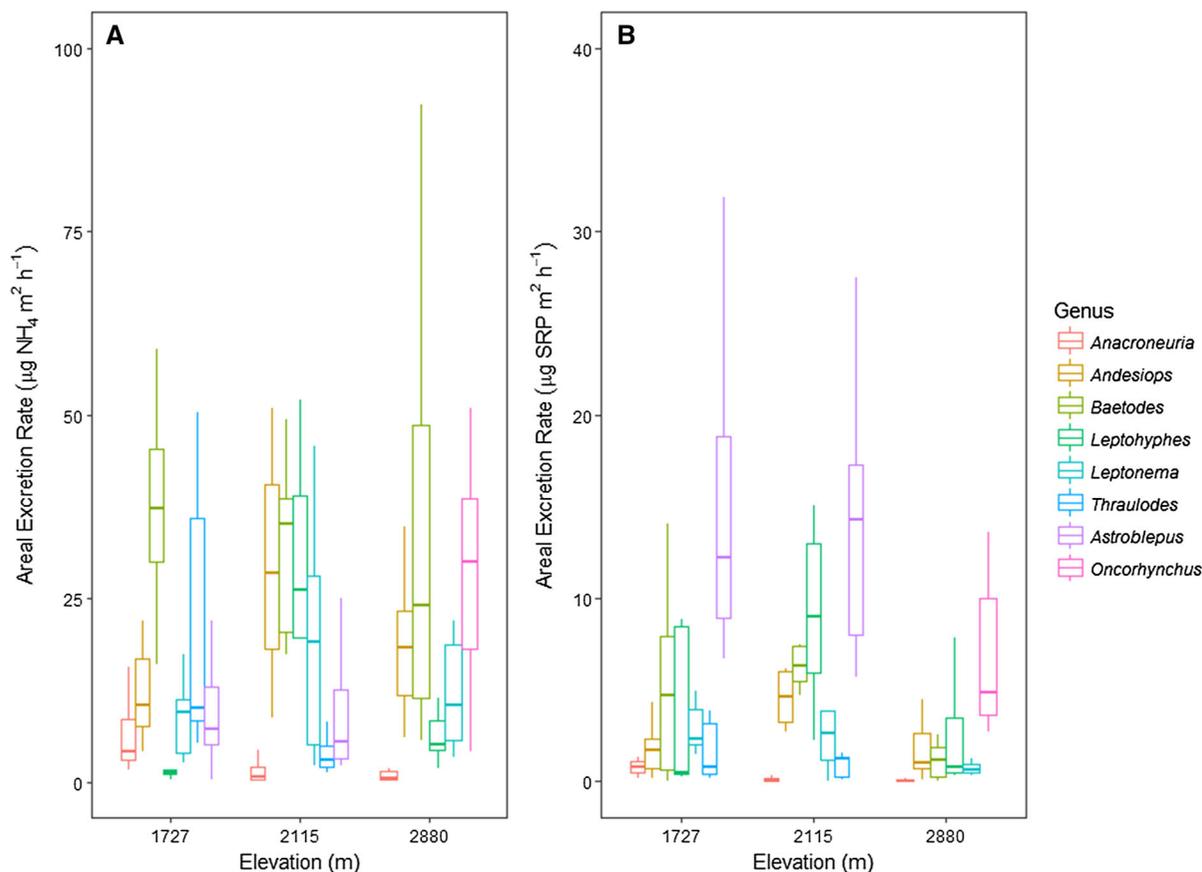


Fig. 3 **A** $\text{NH}_4\text{-N}$ and **B** SRP areal excretion rates of the insect taxa and fish taxa (*Astroblepus* and *Oncorhynchus*) at all of the sites they were collected. The first six taxa are insects and the last two are the fish species studied

streams. Many researchers have examined the functional roles of animals on nutrient dynamics in freshwater ecosystems (e.g., McIntyre et al., 2008; Benstead et al., 2010; Atkinson et al., 2013; Caliman et al., 2013; Whiles et al., 2013), but few have compared multiple taxonomic groups within a system, particularly in understudied tropical streams. Mayflies (i.e., *Andesiops*, *Baetodes*, *Leptohyphes*, and *Thraulodes*) excreted $\text{NH}_4\text{-N}$ and SRP at higher mass-specific rates than both fish species. Further, $\text{NH}_4\text{-N}$ areal excretion rates of native fish were lower than our insect taxa, while areal SRP excretion of both native and introduced fish species were higher than those of insect species. In comparison to the native fish, *Astroblepus*, introduced trout contributed to a greater extent of $\text{NH}_4\text{-N}$ demand. Across all sites, the insect community supplied a larger proportion of $\text{NH}_4\text{-N}$ compared to both fish species. Collectively, the aquatic consumer communities (i.e., insects and fish

