

# Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis

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**Abstract.** The metabolic theory of ecology (MTE) and ecological stoichiometry (ES) are both prominent frameworks for understanding energy and nutrient budgets of organisms. We tested their separate and joint power to predict nitrogen (N) and phosphorus (P) excretion rates of ectothermic aquatic invertebrate and vertebrate animals (10,534 observations worldwide). MTE variables (body size, temperature) performed better than ES variables (trophic guild, vertebrate classification, body N:P) in predicting excretion rates, but the best models included variables from both frameworks. Size scaling coefficients were significantly lower than predicted by MTE ( $<0.75$ ), were lower for P than N, and varied greatly among species. Contrary to expectations under ES, vertebrates excreted both N and P at higher rates than invertebrates despite having more nutrient-rich bodies, and primary consumers excreted as much nutrients as carnivores despite having nutrient-poor diets. Accounting for body N:P hardly improved upon predictions from treating vertebrate classification categorically. We conclude that basic data on body size, water temperature, trophic guild, and vertebrate classification are sufficient to make general estimates of nutrient excretion rates for any animal taxon or aquatic ecosystem. Nonetheless, dramatic interspecific variation in size-scaling coefficients and counter-intuitive patterns with respect to diet and body composition underscore the need for field data on consumption and egestion rates. Together, MTE and ES provide a powerful conceptual basis for interpreting and predicting nutrient recycling rates of aquatic animals worldwide.

**Key words:** animals; biogeochemistry; ecosystems; freshwater; global; global studies; lakes/ponds; limnology/hydrology; marine; physiological ecology; reservoirs; rivers/streams.

## INTRODUCTION

Metabolic ecology and ecological stoichiometry are prominent frameworks for understanding the demands of individual organisms for energy and nutrients, and the resulting relationship between diet, growth, and wastes. Body size and temperature effectively predict many biological rates (Peters 1983), and the metabolic theory of ecology (MTE) provides a firm theoretical basis for these relationships (Brown et al. 2004). Ecological stoichiometry (ES) focuses on the dynamic balance of multiple elements during foraging, maintenance, growth, reproduction, and waste production (Sterner and Elser 2002). Ecologists have long recognized that the processing of energy and matter are intricately linked (Reiners 1986), but the MTE and ES frameworks have not been well integrated, theoretically or empirically (Allen and Gillooly 2009). Indeed, both MTE and ES make independent predictions about energy use and nutrient processing at various levels of biological organization, from subcellular to ecosystems (Sterner and Elser 2002, Brown et al. 2004). Here, we synthesize data from freshwater and marine ecosystems worldwide to test the power of the

MTE and ES frameworks for predicting nutrient excretion rates of aquatic animals in nature.

Body size profoundly affects physiological rates of organisms, particularly energy use (Gillooly et al. 2001, Brown et al. 2004). This relationship is described by the power-function scaling of metabolic rate ( $B$ ) with body mass ( $M$ ) as  $B = B_0 M^b$ , where  $B_0$  is a “normalization constant” and  $b$  is an allometric “scaling coefficient.” MTE provides a theoretical basis for expecting scaling coefficients of  $\sim 0.75$  in order to optimize transport through fractal networks such as circulatory systems (West et al. 1997), although this prediction remains controversial (Isaac and Carbone 2010). Even when scaling coefficients fitted across taxa converge on 0.75, both normalization constants and scaling coefficients for metabolic rates vary greatly among species (Isaac and Carbone 2010, Hudson et al. 2013). MTE also recognizes that biological rates increase with body temperature, generally by  $\sim 1.5$  to  $3\times$  with a  $10^\circ\text{C}$  increase, although this factor (“ $Q_{10}$ ”) varies greatly interspecifically (Clarke 2004). Together, body size and body temperature provide accurate predictions of individual metabolic rates across all organisms (Gillooly et al. 2001). Although MTE mostly focuses on metabolic rates, it is assumed to apply to many physiological processes, including nutrient excretion (Allen and Gillooly 2009).

Based on the law of mass balance, ES predicts that disparities between the elemental composition of an

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organism's body and its food resources will dictate nutrient processing rates and ratios. The ES perspective is often distilled into comparisons of elemental ratios, such as nitrogen to phosphorus (N:P) or carbon to nutrient (C:N, C:P), between consumer and resource (Sternler and Elser 2002). Mismatches between ratios reveal which element is relatively scarce in the diet, and thus could limit consumer growth (Frost et al. 2006), and which is available in excess such that it should be released as waste (Sternler and Elser 2002). By extension, a positive relationship between dietary N:P and waste N:P is expected across consumers of comparable body N:P (Sternler 1990). ES also predicts that an animal with P-rich tissues (low body N:P) must sequester more dietary P in order to grow than a counterpart with high body N:P, resulting in a broad negative correlation between body N:P and waste N:P among consumers with similar diets (Sternler 1990, Sternler and Elser 2002). Often, differences in body P (and N:P) are driven by size- or taxon-specific patterns of investment in P-rich materials such as skeletal bone or RNA (Gillooly et al. 2005). The power of ES lies in using both body and diet composition to predict systematic differences in nutrient recycling among species and size classes of consumers.

Conceptual integration of MTE and ES frameworks has proceeded slowly (Allen and Gillooly 2009) but has been informative (Schindler and Eby 1997, Frost et al. 2006, Jeyasingh 2007, Allgeier et al. 2015, Cross et al. 2015). In the context of nutrient recycling, body size and temperature are recognized as key mediators of nutrient excretion rates even though MTE does not explicitly use nutrients as a currency (Hall et al. 2007, Habeck and Meehan 2008, Sereda and Hudson 2011). Thus, energetics and nutrient mass balance have been combined to determine whether animal growth is likely to be limited by energy or nutrients (Frost et al. 2006), and the consequences for nutrient excretion (Schindler and Eby 1997). These insights show that melding MTE and ES may be requisite to achieving a predictive understanding of controls on nutrient recycling. However, a recent analysis from a subtropical marine ecosystem showed that body size was the primary driver of variation in excretion rates across 102 species of invertebrates and fish, while body nutrient content and trophic position (which broadly reflects diet) explained relatively little variance (Allgeier et al. 2015). The fact that an MTE predictor outperformed ES variables in this landmark study suggests a need for broader tests of the independent and joint power of MTE and ES to predict nutrient recycling rates in nature (Barneche and Allen 2015).

In this paper, we synthesize nutrient excretion data from freshwater and marine animals worldwide to address three issues. First, we assess the relative influence of MTE and ES variables on N and P excretion rates and excreted N:P, and whether merging these frameworks enhances predictive power over using either framework alone. Second, we quantify how broadly scaling coefficients for excretion rates vary among taxa, building on recent evidence for interspecific differences in size-scaling of both metabolic rates (Isaac and Carbone 2010, Hudson

et al. 2013) and nutrient excretion rates (Allgeier et al. 2015). Third, we evaluate the potential for "universal" models to provide reasonable estimates of N and P excretion by individual animals without direct measurements. Our overarching goal was to use extensive natural variation in body size, temperature, diet, and body composition across the world's freshwater and marine animals (Appendix S1: Table S1) to identify the most important MTE and ES predictors.

