Allometric Theory: Extrapolations From Individuals to Ecosystems

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Glossary

Ecosystem model A mathematical representation of the interactions among biological, chemical and physical components in an ecological system.

Epilimnion The upper most layer of lakes when the difference in density due to the warmer surface water create stratification in the water column.

Eukaryotes Eukaryotes whose cells have a nucleus and organelles enclosed within membrane, whereas prokaryotes are unicellular organisms with no membrane-bound organelles.

Functional groups A specific group of organisms (or chemical compounds) that share similar attributes.

Half saturation constant for nutrient uptake The nutrient concentration at which uptake rate of a nutrient is half of the maximum potential rate.

Harmful algal blooms Excessive growth of phytoplankton bloom in aquatic environments dominated by species that cause toxic or harmful effects on people, fish, shellfish, marine mammals and birds.

Homeotherm An organism that maintains their thermal homeostasis. Some rely on internal metabolic processes as a heat source (endotherms), while others maintain their body temperature by behavioral thermoregulation.

Kleiber's rule A rule defining that organism's metabolic rates scale to the $^3/_4$ power of the animal's mass.

Lotka-Volterra models A model that describes predator-prey relationships with a pair of differential equations as function of growth rate of prey, mortality of prey and predator, predator's search/handling efficiency of prey and time.

Meroplankton Organisms that spend only part of their life (early stage, larval) drifting in pelagic environment and spend their adult life in the benthic community.

Parameterization The process of deciding and defining the parameters necessary for a defensible specification of a model.

Poikilotherm An organism whose internal temperature varies considerably as a consequence of variation in the ambient environmental temperature. Many ectotherms, organisms in which internal physiological sources of heat are of relatively limited importance in controlling body temperature. Such organisms rely on environmental heat sources, which permit them to operate at optimal metabolic rates.

Ecological stoichiometry The balance of multiple chemical elements (mainly carbon, nitrogen, phosphorus) and energy in ecological interactions. It particularly deals with the disequilibrium existing between the nutrient requirements of a consumer and the nutrient availability present in their resources (either mineral for autotrophic organisms or organic for heterotrophic organisms).

Occam's Razor Occam's (or Ockham's) razor is a principle attributed to the 14th century logician and Franciscan friar William of Ockham. The most useful statement of the principle for scientists is "when you have two competing theories that make exactly the same predictions, the simpler one is the better."

Fatty acids A fatty acid is a long hydrocarbon chain with variant length and degrees of unsaturation that terminates with a carboxylic acid group. Fatty acids with more than one double bonds are referred to as polyunsaturated fatty acids (PUFA); PUFAs with more than 20 carbons are referred to as highly unsaturated fatty acids (HUFAs). HUFAs are nutritionally critical molecules that animals cannot synthesize but can obtain them through intake of plants.

Abbreviations

AIC	Akaike information criterion
c	Abundance of consumers/predators
E	Activation energy, eV (electron volts, 1 eV $= 23.06$ kcal mol^{-1}, $= 96.49$ kJ mol^{-1})
ES	Ecological stoichiometry
F	Consumer per capita feeding rate
hr	Hour
h	Handling time that predators require to digest resources, s (expressed in seconds)
I	Individual metabolic rate
ind	Individual organisms
k	Boltzmann constant, 8.62×10^{-5} eV/K (see also activation energy)
KH_p	Parameter that represent half saturation constant for phosphorus uptake by primary producer, μmol P L^{-1}
M, m	Mass of organisms, g or kg
MTE	Metabolic theory of ecology
N	Resource abundance in individuals
NH	Parameter represent that half saturation constant for nitrate uptake by primary producer, μmol N L^{-1}
PPMR	Predator-prey mass ratio
QP_{max}	Maximum internal phosphate cell quota, fmol P cell^{-1}
QP_{min}	Minimum internal phosphate cell quota, fmol P cell^{-1}
R	Rate of metabolism, such as rate of respiration, excretion
r	Abundance of resource/prey
SA	Surface area of microorganisms cell, μm^2
SA:V	Surface area to cell volume ratio of individual organism's cell, μm^{-1}
T	Temperature, K
V	Body size as volume, cell volume μm^3
VP_{max}	Maximum phosphorus uptake rate by primary producer, μg P μm^{-3} h^{-1}
W	Organism body size, such as body mass, weight, volume, body length or height and surface area (SA)
wR	Mass specific rate of metabolism
Y	Biological attributes, such as growth rate, metabolic rate, physiological rate
μ_{max}	Parameter that represent maximum growth rate of organisms, day^{-1}

Introduction

Allometry, also known as biological scaling, describes the dependence of a biological variable on an organism's body mass, size, or shape. Originally used to describe the scaling relationships between body size and metabolic rates, allometric relationships can be expanded into a broader context to include morphological (e.g., total body length with body mass of invertebrates), physiological (e.g., metabolic rates with body size among mammals) or ecological traits (e.g., egg size with survival rates of immature stages in butterflies). Allometry offers the foundation for the development of scaling relationships that capture the variation in physiological mechanisms, individual behaviors such as locomotion or dispersal, as well as spatial distributions, population dynamics, and evolutionary patterns. In principle, allometric relationships stipulate that an easily identifiable predictor, the body size, can provide a reliable estimate of a given biological parameter (Fig. 1).

Most allometric relationships are presented as a simple power function of the form:

$$Y = aW^b \tag{1}$$

where W is the organism's body size, Y is a biological attribute, a and b are the experimentally derived constant and scaling exponent, respectively. Often log-log transformation is used to linearize the relationships, and empirically derive values for the coefficients. The logarithmic-scaled equation is thus:

$$\log Y = \log (a) + b \cdot \log W \tag{2}$$

Numerous allometric equations have been developed to estimate biological attributes as a function of body mass/size, or other morphological features, such as length (L), volume (V), surface area (SA), carbon content, or length: height ratio. The selection of the predictor is generally limited by its measurement precision and practicability for a particular organism. For example, the cell volume of microalgae is relatively easy to measure but the vacuoles may occupy most of the cell volume, thereby introducing considerable discrepancy from the actual algal biomass. While fresh biomass is the critical input for the majority of existing allometric equations, it is often difficult to obtain reliable measurements for many microorganisms. Other allometric relationships are based on the length as a proxy variable of the body size to estimate other morphological characteristics (e.g., stem basal diameter
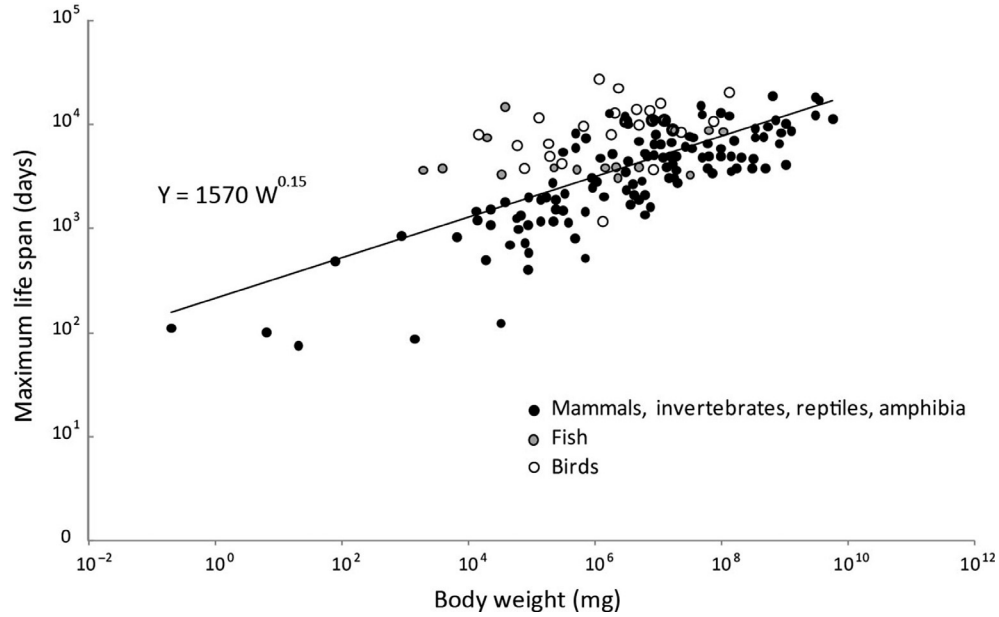
Fig. 1   Maximum life span for a range of animals against adult body weight (mg). Modified with permission from Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., Sams, S., (1978). Relationships between body size and some life history parameters. *Oecologia* 37, 257–272. https://doi.org/10.1007/BF00344996.