together) studied here can supply up to 23% of the $\text{NH}_4\text{-N}$ (mid-elevation site) and 21% of the SRP demand (mid-elevation site) within these small stream ecosystems. Specific effects of these communities on nutrient availability and alleviation of nutrient demand were dictated by the biomass, metabolic rates, and excretion stoichiometry of the taxa and depend strongly on stream discharge and background nutrient concentrations.

When animals comprise a large amount of biomass in ecosystems, they can constitute an essential component of nutrient and energy flux (McIntyre et al., 2008; Rugenski et al., 2012; Atkinson et al., 2018b). Here, we found that despite their small body size, insects can support a larger proportion of nutrient demand than fish. Insects occurred at higher areal biomass than fish at all of our sites (e.g., insect biomass was $\times 3$ higher at our mid-elevation site), owing to their disproportionate impact. Also, insects

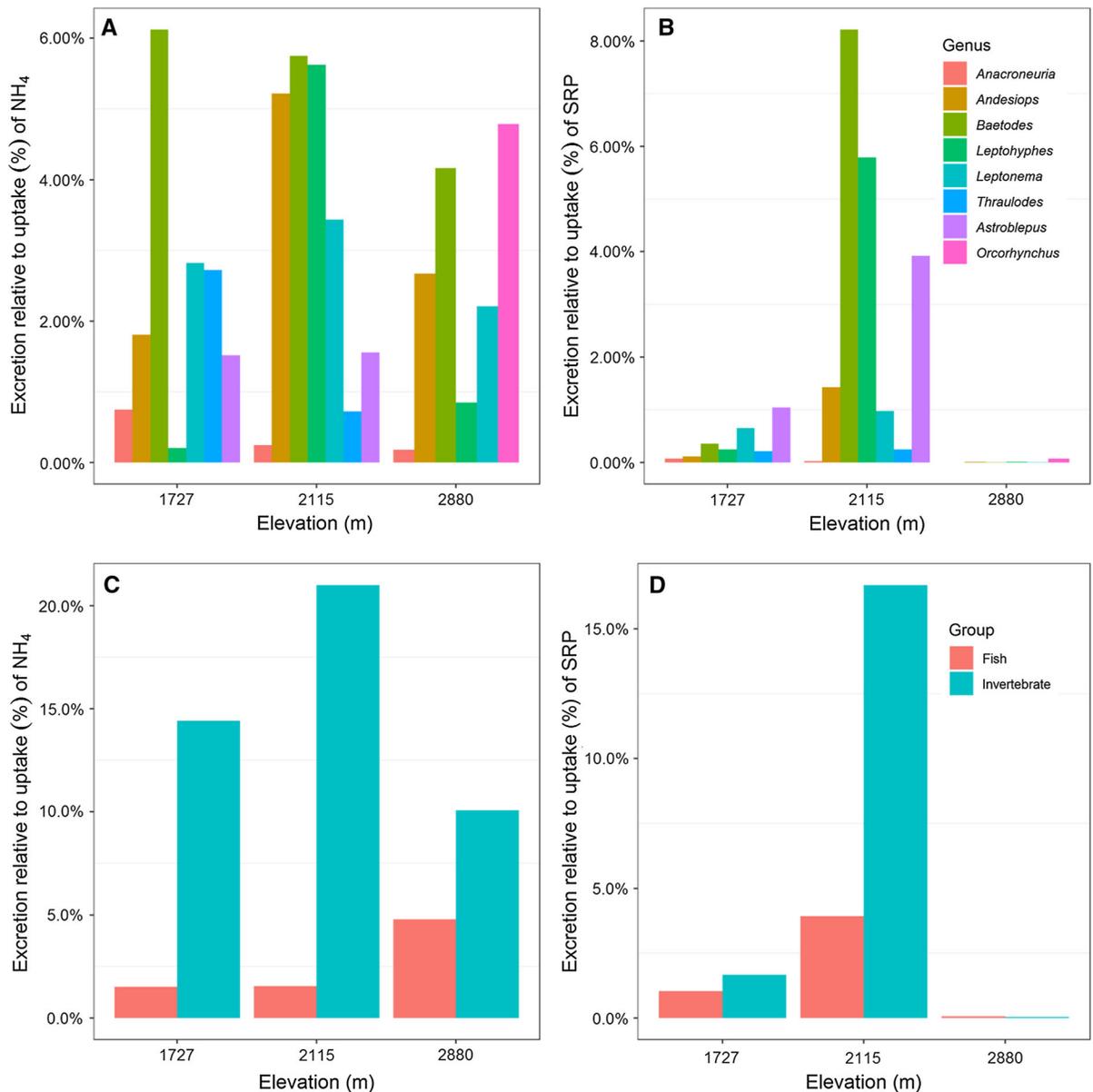


Fig. 4 **A** Areal $\text{NH}_4\text{-N}$ excretion rates of each of our taxonomic groups relative to whole-stream $\text{NH}_4\text{-N}$ uptake at all of our sites. **B** Areal SRP excretion rates of each of our taxonomic groups relative to whole-stream SRP uptake. **C** Areal

$\text{NH}_4\text{-N}$ excretion of invertebrates and fish relative to $\text{NH}_4\text{-N}$ uptake. **D** Areal SRP excretion of invertebrates and fish relative to SRP uptake at all of our sites

had higher mass-specific excretion rates (mayflies in particular), which is in contrast to results found in a previous meta-analysis (Vanni & McIntyre, 2016). However, that analysis included a diverse set of invertebrates (i.e., including molluscs) and vertebrates and our study focused in one system and matches the initial predictions of Vanni & McIntyre (2016).

Another meta-analysis examining variation in excretion rates across taxa (Allgeier et al., 2015) showed that taxonomic identity as well as body size were important predictors and highlighted the complexity in predicting excretion rates; thus, these patterns can be system- and species-specific.