We used mixed effect models to test key variables from each theoretical framework. MTE predictor variables included body size and temperature, and ES predictors included body N:P (when available), trophic guild (a categorical proxy for dietary nutrient content; Cross et al. 2005), and what we call "vertebrate classification." Both invertebrate (57% of observations) and vertebrate (43%) ectothermic animals were well represented in our data set, and fundamental differences in body P arising from building bones (Sternler and Elser 2002) suggest that vertebrate classification could be an informative factor in lieu of direct body composition data. We predicted that models including both MTE and ES would explain more variation in N and P excretion rates than models including either framework alone. We also expected that scaling coefficients ( $b \sim 0.75$ ) and temperature dependence ( $Q_{10} \sim 2$ ) would be similar for N and P. We also expected that excreted N:P would be unrelated to body size (because N and P excretion rates are predicted to scale similarly with body size) but would be consistently higher for vertebrates than invertebrates due to requirements for building P-rich bones, and that differences among trophic guilds in dietary N:P would be reflected in excreted N:P across taxa. Inspired by growing evidence of interspecific variation in normalization constants and scaling coefficients (Isaac and Carbone 2010, Hudson et al. 2013, Allgeier et al. 2015), we began by evaluating the importance of including species identity as a random factor. We then adopted a model selection approach to compare models that differed in their representation of MTE and ES predictors. Fitting the best model structure for each nutrient excretion variable to our database of 491 species offers a strong test of the predictability of nutrient excretion by animals in freshwater and marine environments worldwide.

## METHODS

### *Data sources and selection of variables*

We compiled N and P excretion rates of marine and freshwater animals from a wide range of taxa and ecosystems. Because we were interested in predicting excretion rates in nature, we did not include data from laboratory studies. All excretion rates are derived from experimental incubations of wild-caught animals in measured volumes of water taken from the collection habitat and maintained at or close to temperatures in situ. During incubations, animals are separated from potential food resources because these resources can

release or take up nutrients. Because excretion rates are lower in fasting animals, incubations are typically short (median 1.3 h in our data) so that they can be assumed to reflect excretion rates of animals feeding naturally. Stress can also be an issue for wild-caught animals; Whiles et al. (2009) found that stress induced during collection and incubation can double or triple short-term N excretion rate. However, our synthesis encompasses >6 orders of magnitude variation in nutrient excretion rates, so variation among taxa or studies in incubation stress is unlikely to bias our results.

Searches on Web of Science and Google Scholar yielded thousands of papers that did not report nutrient excretion under field conditions; therefore, we scoured papers that cited, and were cited by, key reviews (Andersson et al. 1988, Sterner 1990, Vanni 2002, Hall et al. 2007, Sereda and Hudson 2011), and repeated this process for each paper found. Our dataset contains 10,534 observations of N and/or P excretion rates from 92 separate sources encompassing 491 species (Appendix S1: Table S1). An observation represents an excretion rate of a single animal or multiple small individuals incubated together. The dataset includes most aquatic invertebrate phyla as well as numerous fishes and some amphibians and turtles. Body size ranged >8 orders of magnitude, from <1  $\mu\text{g}$  to >500 g dry mass (25th and 75th percentiles: 0.0013, 1.43 g), and water temperature ranged from  $-1.9^\circ$  to  $33.5^\circ\text{C}$  (25th and 75th percentiles: 17,  $25^\circ\text{C}$ ).

In our mixed models, predictor variables included  $\log_{10}$  body mass (g dry), temperature ( $^\circ\text{C}$ ), body N:P (molar), trophic guild, and vertebrate classification. Dependent variables were N and P excretion rates ( $\log_{10}$ -transformed) and excreted N:P (molar). Trophic guild was represented by broad categories that reflect an unambiguously increasing rank order of dietary N and P content (Cross et al. 2005). Categories (and their diets) included primary consumer (algae and/or detritus), omnivore (algae/detritus and invertebrates), invertivore, generalized carnivore (invertebrates and fish), and piscivore.

Our set of predictor variables requires three important assumptions. First, about 20% of observations ( $n = 2,081$ ) reported body N:P and excretion rates on the same individuals; for all others, we estimated body N:P using data from the same or related species. This substitution assumes that phylogenetic conservatism constrains conspecific populations or related species to be similar in body nutrient content, although we recognize that phylogenetic influences on body nutrient composition can be inconsistent across lineages and chemical elements (Fagan et al. 2002, González et al. 2011). To test the sensitivity of our inferences to various levels of stringency in body N:P data selection, we compared models fitted to a nested series of datasets for which (1) both body N:P and excretion were measured on the same individuals ( $n = 2,081$ ), or (2) we also included individuals for which mean body N:P was estimated from other individuals of the same species in the same study, or (3) we also included mean body N:P reported for the same species in other

studies, or (4) we also included mean body N:P of congeneric species reported in any study (all data).

Our second key assumption was that N:P is an appropriate representation of body stoichiometry for predicting N or P excretion rates. To test whether alternative measures of body stoichiometry (C:N, C:P) are better predictors because they reflect the balance between energy (C) and nutrient limitation of animals (Schindler and Eby 1997, Frost et al. 2006), we compared the explanatory power of models using body N:P, C:N, or C:P as the predictive metric for body stoichiometry. Finally, our third assumption was that trophic guilds capture qualitative differences in dietary stoichiometry. Direct measurements of ingested items are rarely available and bulk nutrient content of typical diet items fails to appropriately reflect selective feeding (Dodds et al. 2014), hence quantitative dietary data are scarce. Moreover, average dietary nutrient content differs greatly among guilds, generally exceeding variation within a guild (Elser et al. 2000, Cross et al. 2005, McIntyre and Flecker 2010). Thus, trophic guilds offer the only feasible means of characterizing dietary differences in a global synthesis, and provide a useful proxy for profound differences in dietary N and P content (Cross et al. 2005).

#### *Statistical analyses*

We adopted a two-step selection process to optimize the structure of predictive models (Appendix S1: Table S2). First, we assessed the utility of fitting species-specific coefficients, intercepts, or both to quantify random effects on the size-scaling of excretion alongside the fixed effects of MTE and ES predictors. We compared AIC for these three formulations using simple (body size only) and complex (body size, temperature, trophic guild, vertebrate classification, body N:P) predictor sets for N and P excretion and excreted N:P.