for the below-above ground tree biomass, the length-weight relationships of zooplankton) or organismal size-at-age (e.g., size at maturity). Surface area is often used in the allometric equations of nutrient kinetics and toxicology to quantify the transport of compounds through the cell membrane. In some cases, the ratio to the cell volume ($SA{:}V$) has also been used to account for the effects of morphological traits of unicellular organisms. For example, the uptake of chemical compound is largely regulated by the number of uptake receptors at the cell membrane relative to its cell volume, i.e., species with higher $SA{:}V$ demonstrate higher nutrient uptake rates and therefore obtain an advantage when competing for a limiting resource.

Examples of Allometric Principles

Metabolism collectively represents the set of processes in living cells by which energy is provided for vital processes and new material is assimilated in order to maintain life. Metabolism thus determines the demands that organisms place on their environment for all resources. The overall rate of these metabolic processes (often measured as respiration rate; Table 1) sets important constraints on the allocation of resources to all components of fitness. Different facets of metabolic activity can be expressed through this strategy. The most common is the basal metabolic rate, which reflects the rate of a fasting, inactive individual; the field metabolic rate characterizing the rate of a free-living individual in its environment; the maximal metabolic rate describing the metabolism of an individual at maximum aerobic activity.

Early research demonstrated that metabolic rate (R, in Watts) could be predicted from fresh body mass (W, in kg) for vastly different groups of organisms (Fig. 2A). The fitted allometric relationships for each group all scaled to the ¾ power:

$$R_{homeotherms} = 4.1W^{0.751} \tag{3}$$

$$R_{poikilotherms} = 0.14W^{0.751} \tag{4}$$

$$R_{unicells} = 0.018W^{0.751} \tag{5}$$

The common power in Eqs. (3)–(5) implies that the allocation of energy and materials to metabolism follow a similar pattern across most organisms. The positive exponent demonstrates that larger organisms within each metabolic class have a higher metabolic rate than do smaller organisms, while a value <1 predicts that metabolic rate rise more slowly as the body size increases. Adjusting these allometric relationships to be expressed as *mass-specific* metabolic rates (wR, in Watts kg^{-1}) yields scaling exponents of the $-¼$ power:

$$\begin{aligned} wR_{homeotherms} &= R_{homeotherms}/W \\ &= 4.1W^{0.751-1} \\ &= 4.1W^{-0.249} \end{aligned} \tag{6}$$

Table 1   Representative listing of physiological, morphological, and life-history allometric relationships measured for marine and freshwater zooplankton from the 1970s to 2016. n = number of individuals used in the regression analysis; r^2 = coefficient of determination; f = freshwater; m = marine; NA = not available

Taxon or species	Allometric relationship		n	Allometric equation: $\log_{10}Y = a + b \cdot \log_{10}W$				Reference
	Y	W		Intercept(a)	Slope (b)	r^2	P	
Physiology								
Zooplankton (m)	Respiration rate (μL O_2 ind^{-1} h^{-1})	Dry mass (mg)	42	0.21	0.90	0.54	<0.0001	Hébert et al. (2016)[a]
Zooplankton (f)	Respiration rate (μL O_2 ind^{-1} h^{-1})	Dry mass (mg)	17	1.24	0.82	0.94	<0.0001	Hébert et al. (2016)[a]
Daphnia pulicaria (f)	Ingestion rate (μg C ind^{-1} h^{-1})	Body length (mm)	128	−1.067	2.739	0.747	NA	Carotenuto and Lampert (2004)
Cladocerans (f)	Filtering rate (mL day^{-1})	Body length (mm)	519	0.896	2.403	0.867	NA	Knoechel and Holtby (1986)
Daphnia (f)	Clearance rate (mL ind^{-1} h^{-1})	Body length (mm)	30	0.210	2.83	0.98	NA	Demott (1982)
Zooplankton (f, m)	P excretion rate (mmol P-PO$_4^{3-}$ ind^{-1} h^{-1})	Dry mass (mg)	47	0.56	0.70	0.72	<0.0001	Hébert et al. (2016)[a]
Zooplankton (f, m)	P excretion rate (μg P day^{-1})	Body size (μg)	462	−1.65	0.54	0.63	<0.001	Wen and Peters (1994)
Zooplankton (f, m)	N excretion rate (μg N day^{-1})	Body size (μg)	574	−1.38	0.67	0.72	<0.001	Wen and Peters (1994)
Zooplankton (f, m)	N excretion rate (mmol N-NH$_4$ ind^{-1} h^{-1})	Dry mass (mg)	71	2.50	0.84	0.73	<0.0001	Hébert et al. (2016)[a]
Morphology								
Zooplankton (m)	Body dry mass (mg)	Body length (mm)	37	−3.910	2.791	0.94	<0.001	Hébert et al. (2016)[a]
Zooplankton (f)	Body dry mass (mg)	Body length (mm)	148	−4.814	2.075	0.74	<0.001	Hébert et al. (2016)[a]
Cladocerans (f)	Dry weight (μg)	Total length (mm)	283	0.994	2.1	0.84	NA	Peters and Downing (1984)
Life-history								
Copepods (m) (broadcast spawners)	Weight-specific fecundity (day^{-1})	Female body weight(μg C)	35	−0.474	−0.262	0.32	<0.001	Kiørboe and Sabatini (1995)
Copepods (m) (sac-spawners)	Weight-specific fecundity (day^{-1})	Female body weight(μg C)	10	−0.850	−0.260	0.72	<0.001	Kiørboe and Sabatini (1995)
Zooplankton (f, m) (flagellates, ciliates, rotifers, meroplankton larvae, copepods, cladocerans)	Growth rate (hr^{-1})	Body volume (μm^3)	69	−0.52	−0.21	0.69	<0.01	Hansen et al. (1997)
Copepods,cladocerans, rotifers (f, m)	Generation time (°C day^{-1})	Dry body mass (μg)	111	2.26	0.21	0.72	<0.001	Gillooly (2000)

[a]Regression coefficients estimated using natural instead of $\log_{10}$ transformation.

$$wR_{poikilotherms} = 0.14W^{-0.249} \tag{7}$$

$$wR_{unicells} = 0.018W^{-0.249} \tag{8}$$

Thus, the rate of energy expenditure per unit mass declines with increasing body size, while the cost of maintaining a given biomass is less for larger animals than smaller ones.

