

REPORT

Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes

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Abstract

Ecological stoichiometry offers a framework for predicting how animal species vary in recycling nutrients, thus providing a mechanism for how animal species identity mediates ecosystem processes. Here we show that variation in the rates and ratios at which 28 vertebrate species (fish, amphibians) recycled nitrogen (N) and phosphorus (P) in a tropical stream supports stoichiometry theory. Mass-specific P excretion rate varied 10-fold among taxa and was negatively related to animal body P content. In addition, the N : P ratio excreted was negatively related to body N : P. Body mass (negatively related to excretion rates) explained additional variance in these excretion parameters. Body P content and P excretion varied much more among taxonomic families than among species within families, suggesting that familial composition may strongly influence ecosystem-wide nutrient cycling. Interspecific variation in nutrient recycling, mediated by phylogenetic constraints on stoichiometry and allometry, illustrates a strong linkage between species identity and ecosystem function.

Keywords

Allometry, amphibians, biodiversity, ecological stoichiometry, ecosystem function, fish, nutrient cycling, streams, tropical, Venezuela.

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INTRODUCTION

Ecologists are currently in the midst of a vigorous debate about the role of biodiversity in ecosystem function (Naeem *et al.* 1994; Tilman & Downing 1994; Huston 1997; Tilman 1999; Chapin *et al.* 2000). Controversy exists over whether ecosystem processes are affected by the number of species (or functional groups of species) present, leading to a variety of hypotheses linking biodiversity and ecosystem function (Naeem *et al.* 1995; Chapin *et al.* 2000). Central to evaluating these hypotheses is the interdependence of species identity and richness. That is, when species or functional groups are lost from an ecosystem, it is difficult to ascertain whether subsequent changes in ecosystem function result from changes in species richness *per se*, or to the loss of particular species that have disproportionately strong effects (Power *et al.* 1996; Huston 1997). Ecologists therefore need quantitative information on the extent to which species differ or are redundant in mediating ecosystem processes (Grimm 1995; Tilman *et al.* 1997; Vitousek & Hooper 1993; Chapin *et al.* 2000).

The theory of ecological stoichiometry (Sterner 1990; Sterner *et al.* 1992; Elser & Urabe 1999) provides a mechanistic framework for how animal species vary in mediating nutrient recycling, a key ecosystem process. Stoichiometry theory states that animals maintain homeostasis in body nutrient composition. Therefore, the rates and ratios by which animals recycle nutrients reflect the nutrient imbalance between their bodies and their food. Two species with similar food nutrient contents but different body nutrient compositions are predicted to recycle nutrients at different rates and ratios. In addition to stoichiometry, allometry dictates that nutrient cycling rates (per unit body mass) should decline with body mass (Peters 1983; West *et al.* 1997).

Despite the conceptual frameworks afforded by ecological stoichiometry and allometry, and the growing recognition that animals can be important in nutrient recycling in aquatic and terrestrial ecosystems (e.g. Grimm 1988; Pastor *et al.* 1993; Vanni 1996; McNaughton *et al.* 1997; Vanni *et al.* 1997; Covich *et al.* 1999; Sirotnak & Huntly 2000), no studies have systematically explored how animal species

identity affects nutrient cycling rates and ratios. For example, although stoichiometry theory was originally developed for freshwater zooplankton, surprisingly few studies have experimentally determined whether actual nutrient recycling rates and ratios can be explained by stoichiometric models even for this group of animals (Elser & Urabe 1999). More broadly, few studies exist on how animal species richness or identity affects ecosystem function, in contrast to numerous recent studies on primary producers and microbes (e.g. Naeem *et al.* 1994; Tilman & Downing 1994; McGrady-Steed *et al.* 1997; Tilman *et al.* 1997; Hooper & Vitousek 1998; Tilman 1999). This is somewhat surprising, because stoichiometry theory can potentially provide a powerful mechanistic explanation for how animal species vary in mediating nutrient cycling.