Second, we used the most parsimonious model structure from the first step to test the relative importance of MTE and ES predictors. We compared AIC among six models reflecting varying combinations of predictors representing MTE (size, temperature), ES (trophic guild, body N:P, vertebrate classification), and their interactions (Table 1). For this second round of model selection, we used a dataset for which all predictors were available and  $n \geq 6$  observations per species ( $n = 8,028, 6,961$  and  $6,481$  for N, P and N:P, respectively). Each observation was weighted as the inverse of sample size for its species to equalize influence across species. We used  $\Delta\text{AIC} > 2$  as a criterion to guide model selection, supplemented by RMSE comparisons to assess differences in prediction accuracy. Our guiding principle was that if AIC and RMSE are similar, the model with the fewest variables is preferable because it maximizes the potential to predict excretion rates in ecosystems where few data are available.

Finally, the preferred model structures for N, P, and excreted N:P identified by our two-step selection process were fitted to our entire dataset to yield “universal”

TABLE 1. Comparisons of models predicting nitrogen excretion, phosphorus excretion, and excreted N:P using predictors from the metabolic theory of ecology (MTE), ecological stoichiometry (ES), or both (MTE + ES).

Model type	Predictor variables	N excretion ( $n = 8,028$ )		P excretion ( $n = 6,961$ )		Excreted N:P ( $n = 6,481$ )	
		AIC	RMSE	AIC	RMSE	AIC	RMSE
MTE	Mass	8,274	0.0467	11,859	0.0643	<b>84,164</b>	<b>19.99</b>
MTE	Mass, Temp	8,021	0.0463	11,709	0.0638	84,163	19.99
ES	Diet, Vert, Body N:P	12,897	0.0640	13,842	0.0752	84,176	20.00
MTE + ES	Mass, Temp, Diet, Vert	<b>7,916</b>	<b>0.0463</b>	<b>11,629</b>	<b>0.0636</b>	84,170	20.00
MTE + ES	Mass, Temp, Diet, Vert, Body N:P	7,914	0.0463	11,622	0.0636	84,169	19.99
MTE + ES	Mass, Temp, Diet, Vert, Body N:P, Interactions	7,736	0.0454	11,476	0.0625	84,202	19.93

*Notes:* Models of N and P excretion rates (but not excreted N:P) included random effects of species identity on both size-scaling coefficients and intercepts (see Appendix S1: Table S2).  $n$  refers to the total number of individual observations fitted in each model. Bold font indicates our preferred model based on the combination of parsimonious fitting (AIC), prediction accuracy (RMSE), and generality (interactions complicate interpretation; body N:P limits application). Predictors include  $\log_{10}$  dry mass (Mass), water temperature (Temp), vertebrate classification (Vert), body stoichiometry (Body N:P), and all factorial interactions (Interactions).

models. All species were included, regardless of sample size, but weighting was again used to equalize species' influence. The fixed effect coefficients from these models represent our best estimate of how excretion rates and excreted N:P vary across all sites and species after accounting for species-specific variation. From our universal models, we can identify generalized allometric scaling coefficients for comparison to the predicted value of 0.75. In addition, we converted temperature coefficients from the models to  $Q_{10}$  values. Although Gillooly et al. (2001) suggest that "universal temperature dependence (UTD)" is the best way to describe how rates vary with temperature, we present  $Q_{10}$  here because it lends itself to intuitive interpretation, it is more common in the ecological literature, and there is no theoretical advantage of UTD over  $Q_{10}$  (Clarke 2004).

To test how well intraspecific size-scaling coefficients match the generalized coefficients from universal models, we fit scaling coefficients for each species with  $n \geq 6$ . We then compared the frequency distribution of statistically significant species-specific scaling coefficients against the scaling coefficient from the universal model. Separate comparisons were performed for vertebrates and invertebrates. Preliminary analyses indicated that results of these comparisons were unchanged when we also required a minimum range of variation in body size within each species, therefore no such requirement was used.

To fit models, we used Proc Mixed in SAS v9.3 (SAS Institute, Cary, North Carolina, USA) with standard maximum likelihood estimation and Kenward-Roger degrees of freedom for fixed effects.

## RESULTS

### *Model selection*

Using a subset of our data that includes all species with  $\geq 6$  observations, the preferred model structure included

species-specific normalization constants (intercepts) and scaling coefficients (slopes) for both N and P excretion rates (Appendix S1: Table S2). In contrast, the best model for excreted N:P included only a species-specific intercept term. For excreted N:P, the model with both coefficients and intercepts did not converge, but fitting intercepts alone was far superior to scaling coefficients alone ( $\Delta\text{AIC} > 649$ ). To further evaluate whether species-specific coefficients are needed to predict excreted N:P, we tested a size-species interaction term in an ANCOVA model with species treated as a fixed factor. There was no significant interaction in simple or complex predictor sets (both  $P > 0.27$ ), suggesting consistent intraspecific scaling of excreted N:P. Thus, all subsequent models use species-specific coefficients and intercepts for N and P excretion, but only intercepts for excreted N:P.

Though we used a quantitative model selection process to compare MTE, ES, and combined models, choosing final models also involved a subjective balance between explanatory parsimony (based on AIC), prediction accuracy (based on RMSE), and general applicability (based on minimizing data requirements). Body size alone was a strong predictor of N and P excretion rates (Fig. 1), but including water temperature (full MTE model) also reduced AIC significantly (Table 1). For both N and P excretion, the full MTE model was superior to the full ES model based on AIC, but differences in prediction accuracy between MTE and ES models were modest, and the best model included both MTE and ES predictors (Table 1). Accounting for vertebrate classification as a coarse proxy for body nutrient content yielded substantially improved AIC and RMSE for both N and P excretion rates, while the further inclusion of body N:P reduced AIC for P excretion but did not change model RMSE. Thus, differentiating between vertebrates and invertebrates appears to capture most of the effect of body stoichiometry in

