

Opinion

Predicting ecosystem productivity based on plant community traits

Nianpeng He ^{1,2,3,13,*} Pu Yan,^{1,2,13} Congcong Liu,¹ Li Xu,¹ Mingxu Li,¹ Koenraad Van Meerbeek ^{4,5} Guangsheng Zhou ⁶ Guoyi Zhou,⁷ Shirong Liu,⁸ Xuhui Zhou ⁹ Shenggong Li,^{1,2} Shuli Niu,^{1,2} Xingguo Han,¹⁰ Thomas N. Buckley,¹¹ Lawren Sack,^{12,*} and Guirui Yu^{1,2,*}

With the rapid accumulation of plant trait data, major opportunities have arisen for the integration of these data into predicting ecosystem primary productivity across a range of spatial extents. Traditionally, traits have been used to explain physiological productivity at cell, organ, or plant scales, but scaling up to the ecosystem scale has remained challenging. Here, we show the need to combine measures of community-level traits and environmental factors to predict ecosystem productivity at landscape or biogeographic scales. We show how theory can extend the production ecology equation to enormous potential for integrating traits into ecological models that estimate productivity-related ecosystem functions across ecological scales and to anticipate the response of terrestrial ecosystems to global change.

The promise of integrating traits into prediction of ecosystem productivity

For decades, plant functional traits have been used for mechanistic analysis and prediction of processes at a wide range of ecological scales, from organs to species to ecosystems [1–5]. Plant functional traits are defined as properties that influence growth, reproduction, and survival at the individual level [6–8] and are frequently used for predicting plant species responses to changing environments [9–11]. As plants contribute the bulk of ecosystem carbon fluxes, effect traits (i.e., traits that determine the effects of plants on ecosystem functioning [12,13]) in combination with environmental factors can influence ecosystem functioning, such as gross primary productivity (GPP) and net primary productivity (NPP), and therefore modulate the global terrestrial carbon cycle and its responses to climate change [14–16].

Indeed, understanding how plant functional traits modulate primary productivity has attracted wide interest for almost two decades [17–21]. Previous studies have established correlative links between the productivity of natural ecosystems and leaf functional traits averaged across the constituent species [19,20]. However, how best to relate the traits of individual plants or plant species to the functioning of whole ecosystems has remained an open question [9,22]. One major challenge is the need to model ecosystem functions on the basis of land area, as for GPP and NPP, which are considered on that basis from eddy-flux observations and remote sensing [23–25]. Yet, currently, differences in annual GPP among ecosystems are determined primarily by the quantity of photosynthetic tissue and the intensity and seasonality of its activity, not taking into account a wide range of other available traits. While efforts have been made to directly scale up from individual plant traits and community-scale traits to ecosystem productivity, and traits have been used as inputs into dynamic vegetation models to determine photosynthesis and thereby ecosystem productivity, new approaches are needed to incorporate the wide range

Highlights

The integration of plant functional traits to improve predictions of ecosystem productivity holds many opportunities, especially considering that intrinsic links are expected between plant traits and ecosystem function.

We present a novel framework for ‘trait-based productivity’ (TBP) enabling the prediction of productivity-related ecosystem functions from plant community traits and environmental conditions.

The TBP framework takes an emergent perspective considering the ecosystem as a whole, in which individual plant traits scale up to community-scale ‘traits’ that in combination influence ecosystem functions.

The TBP framework has potential to drive a new generation of ecological models at a wide range of spatial scales, informed by species’ traits derived from open access trait databases and high-resolution remote sensing imagery data.

¹Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

²College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

³Center for Ecological Research, Northeast Forestry University, Harbin 150040, China

⁴Division of Forest, Nature and Landscape, Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium

⁵KU Leuven Plant Institute, KU Leuven, Leuven, Belgium



of all available effect traits. This more comprehensive approach, along with taking into account environmental factors, should allow for determining the variation in productivity within and among natural ecosystems.