Tropical aquatic ecosystems offer an excellent opportunity for examining links between animal biodiversity and ecosystem function, because these ecosystems typically exhibit a great diversity of animal species and guilds (Lowe-McConnell 1987; Wootton & Oemke 1992). In addition, some animal species, including fish and invertebrates, can exert strong effects on these ecosystems (e.g. Power *et al.* 1989; Power 1990; Flecker 1992, 1996; Pringle & Hamazaki 1998; Covich *et al.* 1999; Pringle *et al.* 1999; Crowl *et al.* 2001). Here we test the hypothesis that interspecific variation in nutrient recycling rates and ratios can be predicted by ecological stoichiometry and allometry. We show that nutrient recycling rates and ratios of 28 vertebrate species (fish and amphibians) in a tropical stream varied greatly among taxa, and that ecological stoichiometry successfully predicted this variation.

METHODS

Study site

To test the hypothesis that stoichiometry and allometry determine nutrient recycling by animals, we quantified nitrogen (N) and phosphorus (P) recycling (excretion) rates, body mass and body nutrient composition of 26 species of fish and two species of amphibian tadpoles in Rio Las Marias, a fourth-order neotropical stream in the Andean piedmont region of Venezuela. Rio Las Marias contains a diverse assemblage of fish in many taxonomic families and feeding guilds, and fish have strong effects on invertebrates, algae and sediment accrual in this stream (Flecker 1992, 1996; Flecker *et al.* 2002). During the dry season, when this study was conducted, algae in Rio Las Marias are nutrient-limited (Flecker *et al.* 2002), and nutrient excretion by fish may represent a substantial fraction of the N and P needed to sustain algal productivity (Hood 2000). Therefore, interspecific variation in nutrient recycling by consumers has the potential to greatly affect stream ecosystem function.

Quantification of nutrient stoichiometry

We quantified nutrient recycling (excretion) rates and body nutrient composition of 26 species of fish and two species of amphibian tadpoles in the field during three time periods, January, February and March 1998. To quantify excretion rates, we used methods described in Schaus *et al.* (1997). Animals were collected with a backpack electroshocker (Smith-Root Model 15-C; Smith-Root, Inc., Vancouver, WA 98686, USA), seines and dipnets. The electroshocker served mainly to direct animals to seines rather than to stun them, and animals used in this study never lost consciousness. Upon capture, animals were immediately placed in plastic bags (1–20 individuals per bag, depending on body mass) containing 1–3 L of stream water previously filtered through Gelman AE filters to remove particles that might absorb nutrients. When multiple animals were incubated together, all individuals were of similar size. After 1–1.5 h, the contents of bags were filtered through Gelman AE filters to remove faeces and other particles. Animals were removed, measured to the nearest mm and weighed (wet) to the nearest 0.1 g. Filtrate samples were collected in acid-washed Nalgene bottles, frozen and transported on ice to Miami University.

Filtrate samples were analysed manually for ammonia-N using the phenol-hypochlorite method (Solorzano 1969) and total dissolved P (TDP) using the acid-molybdate method (Murphy & Riley 1962) after persulphate digestion. Mass-specific N and P excretion rates were calculated as the change in ammonia-N or TDP per unit time divided by the wet mass of animals. We used TDP instead of the more commonly quantified soluble reactive P (Wen & Peters 1994; Schaus *et al.* 1997) because TDP analyses were more reliable, due to relatively low SRP concentrations in many samples. In total, we measured excretion rates on 332 replicates (bags) over the three time periods. Excretion rate measurements were made roughly in proportion to species abundances, thus the number of excretion replicates varied among species.

To quantify body nutrient contents, entire animals were frozen, then ground to a fine powder with a mortar and pestle and then a dental amalgamator. For some small species, several individuals were ground together, but usually single animals were used. Samples of ground animals were analysed for carbon (C) and N with a Perkin-Elmer Series 2400 CHN analyser and P with HCl digestion followed by SRP analysis (Stainton *et al.* 1977). Although we collected body mass data on all animals used for excretion rate measurements, we could not obtain body nutrient data for all excretion replicates because of difficulties in transporting frozen animals to the USA.

Quantification of nutrient excretion rates by “incubating” animals in containers can conceivably lead to biased estimates if animals behave differently than they do in

nature. However, the method we employed here yields rates very similar to rates obtained from bioenergetics/mass balance modelling in both a temperate fish species (gizzard shad; Mather *et al.* 1995; Schaus *et al.* 1997; Vanni 1996) and two of the armoured catfish (Loricariidae) species examined in this study (Hood 2000). The fact that the two methods agree closely suggests that the rates we present here are not biased by handling methods.