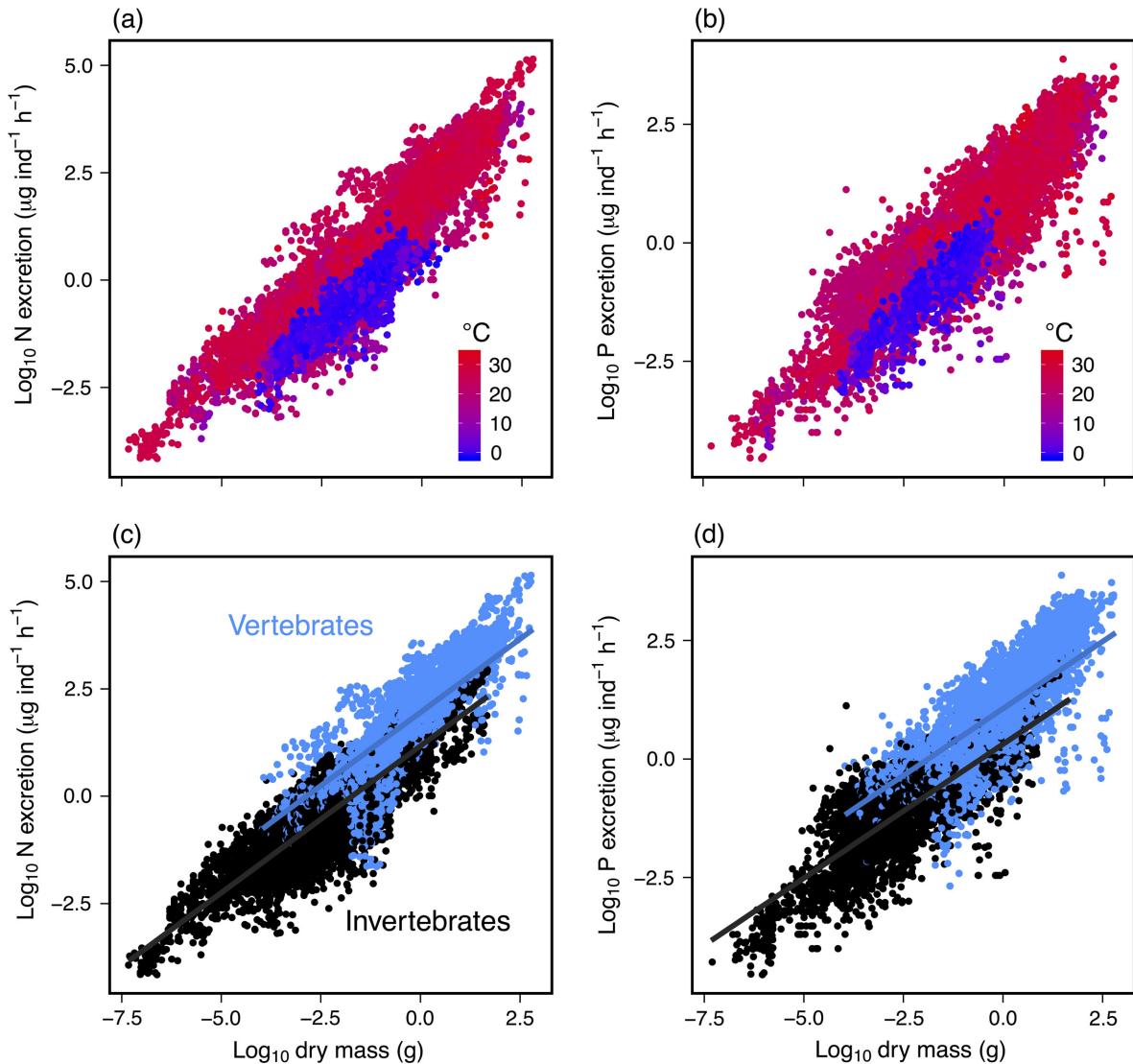


FIG. 1. Nitrogen and phosphorus excretion rates as a function of animal body mass, as mediated by (a, b) temperature and (c, d) vertebrate/invertebrate categorization. The lines in (c) and (d) represent fits of the universal models for excretion rates, using values from Table 2 and assuming a temperature of 20°C (mean temperature for the entire data set is 19.45). (Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).)

predicting nutrient excretion rates. Fitting a model with all factorial interactions among body size, temperature, diet, vertebrate classification, and body N:P yielded substantially lower AIC for N and P excretion rates, yet reduced RMSE by <1.7% (Table 1). Given the large increase in model complexity (25 interaction terms) required for such a small gain in prediction accuracy, we consider models without interaction terms to be most parsimonious despite their higher AIC values. Thus, our preferred model structure for both N and P excretion rates includes only body size, temperature, diet, and vertebrate classification (Table 1).

Overall, our model selection approach indicates that jointly accounting for MTE and ES variables allows robust prediction of N and P excretion rates. However, model

predictive power was much lower for excreted N:P than for N or P excretion rate (Table 1). The MTE models were most parsimonious based on AIC; including ES predictors increased both AIC and RMSE. MTE models with and without temperature were comparable in AIC ( $\Delta\text{AIC} = 0.6$ ) and RMSE ( $\Delta\text{RMSE} < 0.003$ ), and the fitted temperature coefficient was not statistically significant. Therefore, we conclude that the MTE model with species-specific intercepts and body size as the only predictor variable suffices to (weakly) predict excreted N:P (Table 1).

#### Fitting "universal" models

Fitting our preferred model structures for N and P excretion rates and excreted N:P using the complete

TABLE 2. “Universal” models predicting N and P excretion rates and excreted N:P.

	Intercept	Dry mass [log <sub>10</sub> (g)]	Temperature (°C)	Algae or detritus	Diet			Vertebrate classification effect
					Invertebrates	Fish	Invertebrates and fish	
N excretion rate [log <sub>10</sub> (μg N ind <sup>-1</sup> ·h <sup>-1</sup> )]								
Coefficient (SE)	<b>1.4610</b> ( <b>0.0897</b> )	<b>0.6840</b> ( <b>0.0177</b> )	<b>0.0246</b> ( <b>0.0014</b> )	-0.0389 (0.0765)	<b>-0.2013</b> ( <b>0.0771</b> )	-0.0537 (0.2786)	-0.1732 (0.1384)	<b>0.7804</b> ( <b>0.0655</b> )
df	<b>517</b>	<b>309</b>	<b>5,700</b>	394	<b>414</b>	440	1,547	<b>474</b>
P excretion rate [log <sub>10</sub> (μg P ind <sup>-1</sup> ·h <sup>-1</sup> )]								
Coefficient (SE)	<b>0.6757</b> ( <b>0.0992</b> )	<b>0.5656</b> ( <b>0.0205</b> )	<b>0.0194</b> ( <b>0.0020</b> )	0.0173 (0.0953)	<b>-0.2480</b> ( <b>0.0922</b> )	-0.0337 (0.2470)	<b>-0.4525</b> ( <b>0.1534</b> )	<b>0.7504</b> ( <b>0.0768</b> )
df	<b>345</b>	<b>258</b>	<b>3,390</b>	249	<b>235</b>	198	<b>641</b>	<b>293</b>
Excreted N:P (molar)								
Coefficient (SE)	<b>58.526</b> ( <b>4.791</b> )	<b>13.681</b> ( <b>2.042</b> )						
df	<b>367</b>	<b>490</b>						

Notes: Models are presented for the entire data set ( $n = 9,401$ , 7,859 and 7,448 for N, P and N:P), with no minimum number of observations per species but with weighting of observations to equalize the influence of each species (see Appendix S1: Table S3 for additional statistical data). For N and P excretion rates, model selection favored including predictors related to both metabolic ecology and ecological stoichiometry, whereas for excreted N:P the preferred model included only body mass (see Table 1). Bold font highlights statistically significant coefficients ( $P < 0.01$ ); all others,  $P > 0.10$ . Trophic guild (Diet) was categorized as primarily algae/detritus, invertebrates, fish, both invertebrates and fish, or omnivorous (algae/detritus and animals), and the coefficients in the table represent the factor by which log<sub>10</sub>(excretion rate) of an individual in a given diet category differs from that of an omnivore. The “Vertebrate classification effect” is the factor by which log<sub>10</sub>(excretion rate) is higher for a vertebrate, relative to an invertebrate. The coefficients can be used to generate universal equations for excretion rate. For example, the equation for N excretion of a vertebrate that consumes algae/detritus is  $\log_{10}(\text{N excretion}) = 1.4610 + 0.6840 \times \log_{10}(\text{dry mass}) + 0.0246 \times \text{Temperature} - 0.0389 + 0.7804$ .

