

Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food web

Jacob Edward Allgeier^{a,1}, Seth J. Wenger^b, Amy D. Rosemond^b, Daniel E. Schindler^a, and Craig A. Layman^c

^aSchool of Aquatic and Fisheries Science, University of Washington, Seattle, WA 98105; ^bOdum School of Ecology, University of Georgia, Athens, GA 30602; and ^cDepartment of Applied Ecology, North Carolina State University, Raleigh, NC 27695

Edited by Mary I. O'Connor, University of British Columbia, Vancouver, BC, Canada, and accepted by the Editorial Board March 24, 2015 (received for review October 30, 2014)

Reconciling the degree to which ecological processes are generalizable among taxa and ecosystems, or contingent on the identity of interacting species, remains a critical challenge in ecology. Ecological stoichiometry (EST) and metabolic theory of ecology (MTE) are theoretical approaches used to evaluate how consumers mediate nutrient dynamics and energy flow through ecosystems. Recent theoretical work has explored the utility of these theories, but empirical tests in species-rich ecological communities remain scarce. Here we use an unprecedented dataset collected from fishes and dominant invertebrates ($n = 900$) in a diverse subtropical coastal marine community (50 families, 72 genera, 102 species; body mass range: 0.04–2,597 g) to test the utility of EST and MTE in predicting excretion rates of nitrogen (E_N), phosphorus (E_P), and their ratio (E_{NP}). Body mass explained a large amount of the variation in E_N and E_P but not E_{NP} . Strong evidence in support of the MTE 3/4 allometric scaling coefficient was found for E_P , and for E_N only after accounting for variation in excretion rates among taxa. In all cases, including taxonomy in models substantially improved model performance, highlighting the importance of species identity for this ecosystem function. Body nutrient content and trophic position explained little of the variation in E_N , E_P , or E_{NP} , indicating limited applicability of basic predictors of EST. These results highlight the overriding importance of MTE for predicting nutrient flow through organisms, but emphasize that these relationships still fall short of explaining the unique effects certain species can have on ecological processes.

ecological stoichiometry | consumer-mediated nutrient cycling | coastal ecosystems | nitrogen | phosphorus

The degree to which ecological processes and mechanisms are generalizable among taxa and ecosystems, as opposed to being contingent on local context and taxonomic identity of interacting species, remains poorly resolved. Two primary bodies of theory provide a foundation for generalizing across ecosystems: the metabolic theory of ecology (MTE) (1) and ecological stoichiometry (EST) (2). Although these two theories are concerned with different fundamental currencies, energy (MTE) and materials or elements (EST), they are both based on basic principles of physics, chemistry, and biology (3). An alternative perspective is that ecological variation is contingent on species identity, such that certain species have unique effects on ecological processes (4, 5). However, rarely have empirical datasets been used to explicitly test how species level variation may diminish the predictive ability of general models.

Fundamental to MTE is the degree to which metabolic rates of organisms scale with two basic variables: body size and temperature. The generality of this relationship allows investigation of processes that span physiological, ecological, and evolutionary scales (1, 6, 7). Allometric relationships have been successfully applied to generate ecological predictions across vast scales of biological organization and organismal body size (6, 8–10) and provide a framework with which to investigate the influence of additional life history traits (or ecological covariates) on energy and nutrient flows through ecosystems (11–15).

EST attempts to understand the fluxes of multiple nutrients through cells, organisms, food webs, and ecosystems (3). Central to EST is that ecosystem fluxes and storage are constrained by mass balance, which can produce imbalances and, therefore constraints, between supply and demand of nutrients by organisms. For example, the amount of nitrogen (N) excreted by an organism is predicted to be the difference between the rates of N consumed and the rate that N is allocated to growth and reproduction and lost to egestion ($\text{Excretion}_N = \text{Diet}_N - \text{Egestion}_N - \text{Reproduction}_N - \text{Growth}_N$). Thus, these processes are contingent on the stoichiometric traits of organisms (e.g., Reproduction_N and Growth_N) and their dietary resources (Diet_N).

Importantly, these factors, e.g., Reproduction_N , Growth_N , and Diet_N , are typically assumed to be conserved at certain levels of taxonomic resolution (2, 16–18). For these reasons, organism identity has been found to be an important explanatory variable of nutrient recycling by consumers in ecosystems, whereby recycling rates have been found to be most similar within families (16). This hypothesis provides support for the intrinsic importance of taxonomic identity, but renders predicting nutrient recycling difficult until taxa-specific physiology or dietary traits can be identified at the appropriate level of taxonomic resolution.

In theory, MTE should explain a large amount of the variation in recycling rates among individuals, as it accounts for mass-dependent changes in physiological rates. Indeed, evidence of 3/4 allometric scaling of recycling rates has been found in temperate fishes (19). However, EST predicts that the demand for

Significance

A fundamental dilemma in ecology is to reconcile the degree to which ecological processes are generalizable among taxa and ecosystems or determined primarily by taxonomic identity. We apply a unique dataset of organisms from a diverse marine community to test the applicability of two theories, metabolic theory of ecology (MTE) and ecological stoichiometry (EST), and the role of taxonomic identity for predicting nutrient excretion rates by fishes and macroinvertebrates. Excretion rates were principally explained by body mass and taxonomic identity, providing strong support for MTE, but also highlighting the intrinsic importance of taxonomic identity. Little support for basic predictions of EST was found. This research reveals animal-mediated nutrient cycling is largely generalizable by metabolic processes, but refined predictions require tax-specific understanding.