Subsequent research using this simple allometric equation has been successful in describing the relationship between metabolic rate and body mass for diverse groups of organisms, all characterized by scaling exponents of ~3/4. This recurring relationship was adopted as *Kleiber's rule* and its wide applicability suggested that it may be a rare example of a general biological law. However, despite the presence of plausible theoretical explanations for its ubiquity (e.g., processes that control chemical reactions within cells and/or designs of resource distribution networks with functional similarities to all organisms), the debate whether the true value of
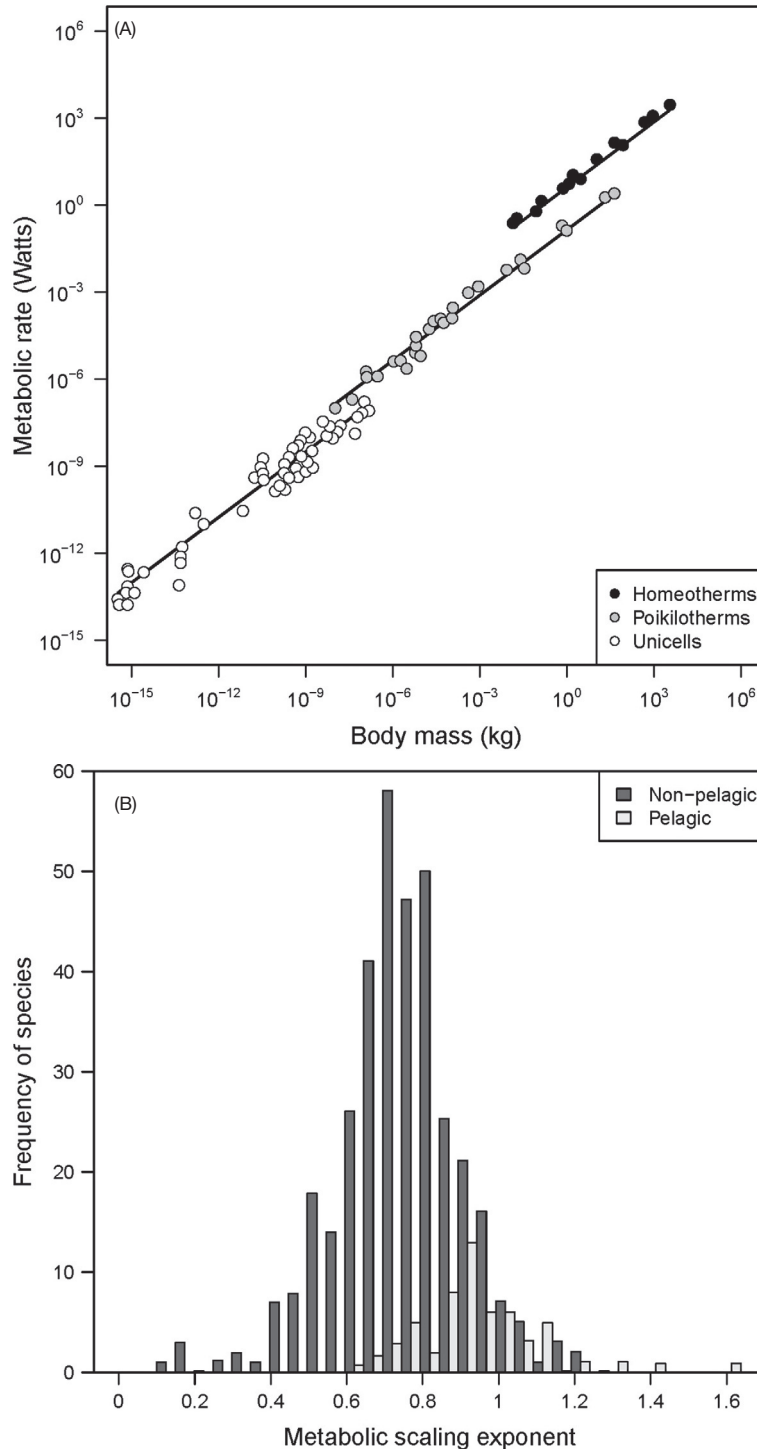
Fig. 2   (A) Standard metabolic rates of homeotherms, poikilotherms, and unicells (Eqs. (1)–(3) in text). (b) Frequency distributions of scaling exponents from regressions of log metabolic rate vs. log body mass of pelagic and nonpelagic marine invertebrate species. (A) Modified from Peters, R. H. The ecological implications of body size. Cambridge, UK: Cambridge University Press, 1983. (B) Modified with permission from Glazier, D.S. (2005). Beyond the "3/4-power law": Variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol. Rev.* **80**, 611–662. https://doi.org/10.1017/S1464793105006834.

the scaling exponent b should be set at $3/4$, $2/3$, or whether it is variable, has continued. For example, a recent survey of 642 published regressions of (laboratory-measured) metabolic rates in marine invertebrates found a wide range of scaling exponents for metabolic rates (Fig. 2B), with similar species exhibiting scaling exponent values from 0.75 up to (or greater than) 0.9. This finding suggests that the $3/4$ power law is not universal. While *Kleiber's rule* is a valid statistical generalization, it is important to note that $b = 3/4$ is an approximation, rather than the "true" value of the scaling exponent for all allometric equations of metabolic rates.

As metabolism represents the total energetic cost of an organism's biological processes, size-related changes in most other biological functions should parallel the scaling of metabolism. To illustrate this scaling for physiological, morphological, and life-history rates, a series of allometric relationships is presented in Table 1 for various groups of marine and freshwater zooplankton. Zooplankton is considered as an ideal organism to develop allometric relationships, due to their numerical abundance and ease of sampling in aquatic environments, while their relatively short generation times are conducive to laboratory studies. Furthermore, the trophic linkages between primary producers and zooplankton are arguably the most important in aquatic food webs, as their interactions control the flow of energy to higher trophic levels.

Grazing (ingestion) sets an upper limit to all other physiological rates, and is one of the most significant interactions between an organism and the surrounding environment. Zooplankton grazing can exert significant control on phytoplankton biomass and species composition. The allometric scaling of ingestion (measured as ingestion, filtration, or clearance rates) with zooplankton body size (measured as body length) suggests that larger zooplankton graze particles at a higher rate than smaller ones (Table 1). Similarly, a unit increase in zooplankton body size results in 2.4–2.8 increase in ingestion rate (Table 1), and therefore larger zooplankton have a greater impact on energy transfer through the food web.

In aquatic ecosystems, zooplankton regenerate mineral nutrients (e.g., nitrogen, phosphorus) via their excretion; thus, changes in the rate of materials recycled can directly impact the abundance and composition of primary producers. Body size has a large effect on excretion rates in zooplankton, where scaling exponents <1 indicate that larger zooplankton excrete at a lower rate for their size than smaller taxa (Table 1). The less than proportional increase in excretion rate is linked to metabolism. Interestingly, the scaling exponents can be higher or lower than $3/4$ depending on the nutrient recycled, as nitrogen excretion rates scale to the 0.67–0.84 power of body mass, while phosphorus excretion rates can be slightly lower ($b = 0.54$–0.70) (Table 1).

The measurement of zooplankton biomass, together with the productivity assessment, is an important component for estimating standing stocks, as well as community structure and dynamics. Only two quantities are required to calculate the production of a population, since multiplying the number of individuals by their average mass yields an estimate of the total population biomass. The production rate is then the amount of biomass accumulated by a population per unit of time. The most common way to estimate average mass of zooplankton involves prediction of animal weight from body length with allometric equations (Table 1). These relationships suggest that there is a greater than proportional increase in zooplankton weight with a corresponding increase in body size. The variation (in scaling exponents) among allometric regressions may relate to environment influences at the study site in question, such as latitude, temperature, and/or food availability.

Body size imposes constraints on the life-history (e.g., growth, fecundity, survival) of organisms. Quantifying the variation of the relationship between life-history processes and body size can offer insights into the natural selection pressures. For example, examining rates of fecundity, mortality, and developmental time as a function of (adult) body mass is critical for understanding zooplankton evolution. Generation time (time span from egg to maturity) is a critical determinant of the rate of population growth in zooplankton, and scales positively to body mass close to the $1/4$ power (Table 1). Weight-specific fecundity rates scale close to the $-1/4$ power for both broadcast and sac-spawning marine copepods, although the intercepts differ, suggesting that weight-specific fecundities are ~2.5 times greater for broadcast spawners than sac-spawners, which in turn may relate to their different life-cycle strategies (Table 1). Maximum specific growth rates appear to scale to the $-1/4$ power, declining with increasing body volume across a wide range of marine and freshwater zooplankton groups (e.g., dinoflagellates, other flagellates, ciliates, rotifers, meroplankton larvae, cladocerans, and copepods), suggesting that small zooplankton have higher mass-specific metabolic rates and grow faster than large ones (Table 1).