database revealed that body mass was the single most important predictor for each excretion variable (Fig. 1a, b; Table 2; Appendix S1: Table S3). Contrary to our expectations, scaling coefficients for body mass were significantly  $< 0.75$  for both N ( $0.684 \pm 0.018$  SE) and P ( $0.566 \pm 0.021$ ), and excreted N:P increased significantly with body mass (Table 2; Fig. 2a). Both excretion rates increased with temperature, but the slope of the temperature effect was steeper for N (Fig. 1a, b; Table 2), translating to a 13% higher  $Q_{10}$  for N (1.76; 95% CI: 1.65–1.88) than P (1.56, 95% CI: 1.43–1.71). Both  $Q_{10}$  estimates were significantly less than 2.

Vertebrates excreted both N and P at rates greater than 5× higher than invertebrates (0.75–0.78 log units; Table 2; Fig. 1c, d). As a result, vertebrate classification had no significant effect on excreted N:P, contradicting our ES-based prediction of higher excreted N:P for vertebrates. Moreover, model results showed that body N:P does not predict excreted N:P after body mass and other predictors are accounted for (Table 2), despite a correlation in the raw data that is apparently driven by the larger body size of most vertebrates (Fig. 2a, b). Only ~20% of our observations included both excretion and body nutrient data from the same individual; thus, in the full models we used data from the same, or a confamilial, species to estimate body N:P in most cases. Supplemental analyses that restricted the dataset based on the source of the body N:P data indicate only minor effects on excretion

regardless of the specificity of body N:P data (Appendix S1: Table S4). In addition, comparisons of models using body N:P, C:N, or C:P to characterize body stoichiometry show that body N:P is the best predictor of all three excretion variables (Appendix S1: Table S5).

Excretion rates differed substantially among trophic guilds, but often in ways that conflict with predictions based on ES (Table 2). Relative to omnivores, invertebrates excreted both N and P at significantly lower rates, as did generalized carnivores (significant only for P). Excretion rates of both primary consumers and piscivores were comparable to those of omnivores.

Our universal models for N and P excretion rates had high prediction accuracy (Table 2). RMSE was 0.049 for N and 0.061 for P, or ~10% of the effect of a 10-fold change in body mass. Accuracy was much weaker for the excreted N:P universal model; its RMSE was 28.38, twice the effect of a 10-fold change in body mass.

#### Species-specific scaling coefficients

Scaling coefficients for excretion rates varied greatly among species, with a high proportion substantially different from the expected 3/4-power scaling. Among 311 species with  $\geq 6$  observations of N excretion, half exhibited a scaling coefficient  $< 0.402$  (25th percentile) or  $> 0.909$  (75th percentile; Fig. 3a). Thus, even though mean (0.692) and median (0.669) N scaling coefficients

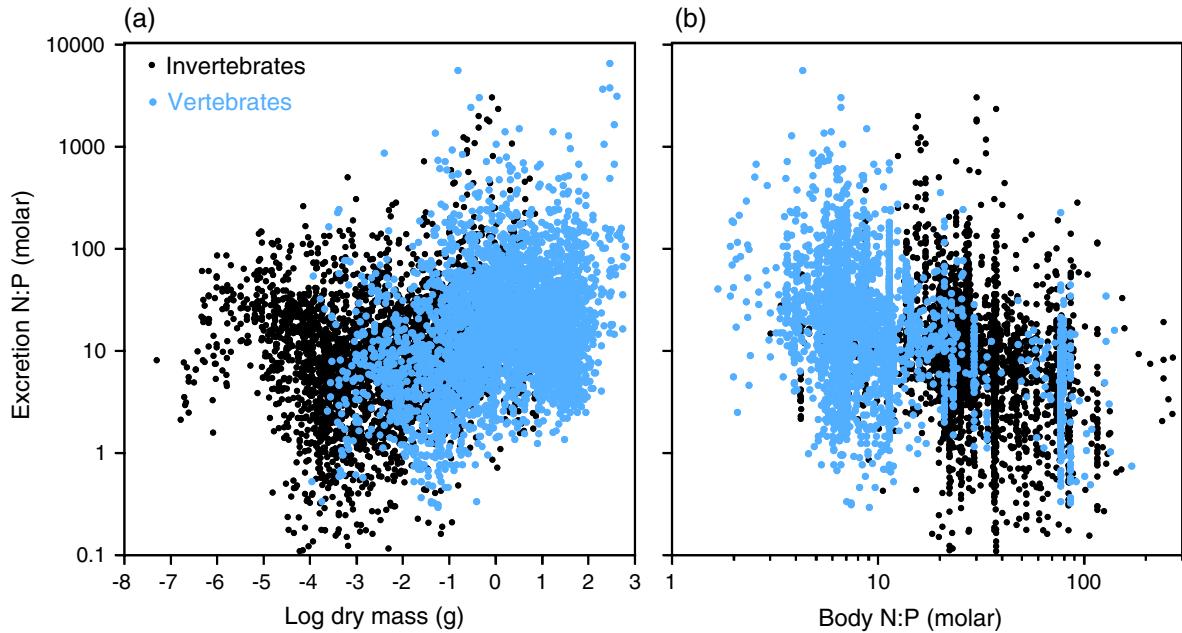


FIG. 2. Excreted N:P of invertebrates and vertebrates in relation to (a) body mass and (b) body N:P. (Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).)

were seemingly close to 0.75, many species displayed much shallower or steeper coefficients. For P, the variation among 269 species-specific coefficients was even greater; 25th (0.255) and 75th (0.913) percentiles were more extreme than for N (Fig. 3b), and the mean (0.597) and median (0.561) deviated more from 0.75. Vertebrates

displayed steeper species-specific scaling coefficients than invertebrates for N and especially P (Fig. 3a, b). Thus, vertebrates not only excrete nutrients at higher average rates than invertebrates at a given body size (Table 2, Fig. 1), but also show greater increases in excretion rates as they grow.