Author contributions: J.E.A. led the research design with substantial contributions from, S.J.W., A.D.R., D.E.S., and C.A.L.; J.E.A. and C.A.L. performed research; J.E.A., S.J.W., and D.E.S. analyzed data; and J.E.A. led the manuscript with substantial contributions from, S.J.W., A.D.R., D.E.S., and C.A.L.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.I.O. is a guest editor invited by the Editorial Board.

¹To whom correspondence should be addressed. Email: zopelote@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1420819112/-DCSupplemental.

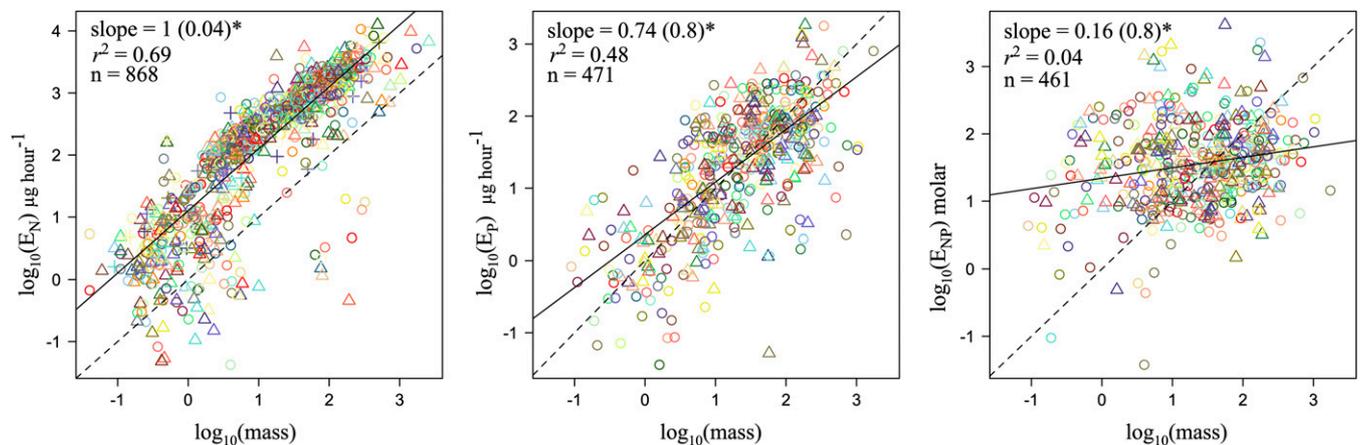


Fig. 1. Linear regression models for excretion rates of N (E_N), P (E_P) ($\mu\text{g}/\text{h}$), and N:P (E_{NP}) and wet body mass of individual organisms. Families are indicated by a unique combination of color and symbol. All values are \log_{10} transformed. *Slope significantly differs from zero ($\alpha < 0.05$).

a given nutrient by an organism ($\text{Reproduction}_N + \text{Growth}_N$) is proportional to the concentration of this nutrient in body tissues (body nutrient content) (2), thus suggesting that specific knowledge of this predictor should explain significant variation in nutrient recycling. That is, as an organism's requirement for a nutrient increases, its excretion of that nutrient must decrease (i.e., the relationship between body nutrient content and excretion rate of that nutrient should be negative), if dietary nutrient concentrations are constant (20). Similarly, the trophic role of a consumer affects the quality of the food it consumes and should likewise explain some of the variation in excretion of nutrients among taxa (2, 19). For example, many fish undergo ontogenetic diet shifts, such that as they achieve large body sizes the proportion of their diet that is fish (a P rich food source) increases, resulting in higher relative P excretion rates through ontogeny (19).

Taken together, EST and MTE should account for a large proportion of variation in nutrient recycling among species and individuals. Recent theoretical developments have already generated novel advances to integrate these theoretical relationships toward a more unified understanding of nutrient recycling by individuals (7, 21). Nonetheless, empirical tests of these basic theoretical assumptions in species-rich ecosystems are needed. Here we apply an extensive dataset to test how various physiological (MTE, body size; EST, body nutrient content), ecological (trophic role, diet), and taxonomic variables explain nutrient recycling at the level of the individual. The response variables of interest are excretion rates of nitrogen (E_N), phosphorus (E_P), and their ratio (E_{NP}). Data are derived from 900 individuals from a diverse community in a subtropical coastal marine ecosystem in The Bahamas. Central to MTE is the role of temperature, in addition to body size, for predicting metabolic rate according to specific scaling coefficients (1). Our data present a novel opportunity because all species are from the same ecological community, are subject to similar environmental conditions (i.e., temperature), and were all held at a similar temperature during excretion experiments. For these reasons, we did not further account for temperature in our analysis, allowing us to focus explicitly on additional factors that may influence excretion rates. These data span large ranges in body size (0.04–2597 g) and levels of taxonomic identity (50 families, 71 genera, and 102 species). We apply these data to address the following question: how complementary are MTE, EST, and additional ecological and evolutionary covariates in predicting processes of nutrient recycling by animals? Specifically we tested three primary hypotheses:

i) E_N and E_P by animals will scale allometrically according to the 3/4 power rule of MTE and, accordingly, E_{NP} will have a

slope of zero. Alternatively, if factors other than metabolic scaling influence recycling rates across body sizes and follow principles of EST, e.g., shifts in diet due to ontogeny, E_{NP} will vary with body size to reflect a systematic shift in diet nutrient composition with increasing body size (e.g., the slope would be negative if larger predators tend to feed on more P-rich prey).

- ii)* Allometric scaling of excretion rates will be modified by taxonomic identity of organisms.
- iii)* In accordance with EST, body nutrient content and trophic position (which influences diet) will improve model performance in explaining variation in excretion rates after accounting for body mass and taxonomy.