The predictive power of scaling laws to life-history processes depends on whether natural selection can alter the scaling exponent value. If the scaling exponent varies with environment, then this reflects the strong role of selection on this exponent. Returning to the large survey of allometric scaling exponents presented earlier, pelagic (open-water) species had significantly greater mean scaling exponents ($b = 0.947$) than those of nonpelagic species ($b = 0.744$) (Fig. 2B). While sampling error can explain some of this variation, it may also reflect real biological differences in metabolic rates across taxa with diverse body characteristics and widely separated phylogenies.

Recent Advances in the Application of Allometric Principles

Metabolic Theory of Ecology

Metabolic and other process rates are strongly affected by both body size and temperature. More recent theoretical advances have combined first principles of allometry and biochemical kinetics to develop the metabolic theory of ecology (MTE). MTE uses scaling functions to incorporate the effects of body size and temperature on individual metabolic rates, which in turn modulate the performance of individual organisms and subsequently the ecology of populations, communities, and ecosystems. The joint effects of body mass (M), and temperature (T, in K) on individual metabolic rate (I), is given as:

$$I = i_0 M^{3/4} e^{-E/kT} \tag{9}$$

where E is the activation energy (0.6–0.7 eV), k is the Boltzmann constant (8.62×10^{-5} eV/K), and i_0 is a normalization constant independent of body size and temperature. Across diverse groups of organisms (from unicellular microbes to the largest vertebrates and trees), this relationship predicts a 100,000-fold variation in metabolic rates over 20 orders-of-magnitude in body size, while

temperature predicts a $\sim$30-fold variation in metabolic rates over the temperature range of normal activity for most organisms (0°C–40°C). The dependence on mass may be a consequence of the scaling of resource supply and exchange surfaces in branching hierarchical networks, while the dependence on temperature reflects its impact on biochemical reaction rates. For ectotherms, this is equivalent to ambient temperature, while for endotherms, this temperature is high (35°C–40°C) and mostly temperature independent.

Taking the logarithm of both sides and rearranging terms yields a linear relationship:

$$\ln\left(IM^{-3/4}\right) = -E(1/kT) + \ln\left(i_0\right) \tag{10}$$

By incorporating the logarithm of mass raised to the ¾ power, the metabolic rate has been "mass-corrected," and the predicted scaling is incorporated into the *y*-axis of bivariate plots. This mass-corrected relationship predicts that the (natural logarithm of) whole-organism metabolic rate is a linear function of inverse absolute temperature; the slope gives the activation energy of metabolism, E, while the intercept represents the (natural logarithm) normalization constant, $\ln(i_o)$. To isolate the effects of body mass, metabolic rates can be "temperature-corrected" using the Boltzmann-Arrhenius factor ($e^{-E/kT}$), to yield:

$$\ln\left(Ie^{E/kT}\right) = \left(^3/_4\right)\ln\left(M\right) + \ln\left(i_0\right) \tag{11}$$

This equation predicts a linear relationship between the (natural logarithm) temperature-corrected metabolic rate and (natural logarithm) body mass. Comparing these relationships to empirical data collected from a wide variety of taxa (e.g., endotherms, fish, amphibians, reptiles, invertebrates, unicellular organisms, and plants) demonstrated that the observed slope of mass-corrected metabolic rates for all groups fell within the predicted range of 0.6–0.7 eV (Fig. 3A). In comparison, temperature-corrected metabolic rates for all groups clustered closely around a common allometric scaling relationship with an exponent of 0.71, which is close to the ¾ power predicted from theory, although the intercepts (normalization constants) vary among groups (Fig. 3B).

By isolating the effect of mass (or alternatively temperature), the MTE can be used to investigate other biological rates, which are predicted to scale as $M^{-1/4}$, and biological times, which are expected to scale as $M^{1/4}$. For example, the MTE has been used to predict ontogenic development as a function of body mass and temperature. Using zooplankton eggs reared in the laboratory and fish eggs collected from the field, plots of temperature-corrected hatching rate (day^{-1}) versus body mass (g) were well fit by straight lines with similar slopes very close to the predicted −¼ power (−0.26 and −0.22, respectively). The MTE has also been incorporated into

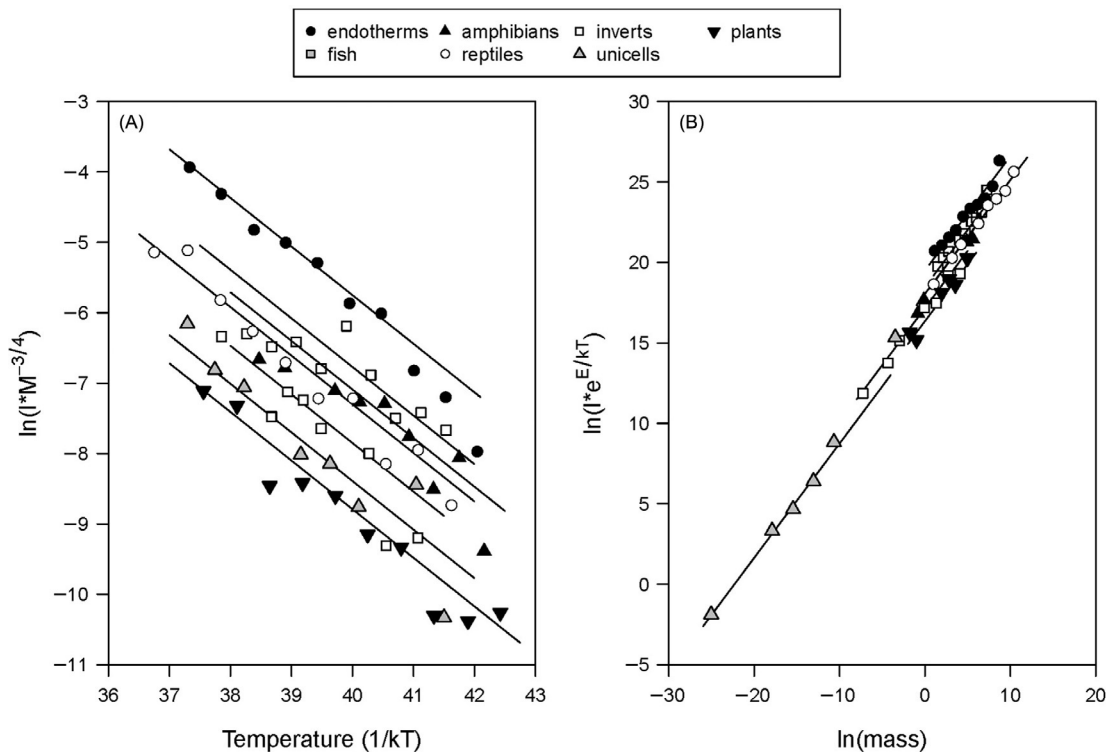**Fig. 3** Allometric scaling relationships of (A) mass-corrected metabolic rate, ln($I \cdot M^{-3/4}$) (in Watts g$^{-3/4}$), or (B) temperature-corrected metabolic rate, ln($I \cdot e^{E/kT}$) (in Watts), as a function of body mass, ln(*M*) (in grams) for endotherms, fish, amphibians, reptiles, invertebrates, unicellular organisms, and plants. k = Boltzmann constant; T = absolute temperature (in K); E = activation energy (in eV). Modified with permission from Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B., (2004). Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–1789. https://doi.org/10.1890/03-9000.

allometric modeling to predict excretion rates of invasive fish species at different temperatures. Accounting for the role of temperature is critical when predicting seasonal excretion rates in freshwater ecosystems. Consistent with the MTE, mass-specific nutrient excretion rates decreased with increasing fish size, such that smaller fish generally excreted more nutrients per gram of body mass than larger fish, and were greater in summer than winter.

