

Embracing general theory and taxon-level idiosyncrasies to explain nutrient recycling

Diego R. Barneche¹ and Andrew P. Allen

Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

At the molecular level, the process of living involves coupled biochemical reactions that result in the uptake and transformation of energy and materials by an organism, yielding biomass to support its growth and reproduction, along with waste products. Ultimately, the dynamics of this process must adhere to constraints imposed by first principles of chemistry and physics, such as mass and energy balance. Still, there is considerable debate regarding the extent to which such constraints can be used to mechanistically understand and quantitatively predict the dynamics of particular ecological processes and systems (1). Although some would argue that first principles can serve as a basis for developing general quantitative theories that account for a broad range of ecological phenomena using few free parameters (2), others would argue that attempts to characterize life in such terms are of more limited value due to the taxonomic and functional distinctiveness of species, and the complexity of their ecological interactions (3). This debate concerning the existence (or lack thereof) of general laws is as old as Ecology itself. Allgeier et al. (4) lend support to both sides of this debate by statistically disentangling general trends and taxon-level

idiosyncrasies in rates of nutrient recycling by individuals. Nutrient recycling is a process fundamental to ecosystem function because it entails the breakdown of organic molecules, thereby releasing dissolved nutrients back into the environment for reuse by plants (5).

Allgeier et al. (4) establish a priori expectations for general trends in nutrient recycling rates using a quantitative framework that arises by combining two emerging ecological theories (6), Metabolic Theory of Ecology (MTE) (7–10) and Ecological Stoichiometry Theory (EST) (11, 12), which respectively deal with energy and material flows in ecological systems. Specifically, the authors investigate whether nitrogen and phosphorus recycling rates vary proportionally with body mass, M , raised to the power of 3/4 (i.e., $\propto M^{3/4}$), and whether an organism's nutrient content and trophic position can account for deviations from this 3/4-power scaling relation. MTE predicts 3/4-power body mass scaling for the total rate of dissolved nutrient excretion (in urine), E_x (grams per hour), based on 3/4-power scaling relations for differences among species in individual-level rates of metabolism (7, 9), biomass production (8), P (grams per hour), and food assimilation (10), $C - E_g$ (grams per

hour), where C is the rate of food consumption and E_g is the rate of food egestion (in feces), because mass balance dictates that $E_x = C - E_g - P$ at the level of the organism (ref. 5; see Fig. 1). Moreover, due to mass balance, recycling rates of particular nutrients in food such as nitrogen, $E_x[N]_{E_x}$, adhere to an equality of similar form: $E_x[N]_{E_x} = C[N]_C - E_g[N]_{E_g} - P[N]_P$, where $[N]_{E_x}$, $[N]_C$, $[N]_{E_g}$, and $[N]_P$ are the respective nitrogen concentrations (grams of nitrogen per gram) for each flux. Consequently, if the nutrient concentrations of food (e.g., $[N]_C$), biomass (e.g., $[N]_P$), and feces (e.g., $[N]_{E_g}$) are all held constant, MTE predicts that nutrient recycling rates (e.g., $E_x[N]_{E_x}$), should also exhibit 3/4-power body mass scaling among species. Moreover, MTE, when combined with EST, predicts that there should be deviations from this predicted scaling relation to the extent that these concentrations vary with body mass and/or among taxa.

To evaluate these predictions, Allgeier et al. (4) collected data on rates of nitrogen and phosphorus recycling from 900 individuals in a single marine ecosystem in the Bahamas. Their database encompasses substantial morphological and taxonomic diversity: Organisms vary by more than four orders of magnitude in body mass, and include vertebrates (fish) and invertebrates (crabs, gastropods, jellyfish, sea cucumbers, and shrimp). To quantify general trends, as well as deviations from these trends for each taxon (e.g., family, species), Allgeier et al. (4) analyzed their nutrient recycling data using mixed effects models (13). They do so by treating taxon as a random factor that could potentially influence both the nutrient recycling rate at fixed mass, and the mass dependence of the nutrient recycling rate. Here taxon serves as a crude surrogate for myriad factors that vary by taxon and affect nutrient recycling rates. Such factors may include, for example, variation among taxa in the scaling of metabolic rates (14–16) or the stoichiometric composition of food, and changes that occur