Several studies find that aquatic invertebrate communities can make significant contributions to ecosystem nutrient demand through excretion and it is commonly assumed that closely related species make similar contributions (e.g., Grimm, 1988b; Vanni, 2002; Hall et al., 2003; Atkinson et al., 2017). However, there can be substantial variation in phenotypic and life-history traits such as functional feeding group (Tomanova et al., 2006), nutrient excretion (see Balik et al., 2018), and voltinism (Huryn, 1990; Usseglio-Polatera et al., 2000). Here we noted variation in excretion rates across insect taxa. The mayflies studied here (particularly *Andesiops* and *Baetodes*) select for and assimilate high-quality autochthonous resources in this system (Atkinson et al., 2018a), which also may contribute to their higher excretion rates in comparison to other insect taxa that feed on a greater proportion of allochthonous resources (e.g., *Leptonema*). Future work incorporating species traits and their secondary production or growth rates (i.e., growth rate hypothesis; Elser et al., 2000) with organismal stoichiometry would be useful for predicting the long-term net effect of these organisms on nutrient availability and fluxes (e.g., Capps et al., 2015b; Atkinson et al., 2017). Many tropical aquatic insects are multivoltine (Jackson & Sweeney, 1995) and may have high growth rates, requiring a high P demand (Elser et al., 2000), which may explain the generally high excretion N:P of some of our insect taxa.

These stream ecosystems may be somewhat unique in that they only contain a single fish species. Lower elevation streams downstream in the Napo basin contain a higher diversity of fish (Bojsen and Barriga, 2002) relative to our upland streams, and thus it is possible that fish may contribute more to nutrient demand relative to aquatic insects in lower elevation streams. Furthermore, ongoing studies in the Napo River Basin show a wide range in fish N excretion relative to demand across sites highlighting the need for further study in this area (A. Alexiades, unpublished data). Further, our work only focused on one mechanism linking animals to nutrient cycling (i.e., nutrient excretion), while other effects such as nutrient bioturbation by animals may be just as significant as excretion (Caliman et al., 2007, 2013; Hölker et al., 2015; Hoellein et al., 2017). Introduced trout are widespread and have pervasive top-down effects on streams (Vimos et al., 2015; Martín-Torrijos et al.,