The MTE framework has been extended to enable predictions regarding population growth. Metabolic rates of organisms determine their rates of growth and reproduction, which in turn fuels population growth. Population growth rate is often measured as net outcome of the maximal growth rate (the capacity of a population to reproduce at maximum rate when resources are not limiting), and the rate of turnover at steady state (where the total number of individuals in the population does not change over time). Allometric scaling relationships of temperature-corrected maximal growth rate as a function of body size for a wide variety of taxa, from unicellular eukaryotes to vertebrates, are suggestive of a single line with a slope of −0.23, across 12 orders-of-magnitude of variation in body size. The rate of population turnover, and thus birth and death rates, scaled similarly. For example, an allometric equation predicting temperature-corrected instantaneous mortality rate for marine fish in the field yields a straight line and a scaling exponent of −0.23, statistically indistinguishable from the predicted −¼ power.

The MTE framework has also been extended to link the processing of energy and elements at the individual level to the flux, storage, and turnover of these elements at the ecosystem level. For example, the constraints that body size and temperature place on C dynamics at all levels of biological organization (e.g., cellular organelles to the biosphere) can be combined to create a model that relates the global C cycle directly to the C flux, storage, and turnover in individual organisms. Compilations of data from major biomes that include forests, grasslands, tundra, and oceans, have demonstrated that allometric relationships between C storage in plant communities as a function of average plant size scale as a 0.24 power, while C turnover expressed as a function of average plant size yielded scaling exponents of −0.22. Both empirically-estimated scaling exponents were very close to their predicted quarter-power scaling values.

To recap, energy and mass are not distinctly different ecological currencies that operate independently of each other to shape ecosystem structure and dynamics. At all levels, from individual organisms to ecosystems, fluxes, reserves, and transformations of energy and materials are constrained by the biochemical and physiological constraints of metabolism. Within this context, the metabolic theory appears to explain much of the variability in process rates and somatic reserves. However, it is important to note that although metabolism is one of the most integrative processes in biology, building connections from molecules to ecosystems, metabolic theory cannot account for all important patterns and processes. The existence of residual variation around the predictions of the metabolic theory underscores the importance of other variables and processes not considered by the contemporary paradigm.

Ecological Stoichiometry and Metabolic Theory of Ecology

Ecological stoichiometry (ES) theory aims to quantify how variations in the balance of biologically important elements impact, and in turn are impacted by, organisms and their environment. Integration of the theory of ES with MTE may offer a useful framework to link the dynamics of energy and mass across different levels of biological organization. The ES and MTE models are founded upon a series of principles that link the energetics and stoichiometry at the level of cellular organelles with individual-level energetics and stoichiometry, and ultimately with higher-order ecosystem processes. The four major principles proposed state that:

1. Links between the fluxes of energy and materials are based on the kinetics and elemental compositions of processes and subcellular structures;
2. Biomass is comprised of metabolic and structural pools, which can have distinct allometric and elemental signature;
3. Metabolic rate (and its determinants) govern the fluxes of energy and elements at the organismal level;
4. The storage, flux, and turnover of energy and mass in a biological community can be estimated by summing across individuals within that community.

Patterns in rates of consumption by herbivores across freshwater, marine, and terrestrial ecosystems, at the individual and population level, have been used to validate joint ES–MTE predictions. Under the combined ES–MTE theory, per-capita rates of herbivory are expected to:

a. increase with body size;
b. increase with ambient temperatures for ectotherms, whereas for endotherms, either be independent of temperature or decrease with increasing temperature if high metabolic costs occur at low temperatures; and
c. increase with increasing stoichiometric mismatch.

In contrast, population-level rates of herbivory are expected to:

d. be independent of body size;
e. increase with increasing ambient temperature for both *endo-* and ectotherms; and
f. decrease with increasing stoichiometric mismatch.

Empirical data have rendered support to the predicted metabolic and stoichiometric constraints on herbivory at individual and population levels (Fig. 4). At the individual level, the body size of herbivores appears to be an important factor of the per-capita consumption rates for large gradients of body size, ranging from small zooplankton to large mammalian herbivores, with larger
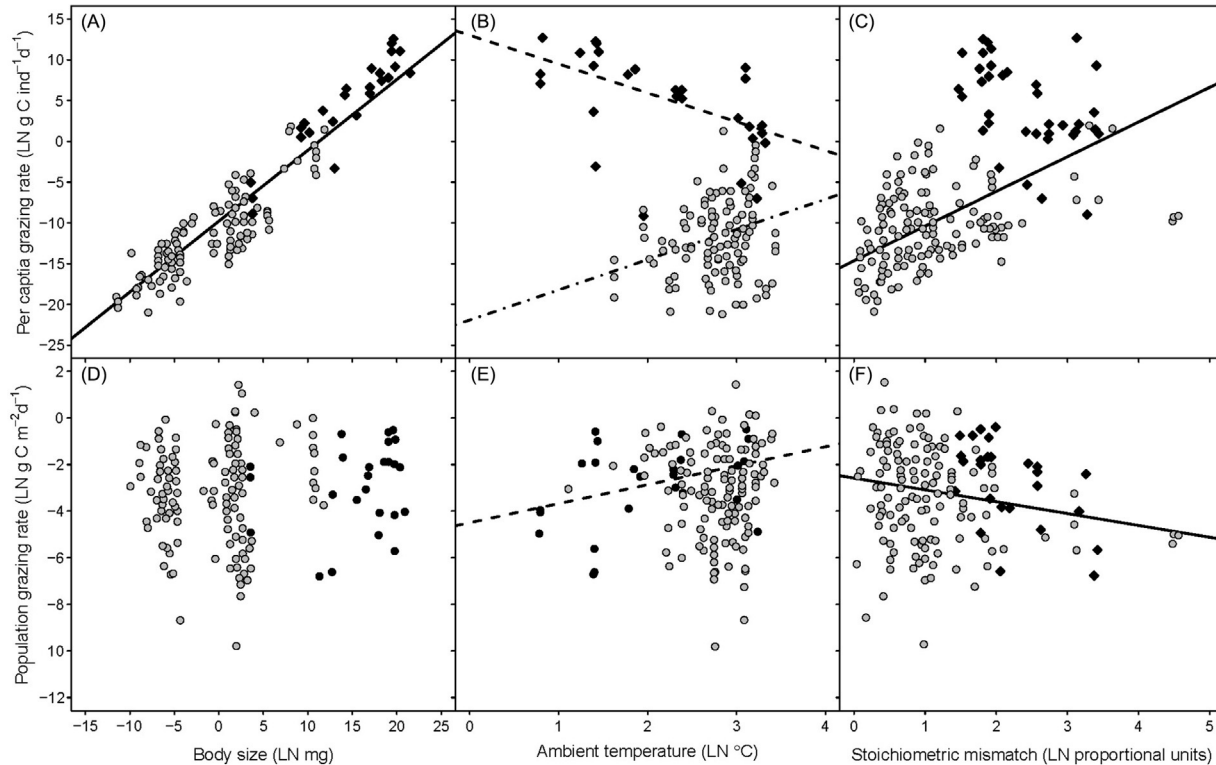
Fig. 4 Per-capita (top panels) and population-level (bottom panels) rates of herbivory as functions of body size, ambient temperature, and stoichiometric mismatch between prey and consumers. *Gray circles* = ectotherms; *black diamonds* = endotherms. Modified with permission from Hillebrand, H., Borer, E.T., Bracken, M.E. S., Cardinale, B.J., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner, D.S., Harpole, W.S., Ngai, J.T., Sandin, S., Seabloom, E.W., Shurin, J.B., Smith, J.E., Smith, M.D. (2009). Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. *Ecology Letters*, **12**, 516–527. https://doi.org/10.1111/j.1461-0248.2009.01304.x.

species consuming more biomass per-capita. Consumption rates in individual endotherms declined at high ambient temperatures, but increased for individual ectotherms. Stoichiometric mismatch had a small, positive effect on per-capita consumption rates. At the population level, consumption rate was invariant with body size, increased with ambient temperature for both ectotherms and endotherms, and declined with increasing stoichiometric mismatch (Fig. 4). Interestingly, examining per-capita consumption rates within ecologically similar groups (e.g., taxa with similar sizes and ecological roles) reduced the explanatory power of body size, while stoichiometric mismatch emerged as a more influential factor. Furthermore, MTE-related variables (body size, temperature) are more closely related to per-capita consumption rates, while ES-related variables (stoichiometric mismatch) appear to shape population-level rates. Overall, these results suggest that the integration of ES-MTE theories offer a microscopic-to-macroscopic strategy that can explicitly relate the energetics and stoichiometry of individuals, communities and ecosystems to subcellular structures and processes.