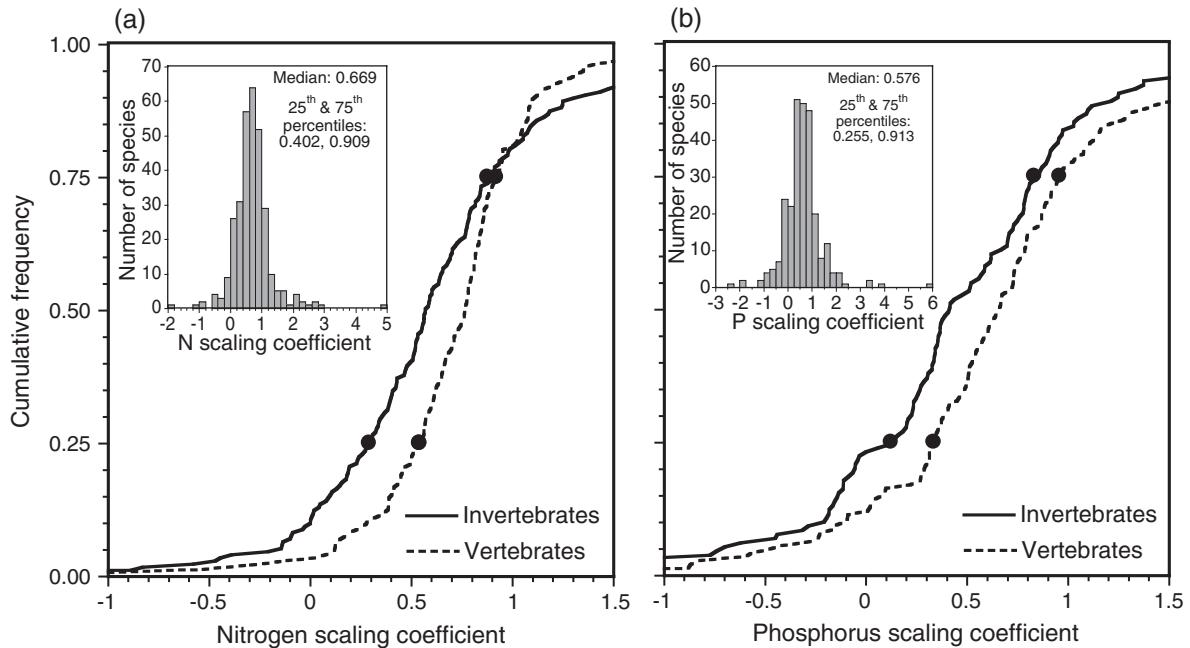


FIG. 3. Distributions of species-specific allometric scaling coefficients for N and P excretion rates. The x-axes of cumulative frequency distributions are truncated to better show differences between invertebrates and vertebrates (<5% of values were excluded); dots represent 25th and 75th percentiles. Inset histograms include all values, showing the full range of variation.

## DISCUSSION

The high predictive power of our joint MTE and ES models suggests that reasonable estimates of natural N and P excretion rates can be made for virtually any aquatic animal. Importantly, our “universal” models require only basic, readily available data on body size, temperature, trophic guild, and vertebrate classification to predict approximate excretion rates. Though generalized models of nutrient excretion rates have been created for fishes using bioenergetics (Schindler and Eby 1997), or for particular metazoan groups using body mass and temperature as predictors (e.g., Sereda and Hudson 2011), ours are the first to address all taxa on a global scale while including both metabolic and stoichiometric predictors.

An important criticism of putatively universal scaling models is that variation around fitted power-function coefficients can yield a wide range of rates at a given body size, but our models show reasonably narrow confidence intervals around fitted coefficients. For example, raising vs. lowering coefficients for the intercept, size scaling, temperature, and body N:P simultaneously by 2 SE yields only a ~2.5- to 3-fold change in predicted N and P excretion rates (Appendix S1: Table S6). However, generalized equations should not be treated as a substitute for field data when very accurate estimates of excretion are needed for a particular species or location.

Our comprehensive evaluation of the relative importance of MTE and ES frameworks for predicting excretion rates leads to the surprising conclusion that MTE predictors—particularly body size—explain far more variance than ES-based predictors. Previous analyses have generally focused on either MTE (body size and temperature; e.g., Hall et al. 2007, Sereda and Hudson 2011) or ES (body and food nutrient ratios; e.g., Sterner 1990, Vanni et al. 2002) variables, but not both (but see Schindler and Eby 1997, Allgeier et al. 2015). Given firm conceptual grounds for expecting ES factors to strongly affect nutrient recycling due to mass balance constraints (Sterner and Elser 2002), it is puzzling that body N:P and trophic guild appear to have only modest influence. Nonetheless, the best models of excretion rates merged key dimensions of both the MTE and ES frameworks.

One notable deviation from MTE predictions revealed by our models is considerably lower scaling coefficients (0.684 for N, 0.566 for P) than the canonical expectation of 0.75 (Gillooly et al. 2001, Brown et al. 2004, but see Hudson et al. 2013). While MTE was developed to explain allometric scaling of metabolic rates, not excretion rates, there are legitimate reasons to expect 3/4-power scaling for excretion. Many other ecological rates show 3/4-power scaling—e.g., individual developmental rates and ecosystem carbon turnover rates—and presumably the scaling of metabolic rates drives these patterns (Brown et al. 2004). More generally, the acquisition and processing of food by individuals is driven by metabolic demands, so it seems reasonable that release of nutrient wastes would scale similarly to metabolism. Finally, a

large survey of marine fish and invertebrates showed 3/4-power for both N and P excretion after accounting for interspecific variation using mixed effect models (Allgeier et al. 2015). Some previous studies also observed steeper scaling of N than P excretion with aquatic animal body size (Hall et al. 2007, McIntyre et al. 2008), while models based on both MTE (bioenergetics) and ES (mass balance) suggest steeper scaling of P than N (Schindler and Eby 1997). The logical basis for these disparities is uncertain. Fish show no consistent intraspecific or interspecific trends in body stoichiometry with size (McIntyre and Flecker 2010), and both ontogenetic diet shifts and size-structured food chain patterns would generally involve either no change in dietary stoichiometry or consumption of increasingly P-rich prey with size. Thus, we are aware of no conceptual explanation for steeper scaling of N than P after distinguishing vertebrates from invertebrates, or for the shallower-than-expected scaling of excretion with size. Nonetheless, our synthesis of excretion rates in nature suggests that both of these patterns are robust.

It is also difficult to explain the enormous interspecific differences in scaling coefficients from a purely MTE perspective. Surveys of many species from the same region have often revealed considerable differences in scaling coefficients among them (e.g., McIntyre et al. 2008, Small et al. 2011, Wilson and Xenopoulos 2011, Allgeier et al. 2015), but our broader data collation yields an even wider range of coefficients (Fig. 3). In some species, ontogenetic shifts in dietary nutrient content could produce steeper or shallower scaling of excretion rates with size than expected from metabolic scaling under an invariant diet. Though ontogenetic diet shifts and other intraspecific resource polymorphisms are widespread (Werner and Gilliam 1984, West-Eberhard 2003), the broad range of scaling coefficients across hundreds of species in this study shows a weaker central tendency than might be expected from specialized diet shifts. These strong effects of species identity also underscore the importance of distinguishing intraspecific vs. interspecific size-scaling coefficients. Our universal models, which account for species-specific size-scaling as well as temperature and ES variables, yield much lower coefficients (0.68 for N; 0.57 for P) than simple linear regressions of excretion vs. body mass across all observations (0.87 for N; 0.81 for P). Indeed, only ~30% of species show intraspecific scaling of excretion rates that equals or exceeds the slope of the relationship across the whole multispecies dataset. Thus, generalized scaling coefficients estimated across taxa (e.g. Hall et al. 2007) should not be applied to conspecific individuals within a population.