Gaps and potential for linking functional traits and ecosystem productivity

Substantial gaps have existed in the ability to link plant traits with productivity in a meaningful way. Although a number of hypotheses exist for relating functional traits to ecosystem productivity (Box 1), challenges arise when trying to generalize these ideas. First, there is no consensus on how the productivity of naturally assembled or experimental systems (such as plantations and crop fields) depends on traits that would contribute to growth [26]. For example, the growth rate hypothesis of stoichiometric ecology postulates that higher productivity would arise from a lower N:P ratio (i.e., a higher concentration of phosphorus) in agricultural fields or controlled experiments due to the increased demand for rRNA production needed to sustain rapid growth, yet no evidence has supported this hypothesis in naturally assembled communities [27,28]. Indeed, tropical forests generally have both higher GPP and N:P ratio than cool temperate forests [28], and grasslands, typically less productive than forests, also have higher leaf N:P [29]. Evidently, in natural communities, dominant species, which contribute strongly to GPP, may have moderate or high N:P ratios but prevail due to stress tolerance, in contrast with agricultural fields and experimental plantations, in which the fastest growing species, with low N:P, would dominate, as these systems are under continuous management and/or protection from drought, competition, pests, and other stresses. Therefore, it remains unclear if there is a general application of stoichiometric principles to derive trait–productivity relationships. Second, the scaling of traits from organ and even species to ecosystem scales often runs into challenging and complex transmutation problems. It is self-evident that a combination of a large number of traits will influence productivity, and, as highlighted by the Jensen’s inequality, the average of a function is not the function of the average due to the perturbation of nonlinearity and variation [30]. Yet, as many studies found that the net assimilation rate of leaves is highly correlated across species with traits such as specific leaf area (SLA) and mass-based leaf nitrogen concentration (N, mg g⁻¹) [31–33], such univariate relationships have inspired many studies to treat complex

⁶Chinese Academy of Meteorological Sciences, Haidian District, Beijing, China

⁷Institute of Ecology, School of Applied Meteorology, Nanjing University of Information Science & Technology, Nanjing, China

⁸Key Laboratory of Forest Ecology and Environment, China’s State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing, China

⁹School of Ecological and Environmental Science, East China Normal University, Shanghai, China

¹⁰State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China

¹¹Department of Plant Sciences, University of California, Davis, CA, USA

¹²Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA

¹³These authors contributed equally to this work.

*Correspondence: henp@igsnr.ac.cn (N. He), lawrensack@ucla.edu (L. Sack), and yugr@igsnr.ac.cn (G. Yu).

Box 1. The basic concepts of the major hypotheses for trait-based ecosystem function

Vegetation, as the primary producer, plays a dominant role in shaping ecosystem function. There are five major hypotheses in trait-based ecology for the role of plants in driving ecosystem functions.

- (i) The mass ratio hypothesis, also known as the dominance hypothesis [83], holds that the traits of the dominant species are more important than species richness *per se*, in determining ecosystem processes, and thus predictions should be made on the basis of scaling the species’ trait values by their contribution to vegetation biomass, often by calculating a CWM [6].
- (ii) The functional complementarity hypothesis holds that the difference in trait values among the organisms in a community influences ecosystem processes through mechanisms such as complementary resource use. Thus, positive relationships are expected between ecosystem functions and indices capturing the community functional diversity [84], including single-trait indicators (1D indices), such as FD_{var} (functional logarithmic variance) and multiple-trait indicators (multidimensional indices), such as FD_Q (Rao’s quadratic entropy) [85].
- (iii) The growth rate hypothesis predicts that organisms with higher growth rate (the rate of change in biomass per unit biomass) also have higher P concentration and lower C:P and N:P ratios [27,28].
- (iv) The vegetation quantity hypothesis (also known as the green soup hypothesis) holds that productivity is mainly driven by vegetation biomass, regardless of traits; that is, vegetation ‘quantity’ is more important than ‘quality’ [45]. This idea has also been referred to as a trait-based approach, if biomass is considered a performance trait [86].
- (v) The ecosystem allometry approach also does not consider plant traits and only biomass, placing an emphasis on the size distribution of individual plants within communities [7,87], and predicting $NPP = \sum_{k=0}^K n_k \times \beta_g \times M_{T(k)}^{3/4}$, where n_k is the number of individuals present per m² in the size class k , and β_g is an allometric coefficient (as a constant regardless of species) linking the absolute growth rate of the whole plant with its total biomass (M_T), and the 3/4 scaling exponent is attributed to constraints imposed by resource distribution within cells and plants [88].

plant communities as a simple big-leaf model (averaging the properties of all leaves) or a multilayer model (treating sunlit and shaded leaves in each layer separately) to scale linearly from organ and leaf levels to processes occurring at the level of groups of leaves or canopies and thereby simulate primary productivity at the ecosystem level [34–36]. This direct upscaling of leaf biochemical traits has not generally been validated, and the associated uncertainty increases with the spatial scale considered (Figure 1) [30]. For example, the optimal temperature for the parameters of leaf photosynthetic physiology, such as electron transport rate and maximum rate of carboxylation by Rubisco, does not predict those considered at the ecosystem level [37]. Indeed, for ecosystems across elevation gradients, leaf-level photosynthetic parameters, such as the maximum rates of carboxylation of Rubisco (V_{cmax}) and electron transport (J_{max}), do not decline with elevation and may even increase, whereas ecosystem-level productivity (such as GPP and NPP) declines with elevation [38]. These challenges point to the necessity for clear matching of processes and scales when estimating ecosystem processes from traits [39], though such matching has not been applied in many recent studies that found weak relationships between ecosystem processes and single traits or finding relationships but of unclear causality [40,41]. Overall, optimism in using this reductionist approach must be tempered.