Food-Web Interactions

The allometric approach has been primarily considered in the context of organismal physiology and less so to elucidate ecosystem processes. More recently, there has been a growing emphasis on the idea that functional traits, as developed through natural selection, can directly affect the intra-specific variations and may ultimately determine demographic performance, spatial distribution (i.e., ecological niche), population dynamics, and food-web organization. In particular, the body size is one of the most fundamental functional traits that shapes predator-prey interactions and may conceivably modulate other ecological processes (e.g., sedimentation, nutrient recycling, foraging, and migration).

Consumer-resource foraging interaction has long been identified as one of the dominant forces that connect individual ecosystem components (i.e., species, populations, trophic groups). Foraging interactions are traditionally characterized by two types of functional response curves: hyperbolic (type II) and sigmoid (type III) curves, where a consumer's per capita feeding rate (F) increases with the resource abundance (N). Originally established by Holling (1959), foraging ecology has yielded many variations of the functional response models. One of the generalized models describes consumer's feeding rate as:

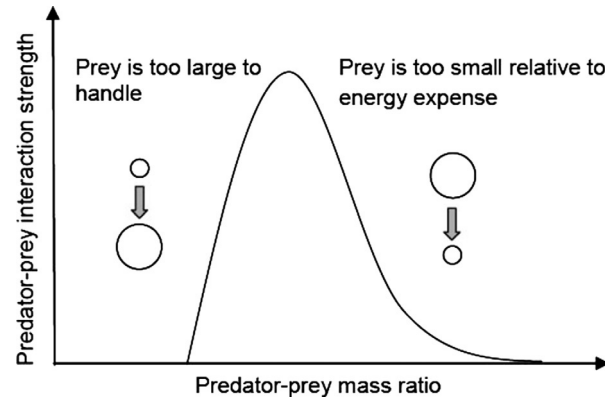$$F = \frac{bN^{1+q}}{1 + bhN^{1+q}} \tag{12a}$$

Fig. 5 Conceptualization of the relationship between predator-prey mass ratio and strength of their interaction. Circles represent the relative mass of predators (top) to the mass of prey (bottom). Modified from Nakazawa, T. (2017). Individual interaction data are required in community ecology: A conceptual review of the predator–prey mass ratio and more. *Ecological Research* **32**, 5. https://doi.org/10.1007/s11284-016-1408-1.

Per capita feeding rate is regulated by the time required to kill, ingest, and digest a resource (handling time, h), as well as the hunting efficiency representing the rate that a resource is captured by a consumer (bN), where b is a coefficient for hunting efficiency. The scaling exponent (q) dictates the response curve type, whose value switches from the hyperbolic type II ($q=0$) into the sigmoid type III ($q>0$) functional response. Although this simple concept around the functional response models has provided mechanistic understanding of consumer-resource interactions, it has failed to characterize more dynamic interactions in natural communities. For example, a predatory spider in central Europe did not follow any of the expected response curves, displaying nonlinear and/or nonmonotonic patterns under conditions of abundant food availability.

In recent years, a size-based perspective has been increasingly recognized as an alternative approach to estimating density-dependent foraging interactions. In size-based functional response models, handling time and/or capturing rate (i.e., hunting efficiency) are expressed as a function of the consumer's body size. For example, handling time (h) in Eq. (12a) can be replaced by:

$$h = h_0 m_r^{\alpha_r} m_c^{\alpha_c} \tag{12b}$$

where h_0 is a constant, m_c, m_r and α_c and α_r are body masses (m) and allometric exponents (α) of consumer/predator c and resource/prey r, respectively.

Originally considered as a constant in functional-response models, capture rate, also known as attack rate, is known to have its own unique body-size dependency. Predator-prey mass ratio (PPMR) has been identified as an indicator to depict body size constraints on the capacity of predators to efficiently utilize excessively large prey. On the other hand, a predator does not fully benefit by targeting excessively small prey because of its limited nutritional value relative to the energy expense for the consumption or handling of the prey. PPMR has been used to measure the strength of the trophic interaction between predators and prey, and to illustrate potential shifts in the energy flows and the reliance on specific resources. In general, capturing rate has a hump-shaped response pattern with PPMR, maximizing at intermediate/moderate PPMR, while energy flows at high and low PPMR may not sustain the predator's biomass or could even risk their survival (Fig. 5). This hump-shaped relationship between capture rate and PPMR is consistent with optimal-foraging and niche theory, and has broad generality across different species in various habitats.

To accommodate body-mass constraints on the capture rate, hump-shaped relationships with PPMR can be further expressed as a combined equation comprising a power-law relationship with prey body mass and an exponential Ricker function for the optimal foraging body-mass ratio. The capture coefficient (b) in Eq. (12a) is then replaced by an allometric scaling relationship, where b_0 is a constant, β_r the exponent for the scaling of m_r, and ε is a constant for the range of the optimal foraging body-mass ratio:

$$b = b_0 m_r^{\beta_r} \frac{m_c}{m_r} e^{\varepsilon \frac{m_c}{m_r}} \tag{12c}$$