In our synthesis, MTE outperformed ES in predicting excretion rates. In addition to the weaker-than-expected overall influence of body stoichiometry on excretion, the observed patterns conflict with the ES-based prediction that vertebrates should excrete less P (and higher N:P) than invertebrates after controlling for body size, temperature, and diet. Despite the fact that growing bones requires far more P sequestration than the structural materials used by invertebrates (keratin, chitin,

calcium-carbonate; Sterner and Elser 2002), we found that vertebrates excreted 5.6-fold more P than invertebrates. The comparable taxonomic disparity for N (sixfold) indicates that vertebrates do not to retain P disproportionately. Moreover, quantitative estimates of body N:P only slightly enhanced our models when vertebrate classification was already included, suggesting that substantial variation among vertebrate species in body P has no consistent effect on P excretion. Together, these results suggest weak overall influence of body stoichiometry on nutrient excretion by aquatic animals when considering all taxa and accounting for body size and temperature effects.

The pattern of differences among trophic guilds also countered expectations from ES theory. All else being equal, consumers of nutrient-rich prey should excrete more than counterparts feeding on nutrient-poor resources. The diets of aquatic animals follow a straightforward progression of increasing dietary nutrient content from detritus to algae to invertebrates to fish (Cross et al. 2005), yet invertivores and generalized carnivores (consuming both invertebrates and fish) excreted both N and P at rates substantially lower than primary consumers, omnivores, and piscivores (Table 2). Even lacking quantitative data on the makeup of diet items for the aquatic animals encompassed in our compilation, it is clear that these differences do not align with gross disparities in N and P content of prey.

The counterintuitive patterns of excretion with respect to both body stoichiometry and dietary nutrient content may in part be explained by undocumented variation in growth or ingestion rates, and consequent differences in the severity of nutrient limitation. If growth rates vary more than body stoichiometry across taxa, then nutrient recycling could be driven primarily by differences in growth. Indeed, body stoichiometry is irrelevant in the absence of growth; consumers should simply release wastes at the same N:P ratio as their food, regardless of body N:P. Thus, one interpretation of the weak effect of body N:P on excretion is that growth rates are low or idiosyncratic across aquatic animals. At the same time, a common strategy for maximizing growth on a low-quality diet is to ingest more material (Bowen et al. 1995). Thus, net intake of nutrients by a primary consumer could match or even exceed that of a species eating higher quality prey. Based on threshold element ratios, aquatic animal growth is often limited by energy rather P (Schindler and Eby 1997, Frost et al. 2006), although P-limitation may arise in primary consumers with an algal or detrital diet low in P (Sterner 1990, Hood et al. 2005, Benstead et al. 2014). Animals that are limited by a particular nutrient should excrete that nutrient at relatively low rates because efficient retention is a necessity for growth. In contrast, energy-limited animals may incidentally ingest excess nutrients while obtaining enough energy for growth, leading to relatively high nutrient excretion rates that are decoupled from dietary nutrient content. Under that scenario, the low excretion rates of carnivores and invertivores that we documented could be

explained by nutrient retention to fuel rapid growth that arises from the abundance and energy-richness of their animal prey. Alternatively, the comparably high excretion rates of primary consumers, omnivores, and piscivores could result from a mixture of high feeding rates but low growth when dietary nutrient content is low (primary consumers, omnivores) vs. low feeding rates and high growth from nutrient-rich prey (piscivores). In either case, explaining surprising patterns of nutrient excretion with respect to vertebrate classification and trophic guild will likely require accounting for growth and ingestion in addition to the MTE and ES predictors analyzed in this study. Furthermore, the relative imbalance of elements for a consumer—summarized by the difference between elemental ratios of the diet vs. consumer tissues—may be a better predictor of nutrient excretion rates and ratios than considering the elemental ratios of food and consumer separately (Sterner and Elser 2002). Unfortunately, in our analysis, the paucity of quantitative data on dietary elemental composition necessitated treating diet as a categorical variable. However, dietary nutrient content is sure to vary within trophic guilds considering the global scope of our database (Cross et al. 2005).

The complexity of predicting excreted N:P of aquatic animals is also evident from aquacultural research and diet manipulations (Moody et al. 2015). Although ration size (i.e., nutrient ingestion rate) and diet heavily influence excretion rates within a species, the effects of dietary N:P on excreted N:P are less clear. Indeed, a recent meta-analysis showed that dietary N:P is a poor predictor of excreted N:P even in single-species lab experiments where diet is controlled, unless N and P ingestion rates are accounted for (Moody et al. 2015). This suggests that quantifying ingestion rates will aid in predicting nutrient excretion in nature. In addition, selective feeding may decouple the actual stoichiometry of ingested material from that expected based on guild designations (Dodds et al. 2014). In our study, addressing a wide variety of taxa and ecosystems came at the cost of limited data on body N:P. Our inferences were consistent regardless of the stringency criteria for sourcing body N:P data (Appendix S1: Table S4), yet we recognize that body stoichiometry varies widely within (El-Sabaawi et al. 2012, Back and King 2013) and among (McIntyre and Flecker 2010) species. Parallel nutrient measurements from the bodies, diet, and excreta of the same animals would surely strengthen inferences about controls on excreted N:P (see Allgeier et al. 2015, Moody et al. 2015).

The surprising mismatches between our findings and ES-based predictions should not be interpreted as violations of mass balance constraints or a rejection of the ES framework. Rather, we interpret these patterns as an indication that additional data are needed to properly describe consumer nutrient budgets. In addition to nutrient contents of consumers and their diets, and growth rates (i.e., somatic retention of nutrients), as discussed above, very few field studies have measured egestion rates, which could be important in the overall balance between intake,

TABLE 3. Simple sensitivity analyses for N and P excretion rates and excreted N:P.