In particular, scaling up from traits to ecosystem functions requires adequate consideration of matching size and units. For a long time, the weighted average of individual traits within a community based on the mass ratio hypothesis has been tacitly adopted to represent community-level traits. Indeed, the community-weighted mean (CWM) trait value reflects the central behavior of species; for example, higher CWM leaf nutrient concentrations, in particular nitrogen, typically

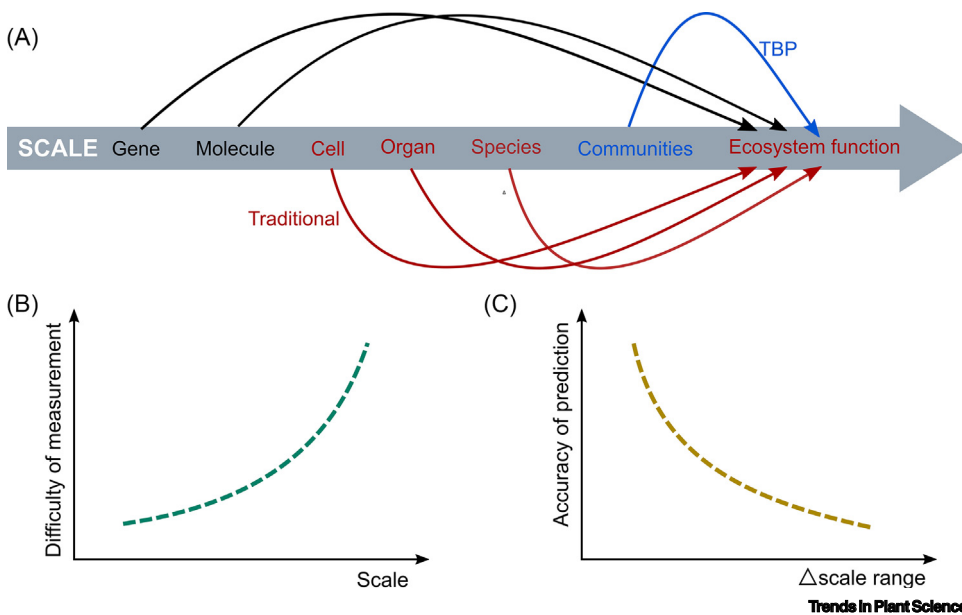


Figure 1. Scaling from traits to ecosystem function, with traits based on characteristics at different scales from gene to ecosystem. Traits can be used to predict high-level processes such as gross primary productivity (GPP), net primary productivity (NPP), or water use efficiency (WUE) in natural ecosystems; the trait-based productivity (TBP) framework predicts ecosystem function from community-level traits (blue arrow), by contrast with previous approaches that directly relate function to the traits of cells, organs, and species (red arrows) (A); the black arrows represent biochemical approaches to tree genetics and breeding, such as improving productivity through genetic engineering (molecular methods). The difficulty of representative trait measurements increases at larger spatial scales (B), whereas the accuracy of prediction may sharply decrease with increasing differences in scales considered (C). The development of TBP to predict primary productivity (GPP, NPP) in natural ecosystems must meet these challenges.

Table 1. Leaf traits scaled to community level

No.	Trait at organ level	Community-scale trait ^a
1	Leaf chlorophyll concentration (Chl, %)	Chl_C (g m ⁻²)
2	Leaf nitrogen concentration (N, %)	N_C (g m ⁻²)
3	Leaf phosphorus concentration (P, %)	P_C (g m ⁻²)
4	Leaf size (leaf, cm ²)	Leaf area index (LAI, cm ² m ⁻²)

^aCommunity-level traits are defined on a ground-area basis.

indicate a community dominated by individuals of fast-growing acquisitive species with higher light-saturated photosynthetic rates [7,42], and with a relatively high ecosystem (production) efficiency [6,10]. Nonetheless, high light-saturated photosynthetic rates per unit leaf area or mass provide limited information about the carbon uptake of the entire plant under typical conditions [43,44], let alone the carbon capture capacity of the ecosystem considered per land area. Meanwhile, both the vegetation quantity hypothesis and the metabolic scaling theory based on allomorphic growth consider biomass as a proxy for community size, an approach supported by a large body of empirical evidence for predicting productivity-related ecosystem functions [45–48]. Nevertheless, the complexity of trait variation and of the ecosystems themselves render them not immediately amenable to the simple reductionist approach of scaling up directly from biomass (Box 1). Furthermore, it is unclear how to scale up from biomass for the prediction of ecosystem function while integrating multiple leaf traits and environmental variables, which a rich body of evidence indicates would influence ecosystem properties. New ways to integrate plant traits and community or ecosystem contextual information are necessary.