Results

Excretion rates of N or P or both and body mass were measured for 667 individual fish and 233 individual macroinvertebrates. Of these individuals, at least one of three additional traits were measured: *(i)* somatic nitrogen (N), *(ii)* somatic phosphorus (P), or *(iii)* $\delta^{15}\text{N}$ (as a proxy for trophic position). Vertebrate species were diverse in taxonomy, morphology, and physiology (28 families, 43 genera, and 72 species, including boxfish, moray eels, and pipefish), as were invertebrates (22 families, 28 genera, and 30 species, including crabs, shrimp, jellyfish, gastropods, and sea cucumbers). Variation in body nutrient content was substantial [%N: 2.32 (pitho crab) to 14.2 (parrotfish); %P: 0.19 (sea cucumber) to 8.7 (purple mouth moray eel); N:P: 0.26–146; %C: 11.1 (pitho crab) to 60.1 (green moray eel) of dry mass]. Mass-specific excretion rates were variable among individuals (N: 0.002–351.2 $\mu\text{g}/\text{g}$ per hour; P: 0.0009–35.9 $\mu\text{g}/\text{g}$ per hour; N:P: 0.038–4,156 molar ratio) and span a broader range than previous studies (e.g., ref. 16: N excretion: \sim 9–30 $\mu\text{g}/\text{g}$ per hour; P excretion: \sim 2–13 $\mu\text{g}/\text{g}$ per hour; NP: \sim 1–7.5; see Table S1 for further information).

Relationships between the logarithm of nutrient excretion and the logarithm of body wet mass (hereafter, mass) were positive and significant for N, P, and N:P (Fig. 1). Evidence for allometric scaling of nutrient excretion at the predicted 3/4 power rule was found for P excretion (slope = 0.73, 95% CI = 0.66–0.80) but not for N excretion, which did not significantly differ from 1 (slope = 1.0, 95% CI = 0.95–1.04), suggesting isometry (8, 19). The slope for N:P excretion was significantly positive (slope = 0.16, 95% CI = 0.16–0.22; Fig. 1), in contrast to predictions.

Linear regression was used to explore the variation in E_N , E_P , and E_{NP} as explained by mass, body nutrient content, and $\delta^{15}\text{N}$. In each case, model residuals (from mass-excretion, body

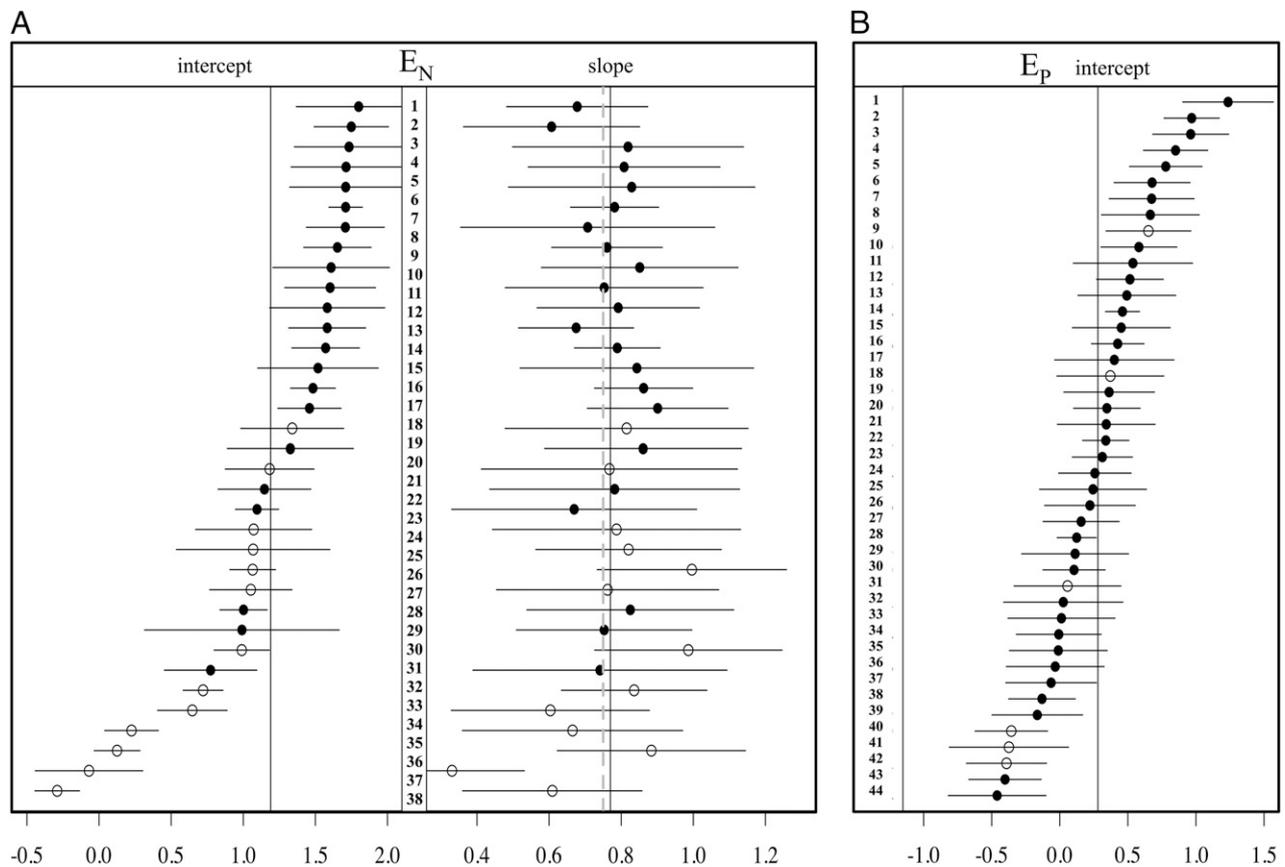


Fig. 3. (A) Random slope and intercept estimates for each family (circles) in the N excretion (E_N) vs. body mass (wet mass) mixed effects model and (B) random intercepts for each family in the P excretion (E_P) vs. body mass mixed effects model. Bars indicate 95% predictive intervals for both the intercept and slope. The vertical black lines indicate the mean intercept and slope. Vertical dashed gray line indicates 0.75, the 3/4 scaling coefficient predicted by MTE. Filled and empty circles indicate vertebrate and invertebrate families, respectively. See Table S2 for family names associated with listed numbers.