Statistical analyses

To quantify relationships between nutrient recycling parameters and animal nutrient content and body mass, we used simple and multiple linear regression. We regressed excretion rates (N and P) and ratio (N : P) against body mass and body nutrient content using log-transformed data. Because the number of replicate excretion measurements varied among species and because we do not have body nutrient content data for all excretion replicates, we standardized data for all species prior to conducting regression analyses. To do so, we obtained a mean excretion rate, body mass and body nutrient content for each species for each time period (January, February and March) and used these means as observations in regressions. Excretion measurements were not made on all species in all three time periods. In addition, because some animal samples perished, in some cases we have excretion and body mass data but not body nutrient content data.

For multiple regressions, we examined variance inflation factors to assess multicollinearity among the two independent variables (body nutrient content and body mass). In addition, we obtained standardized regression coefficients (β_{std}) to assess the relative influence of the two independent variables on excretion rates and ratios. β_{std} is defined as the change in the dependent variable, in units of standard deviations, resulting from a change of one standard deviation in the corresponding independent variable (Neter *et al.* 1996).

We compared body nutrient contents (N, P) and body N : P ratios using one-way ANOVA on log-transformed data, followed by Tukey's multiple comparison test. We tested for variation among taxonomic families, and among species within a family for those families represented by more than two species.

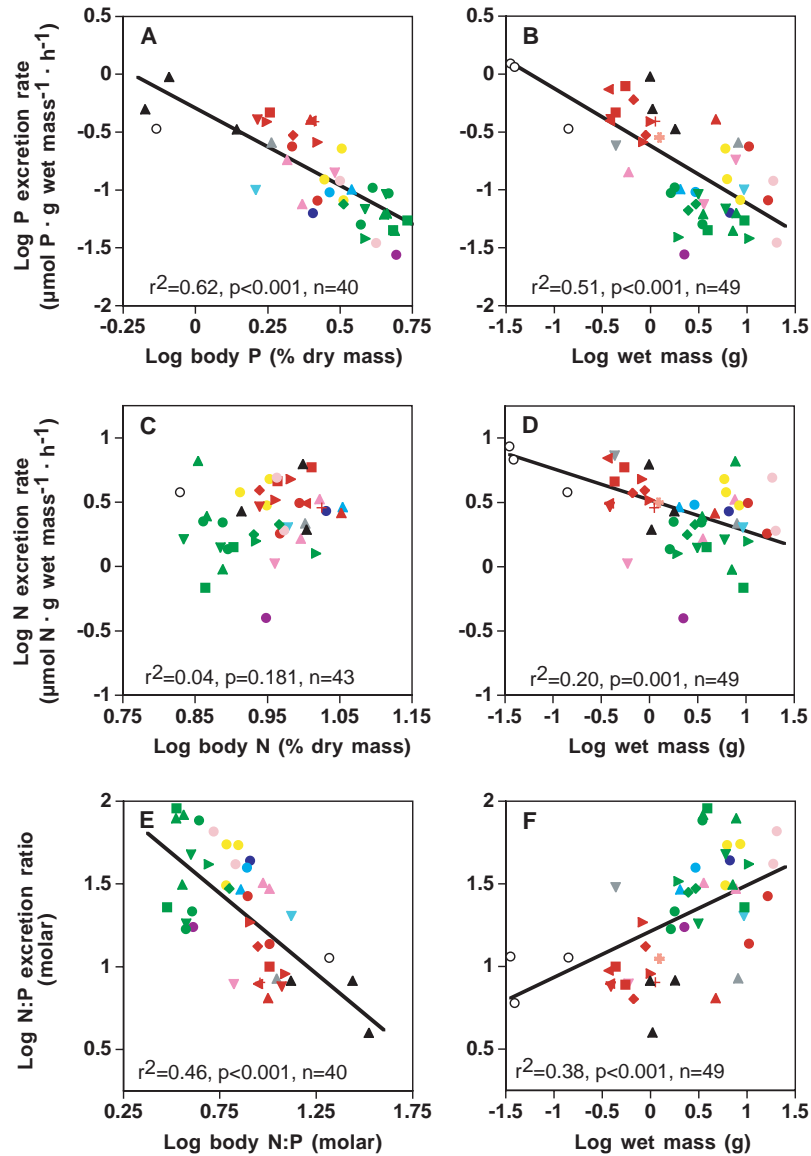
RESULTS

Fish and amphibian species in Rio Las Marias varied more than an order of magnitude in the rates and ratios by which they recycled nutrients (Fig. 1a). Mass-specific P excretion rate was negatively related to body P content (Fig. 1a), in accordance with stoichiometry theory, and negatively related to body mass (Fig. 1b), in accordance with allometry. Body