Efforts to develop a generalized functional-response modeling framework have further advanced our mechanistic understanding of consumer-resource interactions in natural food-web dynamics. Counter to early consumer-resource models, such as the Lotka-Volterra models, where all parameter sets are independently assigned only to fit data points, allometric scaling models ensure that parameters lie within biologically plausible ranges based on their size related capacity. Size-based functional response models highlighted that the coexistence of consumer-resource is restricted within specific body-mass ranges, which in turn regulates the resilience of consumers in the food-web and the broader stability of biotic communities. The consideration of body-mass ratio can also be useful in parameterizing more complex population models. Nonetheless, like any other type of models, allometric scaling models require caution in their use; as the definitions of certain facets of trophic interactions, like the hunting efficiency, are somewhat ambiguous and their complex characteristics (i.e., multiple food-sources, mobility of organisms) are essentially habitat/community-specific.
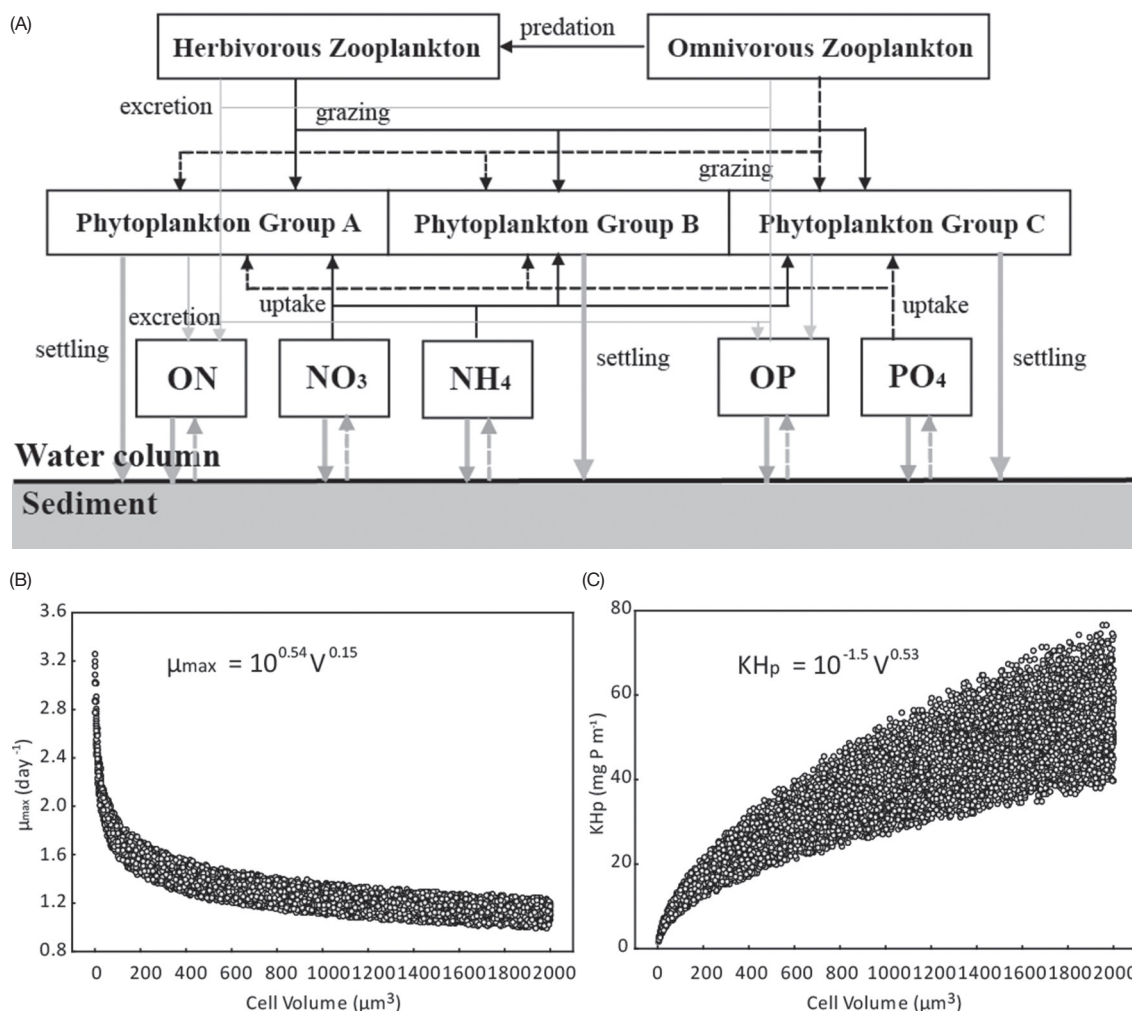
Fig. 6 (A) Conceptual diagram of an aquatic ecosystem model. Parameter values were calculated with allometric equations linking phytoplankton (B) maximum growth rate and (C) half saturation constant for phosphorus uptake with the cell volume. In Shimoda et al. (2016), the cell size variability for a given functional groups was assigned a range between 0.1 and 2000 μm^3 (x-axis). The parametric uncertainty (as seen in the distributed dots in B and C) of the allometric regressions can be propagated with Monte Carlo simulations through the ecosystem model. (B-C) Shimoda, Y., Yerubandi, R., Watson, S., Arhonditsis, G.B. (2016). Optimizing the complexity of phytoplankton functional group modelling: An allometric approach. *Ecological Informatics* 31, 1–17.

Ecosystem Models

Ecosystem models extend the application of consumer-resource interactions to community-level processes, whereby ecologists attempt to reproduce the interplay among organisms and their surrounding physico–chemical environment. Integration of size-based characteristics into ecosystem models may refine the description of community-level processes, such as species seasonal succession and flow of energy and/or matter across trophic levels. Body-size patterns may be more important, or at least more obvious, in aquatic ecosystems than in terrestrial habitats for several reasons. The majority of autotrophic organisms in aquatic ecosystems are very small and grazed by larger consumers, and thus the relative size ratio of consumer to resource more consistently manifests itself than in terrestrial environments. There are significant operational and technical advantages in the collection of datasets from aquatic environments. Reflecting upon these factors, there are a number of allometric equations developed for aquatic organisms and (not surprisingly) many of the existing size-based ecosystem models have been developed for aquatic environments.

The basic concept of size-based ecosystem modeling is that the functional characteristics of the biological components of the studied system can be described by allometric equations. That is, model parameters associated with organismal physiological rates, such as maximum growth rate, nutrient kinetics, and basal metabolism, are determined by the empirically-derived relationships with their body size (i.e., mass, volume, length). Shimoda et al. (2016) employed several allometric equations in an existing aquatic biogeochemical model to describe the physiological processes of multiple phytoplankton functional groups, and thus predict how can the morphological features (i.e., cell volume, surface-to-volume ratio, and shape) influence the response to external perturbations, interspecific competition, and ultimately the seasonal composition of algal assemblages (Fig. 6A). For example, maximum

growth rate μ_{max} (day^{-1}) was replaced by $\mu_{max} = 10^{0.54}V^{-0.15}$, where V denotes algal cell volume (μm^3) (Fig. 6B). Nutrient kinetics were also replaced by several allometric equations such as: half saturation constant for nitrate uptake ($NH : \mu mol\, N\, L^{-1}$), $NH = 10^{-0.72}V^{0.52}$, half saturation constant for phosphorus uptake ($KH_p : \mu mol\, P\, L^{-1}$), $KH_p = 10^{-1.5}V^{0.53}$ (Fig. 6C), maximum phosphorus uptake rate ($VP_{max} : \mu g\, P\, \mu m^{-3}h^{-1}$), $VP_{max} = 10^{-10.7}SA/V^{1.7}$ where SA/V denotes algal cell surface-to-volume ratio (μm^{-1}), maximum internal phosphorus quota ($QP_{max} : fmol\, P\, cell^{-1}$), $QP_{max} = 10^{-0.29}V^{0.767}$, minimum internal phosphorus quota ($QP_{min} : fmol\, P\, cell^{-1}$), $QP_{min} = 10^{-1.04}V^{0.714}$.

The allometric configuration of the process-based model allowed to realistically reproducing the observed phosphate, total phosphorus, nitrate, total ammonia, total nitrogen, chlorophyll *a*, and total zooplankton biomass patterns in the Hamilton Harbor, Ontario, Canada. Consistent with empirical evidence, the allometric-scaled ecosystem model showed that small algal species have a distinct competitive advantage in summer epilimnetic environments across the range of cell volume and nutrient loading conditions examined; especially, when they are characterized by higher optimal temperature for growth. The same study also showed that intense herbivory rates act as a "safety valve" and effectively control the standing biomass of phytoplankton species that can otherwise realize high growth rates under the conditions typically prevailing in the end-of-summer epilimnetic environments. By contrast, when the summer community is released by the zooplankton grazing, the exceedance of critical phytoplankton biomass levels and the likelihood of harmful algal blooms are determined by the multitude of factors that shape inter-specific competition patterns (e.g., relative abundance of competing species, nutrient uptake kinetics). One of the future challenges associated with the allometric approach to plankton modeling involves the characterization of dependence of prey-predator relationships as a function of the interplay among prey morphology, nitrogen, phosphorus, highly unsaturated fatty acids, and other potentially important metabolic congeners through the grazers' digestive tracks.

From a technical standpoint, one of the benefits of the allometric approach to ecosystem modeling is that the characterization of simulated biotic compartments is no longer based on adjustable parameters, often treated as "properties of convenience" for fitting models to the observed data, but instead their morphological features are treated as the common denominator that influences the corresponding physiological rates. In a broader context, this practice may be one of the ways to address the problem of complex over-parameterized models and improve our ability to set quantitative (or even qualitative) constraints while ensuring satisfactory model performance. Model parametric uncertainty is more effectively delineated; namely, the literature-based ranges typically assigned to the calibration parameters can be replaced by the parameter standard error values and/or the estimates of residual variability of allometric equations, which in turn collectively reflect how well does the regression line match the original empirical physiological rates, the variability of the predictor (morphological) variable used to develop the allometric equation as well as the sample size. Using suitable uncertainty analysis techniques, these error estimates can then be propagated through our ecosystem models, whereby we can effectively quantify the degree of confidence in model predictions (Fig. 6C).