for E_N and E_P ($r^2 = 0.65$ and 0.35 , respectively, both positive relationships; Figs. 1 and 2), suggesting the potential importance of trophic position for the recycling of nutrients. However, these relationships are confounded by the positive $\delta^{15}\text{N}$ -body mass relationship ($r^2 = 0.32$, $P < 0.001$), which is highlighted by the relatively weak relationships between $\delta^{15}\text{N}$ and E_N (and in particular E_P) after accounting for body mass (Fig. 2), suggesting effects of trophic position were almost entirely accounted for by body mass.

Taxonomic identity has previously been reported to have important implications for metabolic scaling (22–24). We tested for the importance of taxonomic identity for metabolic scaling coefficients using mixed effects models (22, 23). Two types of models were run. First we fit nested models that included all levels of taxonomic identity (class, order, family, genus, and species), and then we tested models that included only a single taxonomic level (22, 23). To test for potential differences in metabolic scaling of excretion rates by vertebrates and invertebrates, we included a vertebrate/invertebrate level of classification (in addition to all other taxonomic levels) into the second class of models. In all cases, we tested for random effects on the slope, the intercept, or both the slope and the intercept (22) (Table 1). Models that included all levels of taxonomic classifications were within the top two models (as determined by AIC) for E_N (slope and intercept), E_P (intercept only), and E_{NP} (slope and intercept) (Table 1; note that class was excluded as a random effect in the model for E_N because it appeared to be non-identifiable, resulting in an overparameterized model). Only in the case of E_{NP} was the top model a single-taxon model; in this

case, the best model had random effects for slope and intercept at the species level.

For E_N , E_P , and E_{NP} , we then tested the degree to which the allometric scaling coefficient varied within the taxonomic group that produced the best model; i.e., family (slope and intercept), species (intercept only), and species (slope and intercept), respectively (Figs. 3 and 4) (25). Variation around the slope was highly constrained for E_N such that the 95% predictive intervals of the allometric coefficient for all families with the exception of one (*Strombidae*; queen conch, an invertebrate family) overlapped with the predicted 0.75 scaling coefficient (Fig. 3). In contrast, the best fit model for E_P did not include a random slope, indicating species-level differences in the mean excretion rate (Fig. 3), not the scaling of this rate, which was consistent (~ 0.75) among species. Two of the 42 species had positive allometric coefficients with 95% predictive intervals that did not overlap with a zero slope for E_{NP} : the only two negative coefficients did not overlap with zero (Fig. 4).

The best models (lowest AIC) for E_N , E_P , and E_{NP} were used to further test the relative importance of body mass, body nutrient content, and $\delta^{15}\text{N}$. For the E_N and E_P models, strong support was found for body mass as the best predictor. It was the only parameter included in the top four competing models, and in the case of E_P , it had the largest influence on model performance (the model explained $>25\%$ less variation in the data when comparing models with body mass and without). We found support for body nutrient content as a predictor of E_N only. It was retained in the top two models, the 95% CIs did not overlap zero, and the model was not as good when this predictor was

removed (ΔAIC decreased by 7.4; Table 2). Little support was found for effects of $\delta^{15}\text{N}$ for all responses. In all models in which it was retained, the 95% CIs overlapped zero (Table 2).

Discussion

Animals are critical components of nutrient cycles in most ecosystems (26–28). Using a unique dataset from a diverse marine community, our analysis showed that individual level nutrient recycling was highly predictable based on body mass alone, but models were improved substantially when accounting for variation due to taxonomic identity. Surprisingly, neither body nutrient content nor relative trophic position substantially improved model performance, in contrast to the predictions of EST. These results suggest that, among individuals in a diverse community, variation in excretion rates is best explained simply by a combination of allometry and the taxonomic identity of the organism. Our results support theory that seeks to integrate MTE with EST to improve the predictability of material flow through ecosystems (21) but highlights the need for further specificity regarding the unique effects certain species can have on ecological processes.

The slope of the E_P relationship with body mass was consistent with that predicted by allometric scaling laws (~ 0.75), whereas E_N scaled isometrically (slope ~ 1.0) without accounting for taxonomy. When accounting for variability in this relationship among taxonomic levels, both E_N and E_P were found to scale with a $3/4$ coefficient because larger fish, which tended to belong to a few families, excreted higher levels of N than would be predicted by body size alone (Fig. 1). Previous research using bioenergetics models showed that freshwater temperate fishes deviate from the allometric scaling coefficient for E_P , but not E_N , and that accounting for P nutrient content of dietary resources (i.e., stoichiometric imbalances) adjusted the slope for the P models in agreement with the $3/4$ scaling coefficient (19). Our findings, although we did not explicitly test for the importance of body nutrient-dietary imbalances, emphasize the importance of evolutionary factors, e.g., taxonomic identity, for differences among individual nutrient recycling rates in a diverse community.