P explained more variance than body mass in simple regressions (Figs 1a,b), and these two variables together explained 69% of the variance in P excretion rate in multiple regression (Table 1). The standardized regression coefficient (β_{std}) for body P was $> 2 \times$ that for body mass (Table 1), suggesting that body P had a relatively greater influence on P excretion than did body mass. Mass-specific N excretion rate was weakly related to body mass but not to body N (Figs 1c, d). The ratio at which animals excreted N and P (N : P excretion ratio) was negatively related to body N : P ratio, in accordance with stoichiometry theory, and positively related to body mass; body N : P explained more variance in simple regressions (Figs 1e, f). Body N : P ratio and body mass together explained 58% of the variance in N : P excretion ratio in multiple regression. β_{std} was greater for body N : P than for body mass (Table 1), suggesting that body N : P had a relatively greater influence on N : P excretion ratio than did body mass. Body P content predicted N : P excretion ratio almost as well as body N : P (simple linear regression, $r^2 = 0.42$, $P < 0.0001$, $n = 40$), suggesting that interspecific variation in the N : P excretion ratio was caused largely by variation in body P content rather than by body W content. Variance inflation factors for multiple regressions were relatively low (Table 1), suggesting that analyses were not greatly biased by multicollinearity among variables.

The relationship between body P content and P excretion rate was driven largely by variation among families in body P content (Fig. 2a). The families Loricariidae (armoured catfish, represented by six species in this study), Aspredinidae (one species) and Anostomidae (one species) had high body P contents and low P excretion rates (Figs 1a and 2a). At the other extreme, the two tadpole families (one species each) had low body P and high P excretion rates. There was relatively little variation among families in body C or N content, or in body C : N ratio (Figs 2b, c, f). However, body C : P and N : P ratios varied greatly (Figs 2d,e). Loricariids had the lowest body N : P and amphibians the highest. Within families for which we have data on several species (Loricariidae and Characidae), there was relatively little variation among species in body P content (Fig. 3).

Variation among taxa in N : P excretion ratio, and how this relates to body N : P, is illustrated by plotting N excretion rate versus P excretion rate along with isoclines of N : P excretion ratio (Fig. 4). Families with high body P and hence low body N : P (Loricariidae, Anostomidae and Aspredinidae) consistently had high N : P excretion ratios (always > 10 and usually > 20 ; Fig. 4). In contrast, amphibians, which have low body P and high body N : P, usually had N : P excretion ratios < 10 . Other families had intermediate N : P excretion ratios but tended to show some consistency within a family. For example, characid N : P excretion ratios were usually near 10 (Fig. 4). N excretion



- *Ancistrus triradiatus* (LO)
- ▲ *Chaetostoma milesi* (LO)
- *Farlowella vittata* (LO)
- ◆ *Hypostomus* sp. (LO)
- ▼ *Lasiancistrus* sp. (LO)
- ▶ *Spatuloricaria gymnogaster* (LO)
- *Bufo marinus* (BU)
- ▲ *Rana palmipes* (RA)
- *Leporinus striatus* (AN)
- *Bunocephalus amaurus* (AS)
- ▼ *Pseudocetopsis* sp. (CE)
- *Astyanax integer* (CH)
- ▲ *Astyanax metae* (CH)
- *Bryconamericus deuterodonoides* (CH)
- ◆ *Cheirodon pulcher* (CH)
- ▼ *Cheirodontops geayi* (CH)
- ▶ *Creagrutus beni* (CH)
- ◀ *Gephyrochyrax valencia* (CH)
- +
- ◆ *Roeboides dayi* (CH)
- ◆ *Characidium boaevistae* (CR)
- *Cyphocharax spiluris* (CU)
- *Parodon apolinari* (PA)
- ▼ *Microglanis iheringi* (PI)
- ▲ *Pimelodella* sp. (PI)
- ▼ *Ochmanthus alternus* (TR)
- ▲ *Trichomycterus* sp. (TR)
- Regression lines