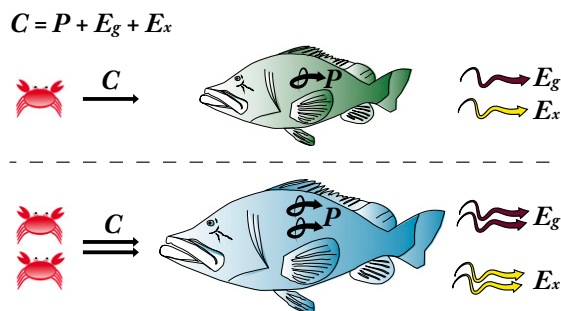


Fig. 1. Heterotrophic organisms take in nutrients via food consumption (C), some of which is egested (E_g) in undigested form as feces, some of which is excreted (E_x) as recycled nutrients in urine, and some of which is allocated to biomass production (P) for growth and reproduction. Mass balance dictates that $E_x = C - E_g - P$ for overall rates of nutrient gain and loss (5). Allgeier et al. (4) show that, after statistically controlling for differences among taxa using mixed effects models (13), the dependencies of nitrogen and phosphorus recycling rates on body mass, M , are both well approximated by 3/4-power body mass scaling relations (i.e., $\propto M^{3/4}$), implying that a species that is 2.5 times larger in adult mass recycles nitrogen and phosphorus at approximately double the rate (i.e., $2.5^{3/4} \approx 2$), as illustrated above.

Author contributions: D.R.B. and A.P.A. wrote the paper.

The authors declare no conflict of interest.

See companion article on page E2640.

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

Table 1. Effects of different predictors on excretion rates, as estimated by the models presented in table 2 of Allgeier et al. (4)

| Predictor variable | Range of variation | |
|----------------------------|--|--|
| | Predictor variable | Estimated effect on rate |
| Best model for N recycling | | |
| Body mass | 64,925-fold (0.04–2,597 g) | 4,543-fold (= 64,925 ^{0.76}) |
| Body [N] content | 6.1-fold (2.32–14.20%) | 4.5-fold (= 6 ^{0.84}) |
| Taxonomy | 35 families (0.52–64.37 µg N·h ⁻¹) | 123-fold (= 64.37/0.52) |
| Best model for P recycling | | |
| Body mass | 64,925-fold (0.04–2,597 g) | 3,640-fold (= 64,925 ^{0.74}) |
| Taxonomy | 44 species (0.35–17.52 µg P·h ⁻¹) | 50-fold (= 17.52/0.35) |

Values were obtained directly from the Allgeier et al. (4) text or were extracted from the figures. Estimated effects over the observed ranges of the predictor variables were calculated based on the parameter estimates of the fitted models. Values for family- and species-level intercepts are estimated random effects, which correspond to recycling rates for organisms at a mass of 1 gram.

within a taxon over ontogeny [e.g., fraction of assimilated food allocated to biomass (10)]. Although the statistical approach of Allgeier et al. (4) is unable to identify the proximate factors responsible for differences in the scaling of nutrient recycling rates among taxa, it is able to quantify the overall effects of taxon-specific factors as deviations from general trends.