Taxonomic identity proved to be a particularly important predictor in all models of nutrient excretion. E_P were most variable among species (as opposed to among other levels of taxonomy) in terms of absolute differences in the mean excretion rate (i.e., random intercept model). However, the scaling of E_P with body size was not dependent on taxonomic differences (i.e., the random slope effect was negligible) and was roughly consistent with the predicted 0.75 in all of the top models regardless of the taxonomic level of the random effects. In contrast, both mean rates (intercept) and the degree to which E_N scaled with body size (slope) varied among families such that only when accounting for these differences did the global scaling coefficient align with MTE predictions (i.e., 95% CIs of the E_N slope overlapped with 0.75). However, almost all families were still found to have 95% prediction intervals that overlapped with 0.75 for E_N (Fig. 3). Interestingly, there were little differences among invertebrates and vertebrates in these scaling coefficients, as may have been predicted given basic physiological differences among these groups (2, 29). Beyond a few exceptions (discussed below), the relative homogeneity in scaling coefficients found in our study contrasted with previous work demonstrating that, whereas scaling coefficients converged at roughly $3/4$ scaling across broad taxonomic grouping values, they were highly heterogeneous among these groups when estimated independently (22, 23).

As hypothesized, E_{NP} was invariant with body mass (slope = 0), but only when accounting for taxonomy (species level). An alternative hypothesis, based on previous evidence that larger individuals (possibly due to ontogenetic shifts in diet) tend to have lower E_{NP} and feed on prey with lower E_{NP} (often because they are higher on the food chain) (19, 27), predicted a negative

relationship with E_{NP} and body size. When accounting for differences in this relationship in both the mean (intercept) and slope among species, only 4 of the 43 species were found to have 95% CIs of slope that did not overlap with zero. Consistent with the alternative hypothesis, two of these species were fish species, *Sparisoma chrysopterygum* (redtail parrotfish) and *Lutjanus apodus* (schoolmaster snapper), both of which have strong ontogenetic dietary shifts and had negative E_{NP} -body size relationships, demonstrating support for the role of ecological interactions for influencing E_{NP} . In contrast, the other two species were invertebrates with positive E_{NP} -body size relationships. This finding, however, opposes expectations based on the growth rate hypothesis (30), which states that at smaller sizes invertebrates with higher growth rate will have an increased demand for P (due to allocation in RNA) and thus would be expected to have a negative E_{NP} -body size relationship. Two aspects must be considered when evaluating these findings (1): these exceptions constitute only a limited subsample of species (4 of 43) (2); in contrast to E_N and E_P , E_{NP} models generally described the data poorly, highlighting the difficulty of predicting E_{NP} with these predictors used herein alone.

Surprisingly little support for the role of additional predictors of ecological interactions (e.g., body nutrient content and $\delta^{15}\text{N}$) for individual nutrient recycling was found in our data. Only with E_N did body nutrient content improve model performance, and even in this case, the effect of body nutrient content explained minimal variation in the data. The lack of importance of body nutrient content for E_P is also surprising for two reasons: (i) the extensive range of P nutrient content found within our dataset (0.19–8.7% dry mass) and (ii) the previous support for this relationship in the literature (16). Although we did not test explicitly for nutritional imbalances in our analysis, the fact that accounting for the trophic position of the consumer did not improve predictive power of individual nutrient excretion raises questions of the importance of dietary nutrient content, a key predictor of EST, as a useful factor in explaining nutrient excretion rates across a diverse group of animals.

Interestingly, the slope of the relationship between body nutrient content and excretion rate was positive for E_N , contrasting theoretical expectations that an animal with lower requirements for a given nutrient should release more of that nutrient back to its environment (2). To some extent this finding can be explained by the natural history and physiology of these animals. For example, E_N by fishes is directly associated with heart rate and thus metabolism (31). Atlantic silversides (*Menidia menidia*) provide an example of an animal that would be expected to have low excretion rates based on its relatively high demand for N (%N ~ 11) and only modestly nutrient-rich diet (zooplankton). However, their family (Atherinopsidae) ranks among the highest in E_N , presumably due to the fact that these are small active pelagic fishes with high metabolic rates. This example highlights the importance of additional factors, namely metabolism, beyond nutritional imbalances for explaining the basic physiological process of nutrient excretion.

The simple, yet highly predictable, nature of allometric relationships and MTE provide a useful framework through which to explore ecological interactions at multiple scales of organization, ranging from potential effects of climate change on ecosystems (14) to scaling C flux from individual to global scales (11). Here, using an unprecedented dataset, we show the applicability of MTE to additionally explain individual-level nutrient recycling, a complex physiological process that encompasses ecological interactions commonly described by EST. Additional predictors of EST may improve predictability, but our analyses suggest that these improvements are negligible without substantially increasing model complexity. Our findings, however, underscore the importance of taxonomic identity in fundamentally regulating these processes, thus confirming a basic expectation of EST and