Figure 1 Regressions of excretion rates and ratio versus body nutrient contents and body mass. Each point represents a mean for a species during a particular time period. Each family is represented by a different colour and, within families, each species by a different symbol. Family codes: LO = Loricariidae; BU = Bufonidae; RA = Ranidae; AN = Anostomidae; AS = Aspredinidae; CE = Cetopsidae; CH = Characidae; CR = Characidiidae; CI = Cichlidae; CU = Curimatidae; PA = Parodontidae; PI = Pimelodidae; TR = Trichomycteridae.

Table 1 Results of multiple regressions to predict P excretion rate and N : P ratio excreted

Parameter	Estimate (SE)	<i>P</i>	Sum of Squares	<i>F</i> -ratio	Variance inflation factor	Standardized regression coefficient
Log P excretion rate						
Intercept	- 0.293 (0.077)	0.0005	-	-	-	-
Log body P (% dry mass)	- 1.120 (0.182)	< 0.0001	1.881	37.825	1.30	- 0.647
Log wet body mass (g)	- 0.218 (0.078)	0.0086	0.383	7.077	1.30	- 0.292
Log N : P excretion ratio						
Intercept	1.842 (0.171)	< 0.0001	-	-	-	-
Log body N : P ratio	- 0.735 (0.170)	0.0001	1.063	18.720	1.22	- 0.507
Log wet body mass (g)	0.274 (0.081)	0.0017	0.647	11.404	1.22	0.396