The allometric approach to ecosystem modeling also offers a different perspective on the optimization of future data collection. Model calibration is not solely perceived as a typical inverse solution exercise, constantly inviting the collection of data on model outputs and subsequently readjusting the parameters to match measurements and predictions. Instead model parameter estimation requires a more robust experimentation focused on the development (or further refinement) of the causal description of model parameters based on the morphological features of the biotic components modeled. Moreover, depending on the nature of the dataset used for the allometric regressions (e.g., marine vs. freshwater algae), the proposed method allows the potential users to delineate the application domain more easily and determine to what extent a particular model has local or universal use.

Cautions, challenges, and future prospects

Allometric theory meets a series of fundamental criteria to be considered as a "good theory." It is extremely simple, quantitative, and most of the dependent and independent variables are easily defined. Empirical relations capture the characteristics of a wide range of organisms, and provide reasonably accurate predictions of many biological processes. Thus, allometric equations have been used to describe biological and ecological processes, ranging from the micro- to macroscale, such as the effects of drugs and other substances on the physiological responses of humans/animals, the estimation of fish stocks, and the prediction of life-stage specific population size in ecosystems, to name a few.

The popularity of the allometric theory, however, appears to have slowed down after its peak around 1970–1980s and much less development and examination of the corresponding equations has been seen in recent literature. It has been argued that its simplicity and generality (supposedly criteria for a good theory) paradoxically represent a "double-edged sword" making it less appealing for research, because any new regressions merely provide validation of the theory. There are also a number of critical viewpoints presented in the literature. First, the precision of the empirical relations is compromised by our desire to achieve generality. It is obvious that capturing the entire range of a physiological characteristic using a regression with only two parameters is nearly impossible. Even though the development of taxa-specific allometric regression models is logical, as phylogenetically neighboring taxa share common physiological traits, other important factors, such as resource availability, may not yield commonality in response to similar selective pressures. For example, the distribution patterns of maximum potential growth rate of phytoplankton vary not only among genera, but also by habitat type (Fig. 7). There is still significant space for advancing allometric theory using scientific creativity and technological innovation.

One of the most significant, yet not frequently explored facets of allometry, involves the scatter around each regression (e.g., model residuals) representing the variability among organisms, missing ecological functions (i.e., adaptation), and measurement errors. Many of the empirical equations used are based on small sample sizes (low degrees of freedoms) and/or capture a fairly narrow range of body/cell sizes typically encountered in natural ecosystems. All these factors inflate the magnitude of the
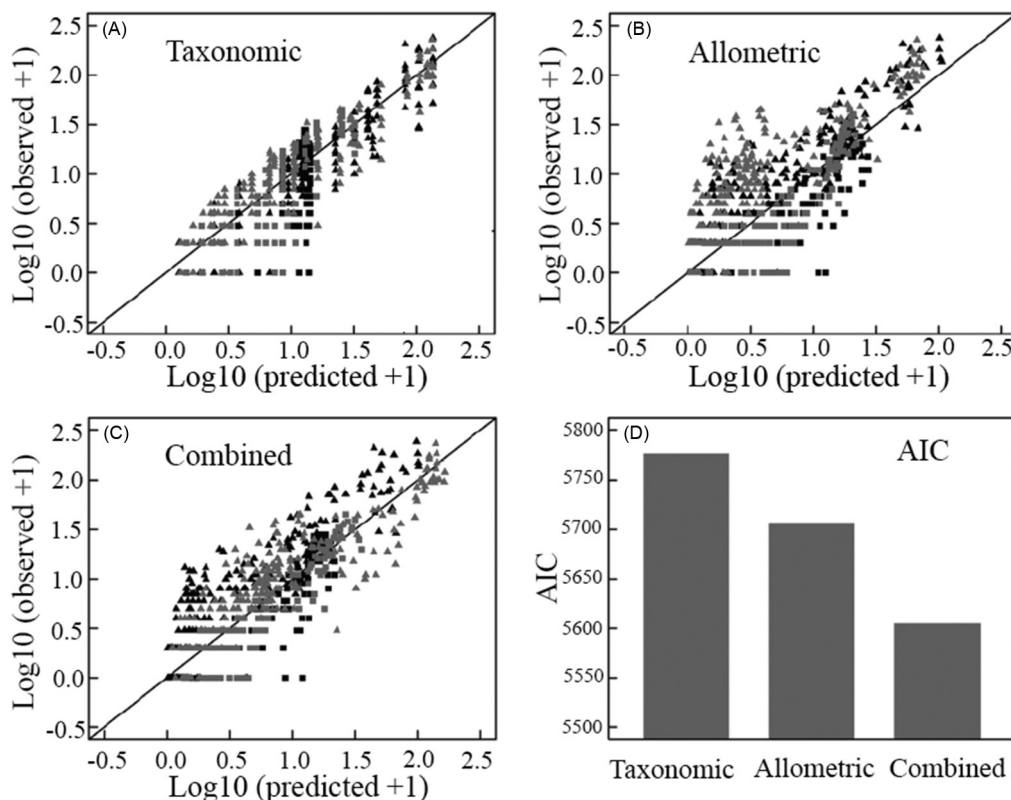
Fig. 7 Goodness of fit comparison of (A) taxonomic, (B) allometric and (C) combined models. The empirically observed values of per capita feeding rates (*y*-axis) are plotted against the values predicted by the models (*x*-axis) using the statistically fitted parameters. (D) AIC of three models. Markers represents: centipedes feeding on fruit flies (*black squares*); centipedes feeding on springtails (*black triangles*); spiders feeding on fruit flies (*gray squares*); spiders feeding on springtails (*gray triangles*). Modified with permission from Rall,B. C., Kalinkat, G., Ott, D., Vucic-Pestic, O., Brose, U. (2011). Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, **120**(4), 483–492. https://doi.org/10.1111/j.1600-0706.2010.18860.x.

uncertainty (confidence, predictive) bands of allometric equations. Rather than perceiving this error as a weakness of the allometric approach, recent viewpoints claim that it offers an excellent piece of information to conduct rigorous uncertainty analysis in complex process-based models and a solid foundation to draw probabilistic inference on important ecological questions.

Many of the existing equations have been derived in experimental controlled settings (i.e., laboratory, mesocosms), and do not necessarily represent the response of organisms that may be observed in the natural world. Unless allometric equations predict maximum potential metabolic/physiological rate under resource saturated environment, more accurate representation of biological traits must be tested with free-living organisms. Although validation of theoretical relationships and existing models is an integral part of science, few studies have attempted to provide a comprehensive review of the existing allometric equations. Often many equations that describe the same phenomenon exist, but objective comparison of these equations has been rarely performed. Further development of new, taxon-specific allometric relationships, expansion of size range for the existing relations may improve their credibility and predictive power.

While Occam's razor is (and should be) the cornerstone of any ecological modeling activity, the integration of process-based models and empirical parameter specification, founded upon the basic allometric concepts, offers an appealing prospect. The development of predictive ecological frameworks that are based on our best mechanistic understanding of biotic processes and ecosystem feedback loops, yet remain within the bounds of data-based parameter estimation and therefore can accommodate rigorous error analysis has both methodological and ecophysiological advantages. Size structure of biotic communities is an important regulatory factor of the biogeochemical fluxes and energy transfer via the food webs that ultimately affects system productivity. The improvement of empirical description of ecological parameters could reconcile the debate regarding the need to balance between simplicity and realism in predictive ecology.

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