So, what does the analysis of Allgeier et al. (4) reveal? The authors show that, after accounting for effects attributable to taxonomy, nutrient recycling rates are well approximated by 3/4-power body-mass scaling, consistent with MTE–EST predictions. Moreover, compared with the effects of body mass, the effects of biomass stoichiometry (as indexed by the body nitrogen and phosphorus contents) and diet (as indexed by body $\delta^{15}\text{N}$ content) are quite small. In fact, only nitrogen content was identified as significant, and its estimated effects were relatively modest (Table 1): Although nitrogen excretion rates are estimated to vary by >4,500-fold over the range of variation in body mass encompassed by this dataset, rates are estimated to vary less than fivefold over the observed range of variation in nitrogen content. Interpretation of these findings entails several caveats. Most importantly, although body mass varies by nearly 65,000-fold among the organisms included in this analysis, nitrogen content varies by less than sevenfold. Therefore, on this basis alone, we might expect body mass to have a greater overall effect

on nutrient recycling rates than organismal stoichiometry. In fact, results of the statistical analysis indicate that a doubling in body mass has a smaller effect on nitrogen recycling rates than a doubling in nitrogen content, suggesting that stoichiometry also plays an important role. Moreover, the effects of nutrient content on nutrient recycling rates may vary depending on whether or not that nutrient is limiting (12), so different patterns may emerge in systems with distinct nutrient regimes. Finally, effects of stoichiometry on rates of nutrient recycling may assume

greater importance at higher levels of biological organization (e.g., population, trophic level). Despite these caveats, the study of Allgeier et al. (4) shows quite convincingly that the constraint of body mass on energy and food requirements is the primary driver of differences in nutrient recycling rates among marine animals in this ecosystem.

What is perhaps most striking about the analysis of Allgeier et al. (4) is how much of the variation in recycling rates is attributable to taxonomy. Specifically, it reveals that, even after controlling for body mass, recycling rates of nitrogen and phosphorus vary ~123- and ~50-fold among families and species, respectively (Table 1). In so doing, the results of Allgeier et al. (4) add to a growing body of literature that quantifies variation in the scaling of biological rates across taxa and systems, e.g., refs. 14–19. Overall, while the results of Allgeier et al. (4) highlight trends that exhibit impressive agreement with theoretical predictions, they also emphasize that we still have much more to learn about the factors governing nutrient recycling rates within and among taxa. Future theoretical advances at the intersection of MTE and EST hold promise in contributing to a deeper understanding of the roles of biota in nutrient cycles at local to global scales.

- 1 Tilman D, et al. (2004) Does metabolic theory apply to community ecology? It's a matter of scale. *Ecology* 85(7):1797–1799.
- 2 Marquet PA, et al. (2014) On theory in ecology. *Bioscience* 64(8):701–710.
- 3 Cyr H, Walker SC (2004) An illusion of mechanistic understanding. *Ecology* 85(7):1802–1804.
- 4 Allgeier JE, Wenger SJ, Rosemond AD, Schindler DE, Layman CA (2015) Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food web. *Proc Natl Acad Sci USA* 112:E2640–E2647.
- 5 Vanni MJ (2002) Nutrient cycling by animals in freshwater ecosystems. *Annu Rev Ecol Syst* 33(1):341–370.
- 6 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.
- 7 West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276(5309):122–126.
- 8 Ernest SKM, et al. (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecol Lett* 6(11):990–995.
- 9 Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85(7):1771–1789.
- 10 Hou C, et al. (2008) Energy uptake and allocation during ontogeny. *Science* 322(5902):736–739.

- 11 Reiners WA (1986) Complementary models for ecosystems. *Am Nat* 127(1):59–73.
- 12 Sterner RW, Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere* (Princeton Univ Press, Princeton, NJ).
- 13 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York).
- 14 Glazier DS (2005) Beyond the '3/4-power law': Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol Rev Camb Philos Soc* 80(4):611–662.
- 15 Isaac NJB, Carbone C (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecol Lett* 13(6):728–735.
- 16 Barneche DR, et al. (2014) Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecol Lett* 17(9):1067–1076.
- 17 O'Connor MI, et al. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc Natl Acad Sci USA* 104(4):1266–1271.
- 18 Killen SS, Atkinson D, Glazier DS (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol Lett* 13(2):184–193.
- 19 Yvon-Durocher G, et al. (2012) Reconciling the temperature dependence of respiration across timescales and ecosystem types. *Nature* 487(7408):472–476.