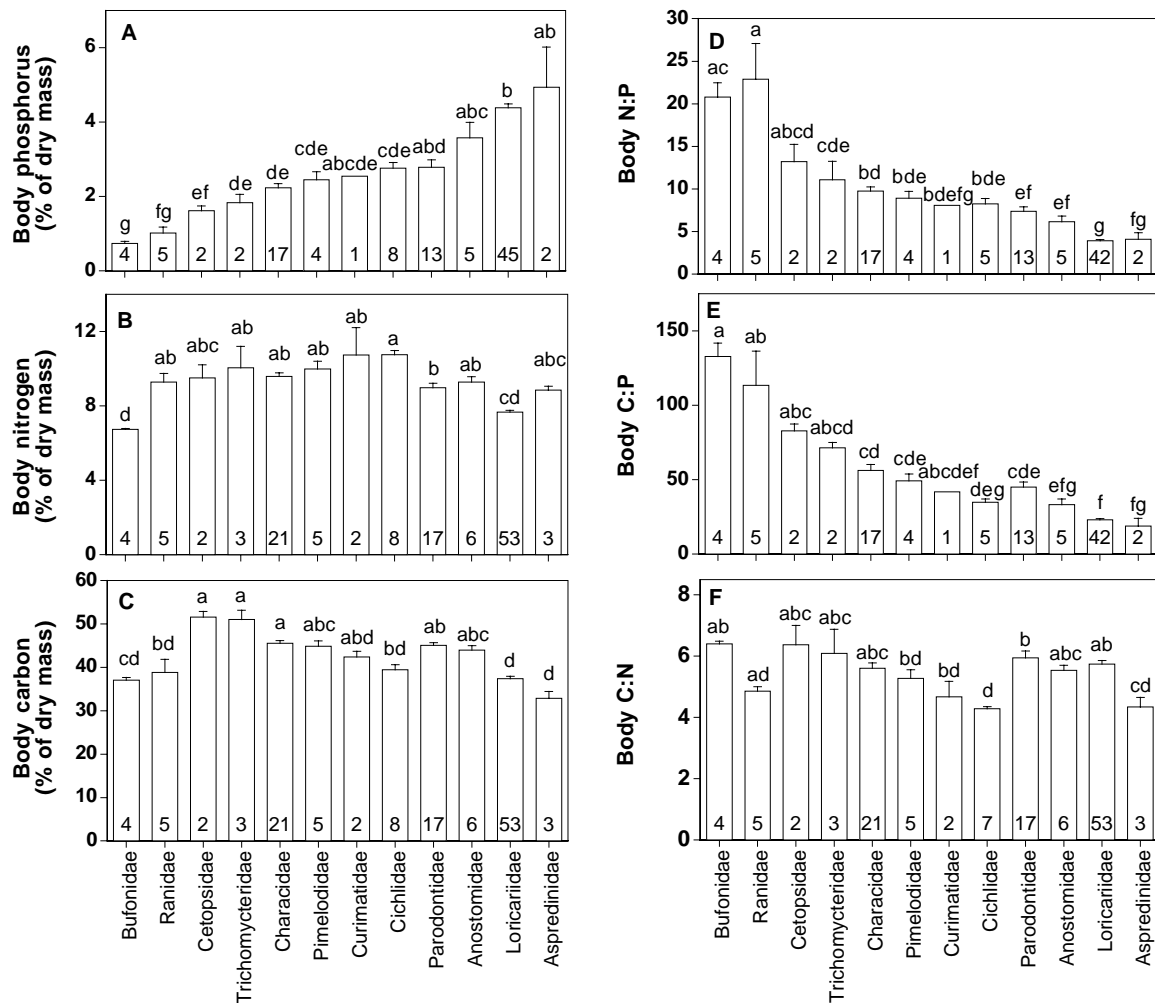


Figure 2 Mean (and SE) whole-body C, N, P contents and nutrient ratios of fish and amphibian families. Numbers at the base of bars represent the number of replicates assayed for nutrient contents. A replicate consisted of a single animal, or of multiple animals ground together, depending on body size. Means sharing common letters (above bars) are not significantly different from one another ($P < 0.05$, one-way ANOVA and Tukey multiple comparison).

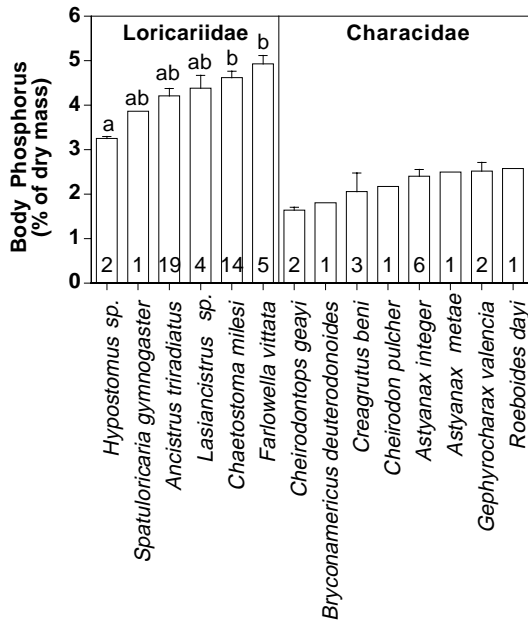


Figure 3 Mean (and SE) whole-body P of individual species in the families Loricariidae and Characidae. Numbers above bars, letters above bars, definition of replicates, and statistical analyses as in Fig. 2. No significant differences existed between characid species.

rate and P excretion rate were highly correlated with each other, but the slope of the regression line was substantially less than unity ($\log N$ excretion rate = $0.772 + 0.438 \log P$ excretion rate, $r^2 = 0.501$). Thus, as P excretion rate increases, N excretion rate also increases but at a slower rate, resulting in a negative relationship between P excretion rate and N : P excretion ratio ($\log N : P$ excretion ratio = $0.783 - 0.642 \log P$ excretion rate, $r^2 = 0.639$).

DISCUSSION

Chapin *et al.* 2000). Our results show that taxonomic identity of consumers may be important in determining the rates and ratios by which nutrients are recycled, and that variation among taxa can be at least partially explained by ecological stoichiometry. In terms of the number of taxa investigated, our study is the most comprehensive assessment to date of how animal species vary in the rates and ratios at which they recycle nutrients, and provides compelling evidence that variation in animal species identity can affect ecosystem function. Variation among consumers in their excretion rates and N : P excretion ratios may be important because this variation may influence overall nutrient flux, primary production rates, and the extent to which primary producers are limited by N vs. P (Elser *et al.* 1988; Sterner 1990; Sterner *et al.* 1992; Vanni 1996; Vanni *et al.* 1997; Elser & Urabe 1999).