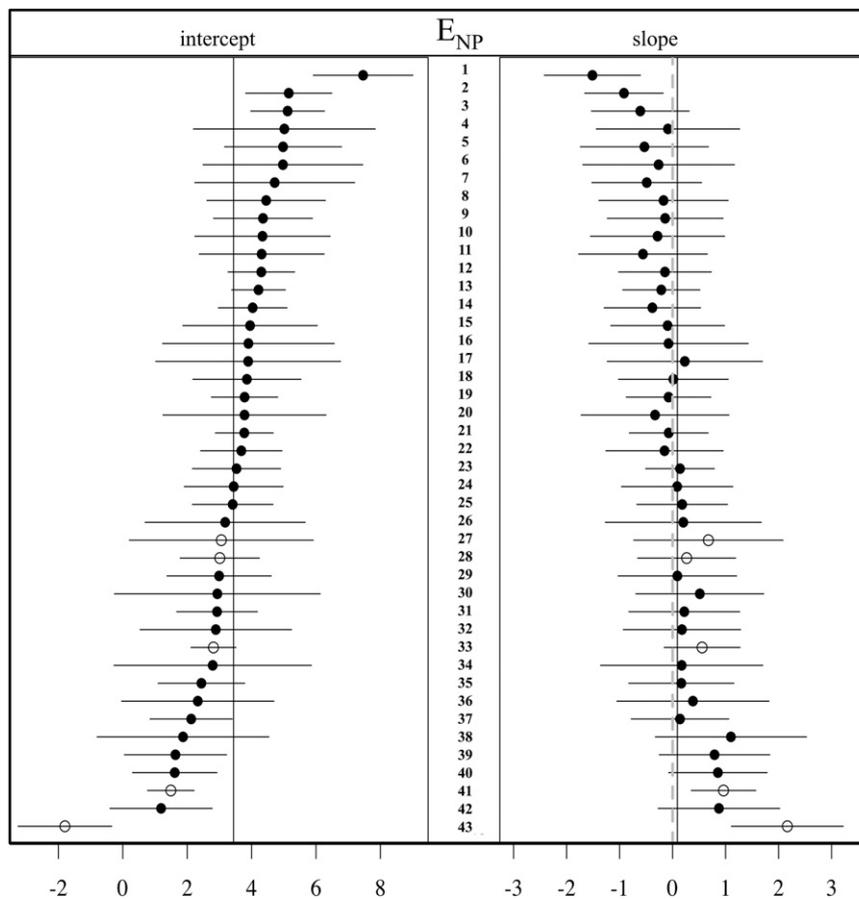


Fig. 4. Random slope and intercept estimates for each species (circles) in the N:P excretion (E_{NP}) vs. body mass (wet mass) mixed effects model. Bars indicate 95% prediction intervals for both the intercept and slope. The vertical black lines indicate the mean intercept and slope. Vertical dashed gray line indicates a slope of 0. Filled and empty circles indicate vertebrate and invertebrate families, respectively. See [Table S2](#) for species names associated with listed numbers.

challenging general theory with an additional layer of biological complexity.

Methods

Individual organisms were collected using hook and line, traps, cast nets, and dip nets between 2008 and 2011, within the same large embayment (the Bight of Old Robinson) on Abaco, The Bahamas. Habitat types within the embayment consisted of seagrass, mangrove, and patch reef complexes (32–34).

Excretion rates, for nitrogen- NH_4^+ and phosphorus-soluble reactive phosphorus (SRP), were measured in situ following the methodologies of ref. 35, as modified by ref. 36. In each case, animals were placed into clean plastic zippered bags (1- to ~37-L bag sizes) for either 30 (vertebrates) or 60 (invertebrates) min. Experiments were conducted in situ, and bags were placed in bins of ambient seawater. As such, temperature was highly regulated for all experiments (~22–23 °C) and was similar to the temperature of the environment from which the subject animals were extracted. The volume of water per experiment varied according to the size of the individual (0.15–22 L), and net excretion rates were corrected for water volume to achieve rate of excretion in grams of nutrient per unit time. Values were control corrected through the use of multiple (typically $n = 6$) identical control incubation bags without fish. Each individual used for excretion experiments [$n = 667$ individual fish; size range: 0.14–2597 g (range, 2–107 cm), $n = 233$ invertebrates, size range: 0.04–487 g, 900 total individuals] was weighed for wet mass and measured to standard length. Fish were dissected to remove stomach contents, and invertebrates were incubated in seawater (for at least 6 h but typically 10–24 h) to allow for gut evacuation, and after identification, all animals were frozen for transport to Odum School of Ecology and processed for elemental content (see below). The University of Georgia's (UGA) Institutional Animal Care and Use Committee approved protocols for the capture and handling of fish (AUP A2009-10003-0). Water samples (filtered with 0.45- μm Whatman nylon membrane filters) were immediately placed on ice and, within 10 h, analyzed for NH_4^+ using the methodologies of ref. 37 or frozen

for transport to the Odum School of Ecology (UGA) for SRP analysis using the ascorbic acid method and colorimetric analyses (American Public Health Association 1995) (38).

Individuals used for somatic nutrient content analyses ($n = 494$ vertebrates, $n = 164$ invertebrates, and $n = 658$ individuals total) were weighed for wet mass and measured to standard length. Samples were lyophilized to a consistent dry weight and then ground to a powder with a ball mill grinder. Larger individuals required blending to homogeneity before mill grinding. Ground samples were analyzed for %C and N content and $\delta^{15}\text{N}$ with a CHN Carlo-Erba elemental analyzer (NA1500) CN Analyzer and for %P using dry oxidation-acid hydrolysis extraction followed by a colorimetric analysis (Aplkem RF300). Elemental content was calculated on a dry weight basis. $\delta^{15}\text{N}$ values were used as a proxy measure for the trophic position of an individual following the rationale that the higher the $\delta^{15}\text{N}$ value, the higher on the food chain an individual is feeding (39–41). We did not correct for potential temporal variation in isotopic baselines for three reasons: (i) because the myriad basal resources within these systems makes correcting for specific isotopic baselines impossible (39, 41), (ii) because we are not attempting to use these data to calculate trophic position *sensu stricto* (42), and (iii) because previous research using the same species from the same study area found clear gradients of $\delta^{15}\text{N}$ values that accurately depict relative trophic levels in this system with relatively little interannual variation in isotopic values among consumers (40). We acknowledge some potential error associated with this approach, but suggest the continuous nature of $\delta^{15}\text{N}$ renders it preferable to simply assigning species to exact trophic levels based on presumed natural history or literature sources from studies conducted in other systems.