2016) and here we found that their bottom-up effects can also be strong. Introduced trout had high $\text{NH}_4\text{-N}$ and SRP areal excretion rates that exceeded rates of any single insect taxa at the high-elevation site, but their overall contribution to nutrient demand was low. Introduced trout are common in Andean streams (Alexiades & Encalada, 2017), suggesting more work needs to be conducted to elucidate their bottom-up roles across streams with varying densities. The areal excretion rates of the introduced trout found in these tropical highland streams pale in comparison to the areal rates in temperate settings where regular high-density trout stocking is conducted. Nonetheless, these results suggest that non-native fish contribute to the regeneration of nutrients in these headwater tropical streams and further introductions and stocking efforts could affect nutrient dynamics in these systems. While our results suggest that introduced fish may change nutrient availability to primary producers, their top-down impacts via predation, bioturbation, or induced behavioral drift (Schaus et al., 2010; Vimos et al., 2015) could also potentially reduce nutrient recycling rates via consumer communities not assessed in this study (Atkinson et al., 2017).

Our results support the idea that characteristics (e.g., invertebrate vs. vertebrate) of aquatic organisms may be used to predict changes in nutrient availability in the wake of species introductions and species loss (Capps & Flecker, 2013a; Capps et al., 2015a). Changes in nutrient dynamics can be nutrient specific, and organisms may influence remineralization of N and P differently (Small et al., 2011; Atkinson et al., 2017). Capps et al. (2015a) compared three systems to examine the influence of different consumers on nutrient regeneration and storage, and found that freshwater mussels, stream-dwelling tadpoles, and invasive armored catfish were all net remineralizers of N, but the catfish acted as a net sink for P and the mussels and tadpoles acted as sources. Nutrient excretion by consumers has resultant impacts on the recipient ecosystem. Previous work in Panamanian streams has shown that grazing tadpole amphibians can supply up to 40% of nutrient demand and indirectly enhance litter decomposition through their nutrient regeneration (Rugenski et al., 2012; Whiles et al., 2013). Here, fish taxa enhanced P availability more than most of the insect taxa, especially relative to N. This result may be a result of potentially high growth rates, which increases P demand (due to

allocation in RNA; Elser et al., 2000), of some of the invertebrates, reducing their remineralization of P. By further studying the roles of various taxonomic groups on essential functions such as nutrient regeneration and how it varies as a result of gradients in food quality, growth, and predation (Atkinson et al., 2018a; Dalton et al., 2018), we may be able to better understand the impacts of both species invasions and declines on ecosystem structure and function (Capps et al., 2015a).

We found high variability in both the excretion of nutrients by animals and rates of ecosystem scale nutrient uptake across sites. This is due to multiple factors including site variation in mass-specific excretion rates, consumer biomass, and background stream nutrient concentrations (Vanni, 2002; Atkinson et al., 2017). In particular, the streams varied greatly in the biomass of particular taxa. For example, the mid-elevation site had high abundances of mayflies (i.e., *Andesiops*, *Baetodes*, and *Leptohyphes*), exacerbating their larger contribution to nutrient availability at that site. Further, mass-specific excretion rates across all taxa tended to be higher in the smallest mayfly taxa, *Baetodes*, at the warmer, lowest elevation site. When examining site effects, the highest elevation site had the highest background SRP concentration, which is at least partly explains why SRP uptake rates were so high at that site (Dodds et al., 2002; Mulholland et al., 2002), reducing the impact of consumer excretion relative to demand. These higher phosphorus concentrations and the higher uptake rates resulted in animals supplying less of the overall nutrient demand. Our analyses are limited in that we were unable to estimate excretion rates of all aquatic insects, only a subset of the most common species. Also, our metric for estimating uptake has limitations in that it estimates whole-stream uptake and does not discriminate between biological versus non-biological uptake, so actual biological uptake is likely a bit lower. Further work incorporating more taxa would be useful for further examining the importance of different taxonomic guilds and functional feeding groups.

Aquatic consumers can function as essential nutrient remineralizers by strongly influencing the availability of nutrients relative to their demand (McIntyre et al., 2008; Benstead et al., 2010; Atkinson et al., 2014, 2018b). We found that both aquatic insect and fish consumer groups can act to supply a substantial proportion of nutrient demand, but that this was

dependent on the biomass and excretion rate of the consumer group as well as the nutrient demand of the system. Our work builds on the growing body of literature highlighting the essential roles animals play in modifying nutrient cycling (Vanni, 2002; Atkinson et al., 2017). Future work needs to expand to investigations of a larger proportion of the consumer community matched with ecosystem metrics such as nutrient demand and ecosystem metabolism so we can fully understand the role of intact communities on ecosystem function.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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