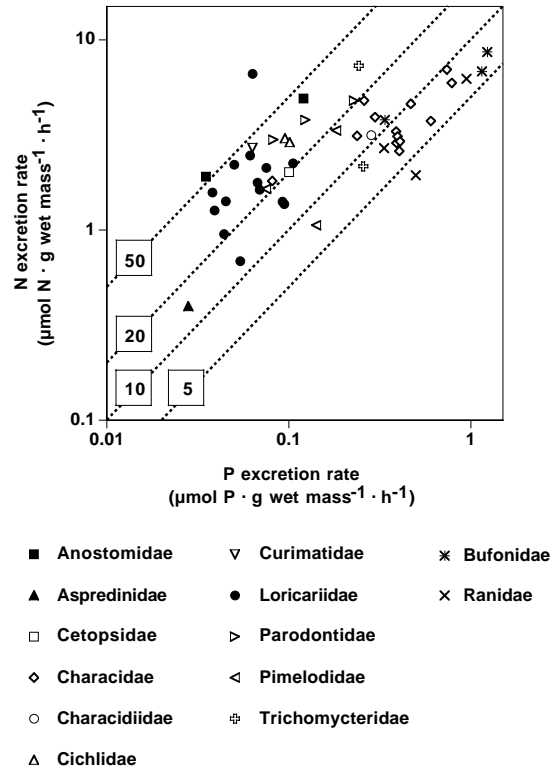


Figure 4 Plot of N excretion rate versus P excretion rate. Each point represents a species mean, as in Fig. 1. Solid symbols represent species with high body P content, open symbols represent fish species with low body P, and stars/crosses represent amphibians. Dashed lines represent N : P excretion ratios.

From the perspective of ecosystem functioning in Rio Las Marias, variation among taxa in excretion rates and ratios will be important only if vertebrates supply a significant quantity of nutrients relative to nutrients needed to sustain algal and bacterial production. Hood (2000) showed that two abundant loricariids, *Ancistrus triradiatus* and *Chaetostoma milesi*, could together supply 10–13% of N and 9–48% of P demand by algae in Rio Las Marias. Algal demand estimates were based on measurements of primary production, using oxygen evolution in light and dark containers, and algal nutrient composition, on two dates in 1999 (Hood 2000). To evaluate the importance of the entire fish assemblage in sustaining primary production, we used excretion rates from our study (Fig. 1) and fish population density estimates from 1999 (Hood 2000) to obtain a population-wide nutrient excretion estimate for each of the 22 most abundant fish species. (Amphibian densities are not available but they are low in most years). One important fish species, *Prochilodus mariae*, was not included in our 1998 excretion survey (Fig. 1), so we used *Prochilodus* excretion estimates from 1999 (Hood *et al.*, unpublished data). Population-wide

excretion rates were summed to obtain total excretion by the assemblage and compared with the algal nutrient demand estimates in Hood (2000). Based on these calculations, the Rio Las Marias fish assemblage can provide 49% and 126% of algal demand for N and P, respectively. It is possible that we underestimated primary production (hence algal nutrient demand) because there was no water flow in the containers used to measure primary production (Stevenson 1996). However, even if actual algal nutrient demand is twice as high as our estimates suggest, nutrient cycling by fish appears to be very important for ecosystem functioning in Rio Las Marias.

Our results suggest that consumer family identity, more so than species identity, may be critical in explaining variance in nutrient recycling rates and ratios in neotropical streams. Within families for which we have data on several species (Loricariidae and Characidae), differences among species in nutrient excretion rates were relatively small, suggesting that species within a family show considerable "biogeochemical redundancy" (Grimm 1995), at least in terms of nutrient cycling. In contrast, differences among families in P excretion rate and N : P excretion ratio were sometimes quite large, suggesting that there is considerably less biogeochemical redundancy among families than among species within a family. In tropical ecosystems, the relative abundance of the family Loricariidae (armoured catfish) may be particularly important for nutrient dynamics. Loricariids are abundant and widespread (> 600 species in the neotropics; Lowe-McConnell 1987), and often have strong effects on tropical stream food webs (Power *et al.* 1989; Power 1990; Flecker 1992). Several other fish families represented in our study (e.g. Characidae, Pimelodidae, Trichomycteridae), as well as amphibians, are also common in many tropical waters (Lowe-McConnell 1987). Loricariids have high body P, low P excretion rates and high N : P excretion ratios (Fig. 1), while these other common taxa have low body P, relatively high P excretion rates and/or low N : P excretion ratios. Thus the relative abundance of loricariids versus these other families may be critical in determining ecosystem-level nutrient cycling.