Simple linear regression was used to first explore the role of body mass in predicting excretion rates for all individuals for which we had excretion rate and body mass ($n = 868$, 471, and 461 for N, P, and N:P, respectively). To understand the degree to which body nutrient content and a species' trophic position ($\delta^{15}\text{N}$) complement allometric relationships, we consolidated

Table 2. Results from the top for models for excretion rats of N, P, and N:P (E_N , E_P , and E_{NP} , respectively) and the null model with no fixed effects

Response	Taxonomy	Rank	$\delta^{15}\text{N}$	Body nut.	Mass	LogLik	AICc	ΔAIC	Weights	r^2_{fixed}	$r^2_{\text{cond.}}$
E_N	O,F,G,S (S&I)	1	—	<i>0.84</i>	<i>0.76</i>	-259.37	551.6	0.0	0.71	0.49	0.92
		2	0.01	<i>0.84</i>	<i>0.75</i>	-259.27	553.5	1.9	0.27	0.50	0.92
		3	—	—	<i>0.77</i>	-264.19	559.2	7.5	0.02	0.39	0.92
		4	0.01	—	<i>0.76</i>	-264.07	561.0	9.4	0.01	0.40	0.92
		7	—	—	—	-272.93	574.5	22.9	0.00	0.00	0.93
E_P	O,F,G,S (I)	1	—	—	<i>0.74</i>	-265.66	545.6	0.0	0.55	0.36	0.79
		2	-0.01	—	<i>0.75</i>	-265.65	547.7	2.1	0.19	0.36	0.79
		3	—	-0.001	<i>0.74</i>	-265.66	547.7	2.1	0.19	0.36	0.79
		4	-0.01	0.0002	<i>0.75</i>	-265.65	549.8	4.2	0.07	0.36	0.79
		7	—	—	—	-347.00	706.2	160.6	0.00	0.00	0.71
E_{NP}	Species (S&I)	1	—	—	—	-608.12	1,226.4	0.0	0.24	0.00	0.34
		2	—	0.37	—	-607.20	1,226.6	0.2	0.21	0.01	0.33
		3	—	0.39	0.16	-606.63	1,227.6	1.2	0.13	0.01	0.32
		4	—	—	0.14	-607.68	1,227.6	1.2	0.13	0.01	0.33

Fixed effects include the following: body nutrients (Body nut.), Mass and $\delta^{15}\text{N}$. Random effects are set on the taxonomic level at which best explained variation in the response (Table 1). Both the E_N and E_P random effects were nested and included the following: order (O), family (F), genus (G), and species (S). The E_{NP} model had a random effect at the species level (S and I indicate slope and/or intercept models). The LogLik = negative log likelihood estimate, AICc = AIC value corrected for the number of predictors within the model, ΔAIC = change in AICc relative to lowest AICc value, weights = model weights are calculated relative to all competing models. r^2_{fixed} is the variance explained by the fixed effects alone, and $r^2_{\text{cond.}}$ indicates the variance explained by the full model. Values indicate the parameter estimates for that respective column. —, associated predictor was not in the model. Italicized values indicate 95% CIs did not overlap with zero.

data to individuals for which all predictors of interest were available ($n = 625, 371, \text{ and } 365$ for N, P, and N:P, respectively). Simple linear regression was used to test allometric relationships, and the model residuals were then regressed against the additional predictors independently. Model r^2 and significance ($\alpha < 0.05$) were reported. This process was repeated for N, P, and N:P excretion.

To explore the importance of taxonomy variation in the relationship between body mass and nutrient recycling, we used mixed effects models testing for variation in slope or intercept or both across (i) all taxonomic levels (class, order, family, genus, or species) using a nested model structure and (ii) each taxonomic level independently; models were fitted by restricted maximum likelihood. Because we were interested in testing for species-level random effects, we used a subset of our data that included only species with three or more individuals ($E_N = 56$ species, 789 individuals, 14.8 individuals per species; $E_P = 44$ species, 430 individuals, 9.8 individuals per species; $E_{NP} = 43$ species, 420 individuals, 9.8 individuals per species). In the case of one model for E_N containing random slope and intercept for all nested taxonomic levels, the random effect for class appeared to be unidentifiable and thus was removed from the model.

The model with the lowest AICc values was then used to further explore how other covariates (body nutrient content, $\delta^{15}\text{N}$, i.e., fixed effects only) may explain additional variation in nutrient excretion rates using mixed effects models fitted by maximum likelihood using the dredge function in the R package *MuMIn*. Comparisons among competing models were made using information theory (AIC; note AICc was used in our analysis, but yielded the same ranking as AIC) (43, 44) and the r^2 statistic (conditional; which includes fixed and random effects, as well as for fixed effects alone). Mixed effects models were run using the lme4 package in R (25, 45). All other data analysis was conducted using R software (44).

ACKNOWLEDGMENTS. We thank D. Haynes, F. DeRosa, R. Appaldo, K. Rennert, J. Richard, and Friends of the Environment for logistic and field support. M. Vanni and P. McIntyre were helpful in discussions about excretion methods, and T. Maddox provided invaluable support for nutrient analyses. The manuscript was greatly improved by comments from three reviewers and the editor. Funding was provided by an Environmental Protection Agency Science to Achieve Research Fellowship, National Science Foundation (NSF) Doctoral Dissertation Improvement grant, and NSF Postdoctoral Research Fellowship in Biology (to J.E.A.) and NSF Biological Oceanography Grants 0746164 and 1405198 (to C.A.L.).

- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85(7):1771–1789.
- Sterner RW, Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere* (Princeton Univ Press, Princeton).
- Reiners WA (1986) Complementary models for ecosystems. *Am Nat* 127(1):59–73.
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100(910):65–75.
- Hooper DU, et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr* 75(1):3–35.
- West GB, Brown JH, Enquist BJ (1999) The fourth dimension of life: Fractal geometry and allometric scaling of organisms. *Science* 284(5420):1677–1679.
- Gillooly JF, et al. (2005) The metabolic basis of whole-organism RNA and phosphorus content. *Proc Natl Acad Sci USA* 102(33):11923–11927.
- Peters RH (1983) *The Ecological Implications of Body Size* (Cambridge Univ Press, Cambridge, UK).
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276(5309):1221–1226.
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293(5538):2248–2251.
- Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. *Funct Ecol* 19(2):202–213.
- López-Urrutia A, San Martín E, Harris RP, Irigoien X (2006) Scaling the metabolic balance of the oceans. *Proc Natl Acad Sci USA* 103(23):8739–8744.
- Enquist BJ, West GB, Brown JH (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proc Natl Acad Sci USA* 106(17):7046–7051.
- O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. *PLoS Biol* 7(8):e1000178.
- Barneche DR, et al. (2014) Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecol Lett* 17(9):1067–1076.
- Vanni MJ, Flecker AS, Hood JM, Headworth JL (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: Linking species identity and ecosystem processes. *Ecol Lett* 5(2):285–293.
- Lemoine NP, Giery ST, Burkepile DE (2014) Differing nutritional constraints of consumers across ecosystems. *Oecologia* 174(4):1367–1376.
- Fagan WF, et al. (2002) Nitrogen in insects: Implications for trophic complexity and species diversification. *Am Nat* 160(6):784–802.
- Schindler DE, Eby LA (1997) Stoichiometry of fishes and their prey: Implications for nutrient recycling. *Ecology* 78(6):1816–1831.
- Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. *Annu Rev Ecol Syst* 33:341–370.
- Allen AP, Gillooly JF (2009) Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. *Ecol Lett* 12(5):369–384.
- Isaac NJB, Carbone C (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecol Lett* 13(6):728–735.
- Hudson LN, Isaac NJB, Reuman DC (2013) The relationship between body mass and field metabolic rate among individual birds and mammals. *J Anim Ecol* 82(5):1009–1020.
- Capellini I, Venditti C, Barton RA (2010) Phylogeny and metabolic scaling in mammals. *Ecology* 91(9):2783–2793.
- Bates DM (2010) *lme4: Mixed-Effects Modeling With R* (Springer, New York).

26. Kitchell JF, et al. (1979) Consumer regulation of nutrient cycling. *Bioscience* 29(1): 28–34.
27. Allgeier JE, Yeager LA, Layman CA (2013) Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. *Ecology* 94(2): 521–529.
28. McNaughton SJ, Ruess RW, Seagle SW (1988) Large mammals and process dynamics in African ecosystems. *Bioscience* 38(11):794–800.
29. Elser JJ, Urabe J (1999) The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology* 80(3):735–751.
30. Elser JJ, et al. (2000) Biological stoichiometry from genes to ecosystems. *Ecol Lett* 3(6):540–550.
31. Anderson P (2001) *Fish Physiology: Nitrogen Excretion*, eds Write PA, Anderson PM (Academic Press, San Diego), pp 201–229.
32. Yeager LA, Layman CA, Allgeier JE (2011) Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* 167(1):157–168.
33. Hammerschlag-Peyer CM, Allgeier JE, Layman CA (2013) Predator effects on faunal community composition in shallow seagrass beds of The Bahamas. *J Exp Mar Biol Ecol* 446:282–290.
34. Allgeier JE, Rosemond AD, Mehring AS, Layman CA (2010) Synergistic nutrient co-limitation across a gradient of ecosystem fragmentation in subtropical mangrove-dominated wetlands. *Limnol Oceanogr* 55(6):2660–2668.
35. Schaus MJ, et al. (1997) Nitrogen and phosphorous excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnol Oceanogr* 42(6):1386–1397.
36. Whiles MR, Huryn AD, Taylor BW, Reeve JD (2009) Influence of handling stress and fasting on estimates of ammonium excretion by tadpoles and fish: Recommendations for designing excretion experiments. *Limnol Oceanogr* 7:1–7.
37. Taylor BW, et al. (2007) Improving the fluorometric ammonium method: Matrix effects, background fluorescence, and standard additions. *J N Am Benthol Soc* 26(2):167–177.
38. Allgeier JE, Layman CA, Mumby PJ, Rosemond AD (2014) Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Glob Change Biol* 20(8):2459–2472.
39. Layman CA (2007) What can stable isotope ratios reveal about mangroves as fish habitat? *Bull Mar Sci* 80(3):513–527.
40. Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: A case study on the invasive Lionfish *Pterois volitans* in the Bahamas. *Mar Ecol Prog Ser* 448:131–144.
41. Layman CA, et al. (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev Camb Philos Soc* 87(3):545–562.
42. Post DM (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83:703–718.
43. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach* (Springer-Verlag, New York), 2nd Ed.
44. Gelman A, Hill J (2007) *Data Analysis Using Regression* (Cambridge Univ Press, New York).
45. R Core Development Team (2012) R: A language and environment for statistical computing. Available at www.r-project.org. Accessed August 2012.