Excretion rate or ratio	Predictor varied by 2×									
	Baseline	Log body dry mass (g)			Temperature (°C)			Body N:P (molar)		
		Upper	Lower	Log ratio	Upper	Lower	Log ratio	Upper	Lower	Log ratio
Nitrogen ( $\mu\text{g N ind}^{-1}\cdot\text{h}^{-1}$ )	8.254	17.14	3.974	0.635	11.92	5.717	0.319	7.808	8.724	-0.048
Phosphorus ( $\mu\text{g P ind}^{-1}\cdot\text{h}^{-1}$ )	2.066	3.781	1.129	0.525	2.760	1.547	0.252	2.144	1.991	0.032
Excreted N:P (molar)	8.845	10.04	7.794	0.110	9.559	8.185	0.067	8.069	9.702	-0.080

*Notes:* Baseline excretion rates are those for an invertebrate omnivore, calculated with the universal equations (Table 2), using mean values for the entire data set for each predictor variable [ $\log_{10}(\text{body dry mass})$  (g) = -1.39; temperature = 19.45°C; body N:P = 24.08 molar]. Excreted N:P is equal to predicted N excretion divided by predicted P excretion, using the rates given here. Sensitivity was assessed by varying the predictor variables two-fold, centered around the baseline value. In each case, the other two predictor variables were held at baseline values. log ratio =  $\log_{10}(\text{upper rate/lower rate})$ .

sequestration, and recycling of nutrients. Indeed, nutrient egestion rate may be comparable to excretion rate of dissolved nutrients (Halvorson et al. 2015), yet field data on egestion are scarce because it is harder to measure. Thus, a definitive test of ES predictions of nutrient recycling rates must await datasets that include complete data on intake (dietary nutrient content, ingestion rate), sequestration (growth rate, body nutrient content), and both components of nutrient recycling (excretion and egestion).

Three additional caveats must be noted to avoid misinterpretation of our universal equations. First, our analyses and other recent metabolic (Isaac and Carbone 2010, Hudson et al. 2013) and stoichiometric (McIntyre et al. 2007, Allgeier et al. 2015) studies underscore the importance of accounting for taxonomic identity when estimating overarching scaling coefficients from disparate datasets. As a consequence, estimates of excretion rates derived from our universal equations should be interpreted as informed approximations rather than accurate predictions.

Second, our capacity to predict excreted N:P remains remarkably weak. This disappointing outcome could reflect an amplification of independent measurement errors in N and P excretion estimates. More generally, the ES-related factors that are most likely to affect excreted N:P are themselves difficult to quantify compared to MTE predictors, leading to both low data availability and greater analytical uncertainty regarding body and dietary stoichiometry. Thus, we recommend against applying our excreted N:P model to taxa for which no field measurements are available.

A third potential caveat is that the greater range in body size (~10 orders of magnitude) than temperature or body N:P (~1 to 2 orders of magnitude; Fig. 2) could exaggerate body size effects (Barneche and Allen 2015). However, our synthesis encompasses much of the natural range of body size, temperature, diet, and body nutrient content among the world's aquatic animals, providing more than enough variation in each predictor to quantify its influence within natural limits. In studies of a single ecosystem or a small

set of species, the range of variation in these predictors may be more similar, potentially leading to lower apparent influence of body size than in our analysis. Nevertheless, it is worth exploring the sensitivity of excretion rates to relative variation in body size, temperature or body N:P (Barneche and Allen 2015). To that end, we conducted a simple sensitivity analysis. We calculated "baseline" N and P excretion rates for an invertebrate omnivore by inserting mean values for log body mass, temperature and body N:P into the universal equations (Table 2). Then, we separately varied body mass (not log body mass), temperature, or body N:P by 2×, centered around each mean value, while holding the other two predictors constant at their mean values. As a measure of effect size, we calculated the log ratio [ $\log_{10}(\text{higher excretion rate or ratio/lower excretion rate or ratio})$ ] for each predictor variable. This analysis confirmed that body mass is the primary driver of excretion rates. Doubling body N:P changed excretion rates by only 4–5% or 11–12% of the effect of doubling body size or temperature, respectively (Table 3). Excreted N:P, calculated as the ratio of predicted N to predicted P excretion, was also most sensitive to doubling of body mass but the difference in effect size among predictors was much smaller than for excretion rates (Table 3).

Our results suggest a need to revisit the relative importance of vertebrates in nutrient cycling. Due to the inverse relationship between body size and mass-specific excretion rate (i.e., scaling coefficients <1), the contribution of vertebrates to whole-system nutrient recycling is often discounted compared to microbes and invertebrates (Grimm 1988a, b, Hudson et al. 1999, Sereda et al. 2008). Although lower-than-expected scaling coefficients (0.684 for N, 0.566 for P) would decrease the contribution of vertebrates to aggregate nutrient recycling compared to smaller heterotrophs, this might be more than offset by elevated normalization constants and steeper species-specific scaling coefficients of vertebrates (Fig. 1, Table 2). Higher excretion rates of vertebrates may simply reflect differential metabolism; temperature-corrected metabolic rates of fishes are ~3.7× greater than those of

invertebrates (Brown et al. 2004). In any case, given the equivalence of energy processing (Damuth 1993) across populations representing different body size classes, our results suggest that vertebrates may mediate substantial nutrient fluxes in aquatic ecosystems despite their larger body size (see also Habeck and Meehan 2008).

In the context of global environmental change, our excretion models suggest yet another mechanism by which humans can affect the balance between N and P recycling. For instance, fisheries disproportionately harvest large species (Pauly et al. 1998, Allan et al. 2005, McIntyre et al. 2007, Doughty et al. 2015), and climate warming is expected to reduce body size across entire assemblages (Cheung et al. 2012). The fitted coefficients in our universal models suggest that such body size reductions would depress excreted N:P more strongly than warming temperatures would enhance it via stronger temperature-dependence of N excretion (Table 2), leading to net reduction in N:P of animal excretion. Both low N:P supply and warming favor cyanobacteria (Paerl and Scott 2010), which could alter ecosystems in many ways. Given that median excreted N:P for the entire data set (11.7 molar) is fairly close to the Redfield ratio, it is even possible that major shifts in the body N:P of dominant species could have important effects on excreted N:P, all else being equal (Table 3). Though speculative, it is important to consider the potential for subtle effects of environmental change arising from the dependence of animal nutrient excretion on temperature, body size, and body N:P.

Overall, the remarkably high predictive power of both N and P excretion rate models indicates that general rules govern nutrient excretion rates across aquatic animals and ecosystems. While these models provide approximate estimates of excretion in lieu of direct measurements, we hasten to emphasize that additional field data are sorely needed. In particular, we need more data on growth, ingestion, and egestion rates (rarely measured in nature) in conjunction with excretion and body stoichiometry (more commonly measured) from the same individuals. Such datasets would enable the use of elemental imbalance between diet and body as an independent variable, potentially increasing the capacity of ES-based models to explain excretion rates and ratios. Nevertheless, our synthesis of excretion data from hundreds of species reveals unexpected differences in excretion rates between major types of organisms (vertebrates vs. invertebrates), individual species, trophic guilds, and elements (N vs. P). The mechanisms underlying these differences in nutrient recycling are largely unknown, offering a rich agenda for future research at the interface between organismal biology and ecosystem ecology.

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