Family affiliation appeared to have a greater effect on nutrient cycling than feeding guild affiliation in our study. For example, tadpoles, *Parodon* and most loricariids are grazers, consuming algae and detritus, yet they recycle nutrients at very different rates and ratios (Fig. 1). Likewise, the loricariid *Spatuloricaria gymnogaster* has a diet comprised largely of invertebrates (A.S. Flecker and B.A. Daley, unpublished data), yet recycled nutrients at rates and ratios similar to other loricariid species that are grazers. The lack of a functional group effect contrasts with studies on plants that show strong effects of functional group identity on ecosystem processes, including nutrient cycling (Tilman *et al.* 1997; Hooper & Vitousek 1998).

Although family affiliation emerged as a key variable in explaining nutrient stoichiometry, variation in nutrient cycling was not readily predicted by higher levels of taxonomic organization. Thus, while amphibians have P excretion rates and N : P excretion ratios that are somewhat distinct from fishes, different taxonomic orders of fish are not clearly separable in terms of nutrient cycling. For example, there was no overall distinction in nutrient cycling between catfish (Order Siluriformes), tetras (Characiformes) and cichlids (Perciformes). Some catfish families (Loricariidae, Aspredinidae) had low body N : P, low P excretion rates and high N : P excretion ratios, while other catfish (Cetopsidae, Pimelodidae and Trichomycteridae) did not (Figs 1 and 2). Similarly, the characiform family Anostomidae was more similar to loricariids and aspredinids in terms of body nutrients and nutrient cycling than to other characiform families (Characidae, Characidiidae, Curimatidae and Parodontidae). With regard to even broader phylogenetic patterns, vertebrates will generally sequester relatively more P in their bodies than invertebrates because of the higher P content of vertebrate bodies. For example, the mean P content of fish bodies in our study is about $2.5 \times$ higher, and the C : P and N : P ratios about $2.5 \times$ lower, than the bodies of herbivorous zooplankton or terrestrial insect herbivores (Elser *et al.* 2000). Thus, the relative abundance of invertebrates versus vertebrates may play a large role in determining the rates and ratios at which animal assemblages recycle nutrients.

Our results show that body size is also important in determining nutrient recycling rates and ratios, in accordance with prior studies (Peters 1983; Wen & Peters 1994; Schaus *et al.* 1997). Both natural and anthropogenic influences can affect body size. Fish, birds and humans all are size-selective predators and can greatly affect size structure and species composition of tropical fish assemblages (Power 1984; Lowe-McConnell 1987; Power *et al.* 1989). Loricariids, for example, are fished commercially in many neotropical areas (Lowe-McConnell 1987). Our results indicate that disruptions of size-structure, as well as taxonomic composition, could have important indirect effects on nutrient cycling.

Our results demonstrate a phylogenetic constraint on the stoichiometry of consumer nutrient recycling. Loricariids have evolved bony armour, presumably as a defence against predators (Vermeij 1987). Because armour contains much phosphorus, loricariids must sequester relatively more dietary P in their bodies than most other groups of fish. Amphibians have evolved a complex life cycle, including tadpoles that sequester little P, presumably because they do not ossify their bones until late in development (Burggren & Just 1992). Thus, taxonomic variation in body nutrient composition may be constrained by selective pressures on traits seemingly unrelated to

nutrient balance, with potentially profound effects on the relationship between biodiversity and ecosystem function. A close association between anti-predation defence and nutrient cycling is not unprecedented. Indeed, in terrestrial plants, the relative availability of light and nitrogen determines the C : N ratio in plant tissue as well as the production of carbon-based versus nitrogen-based chemical defences against herbivores (Bryant *et al.* 1983).

The debate over whether biodiversity affects ecosystem function has focused largely on how the number and identity of species (or functional groups of species) affect ecosystem processes, and has centred mostly on plant and decomposer species. Our results suggest that it may be fruitful to further explore how variation in the number and identity of consumer families mediates ecosystem processes, and that ecological stoichiometry can provide a predictive framework to guide exploration of this variation.

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