As a new approach to predict ecosystem function from underlying processes (Box 1), the calculation of ‘ecosystem traits’ (‘community traits’) was recently proposed [9] (Table 1 and Box 2). Calculation of plant community traits involves scaling-up and scale-matching traits measured at the organ level to derive a trait value per land area; these plant community traits can then be tested for correlation with ecosystem functioning across natural ecosystems [9,49]. Such scaled-up versions of ‘effect traits’ [50] have strong promise for predicting ecosystem productivity, especially given the increasing availability of plant trait data based on remote sensing [24,51]. For example, hyperspectral approaches in remote sensing provide an opportunity to retrieve plant functional traits, such as pigment and mineral nutrient concentrations, and derived functional parameters for improved estimation of vegetation processes, including photosynthetic rate [52,53]. Meanwhile, trait databases based on field investigations, such as TRY [54] and BIEN [55], are rapidly expanding, allowing the synthesis of community-level traits [56–58]. However, species occurrence biases are a concern when one uses plant trait data to infer ecosystem function. Studies have shown that in multiple dimensions, including taxonomy, space, and time, there is widespread bias and uncertainty in plant occurrence information [59–61]. This uncertainty will affect the accuracy in calculating community-level traits, especially in extreme habitats [62]. Therefore, even relatively widely used plant occurrence databases, such as GBIF, should be checked thoroughly at the species level to ensure the accuracy of subsequent calculations of community-level traits. Trait values for specific extreme habitats should be carefully treated and retrieved from the corresponding regional database [62]. Setting up or capturing data from multiple plots for the same habitat to minimize the impact of outliers is also encouraged.

Integrating plant traits to the prediction of productivity-related ecosystem functions

To explicitly integrate the influence of community-level traits on ecosystem productivity, we consider an analogy to an engine (Figure 2). Engine power (in kilowatts) is mainly determined by the amount of fuel, engine capacity, utilization efficiency of fuel, and working time. Clearly, natural

Box 2. Normalizing plant traits per unit land area as potential drivers of ecosystem function

Ecosystem traits represent the capacity for resource uptake and carbon fixation, calculated as an intensity (or density) normalized per unit land area [9]. We focus on plants, as the major determinant of terrestrial ecosystem productivity is leaf photosynthesis, and thus ecosystem traits may also be referred to as plant community traits. Leaf traits can be converted to plant community traits and thereby considered as drivers of ecosystem function, including leaf traits that are area-based, mass-based, or ratios [7,8]. Plant community traits can be derived directly from the traits at the individual or species level, or from the CWM trait value ($Trait_{cwm}$) [84]:

(i) For mass-based traits:

$$Trait_{ecosystem} = \sum_{i=1}^n Trait_i \times LMI = \sum_{i=1}^n Trait_i \times \frac{B_i}{\sum_{i=1}^n B_i} \times \frac{\sum_{i=1}^n B_i}{S} = Trait_{cwm_{biomass}} \times LMI \quad [I]$$

where i and n are the species i and the number of species in the community, respectively; B_i is the biomass of species i , S is community or plot area, LMI is the leaf mass index, that is, the leaf mass per unit land area (unit: $kg\ m^{-2}$). Notably, community weighting can be performed on the basis of biomass ($Trait_{cwm_{biomass}}$), or, alternatively, abundance (A_i ; $Trait_{cwm_{abundance}}$).

(ii) For area-based traits:

$$Trait_{ecosystem} = \sum_{i=1}^n Trait_i \times LAI = \sum_{i=1}^n Trait_i \times \frac{LA_i}{\sum_{i=1}^n LA_i} \times \frac{\sum_{i=1}^n LA_i}{S} = Trait_{cwm_{cover}} \times LAI \quad [II]$$

where LAI is the leaf area index, that is, the leaf area per unit land area (unit: $m^2\ m^{-2}$);

(iii) For ratio traits (taking specific leaf area [SLA= leaf area/ leaf mass] as an example):

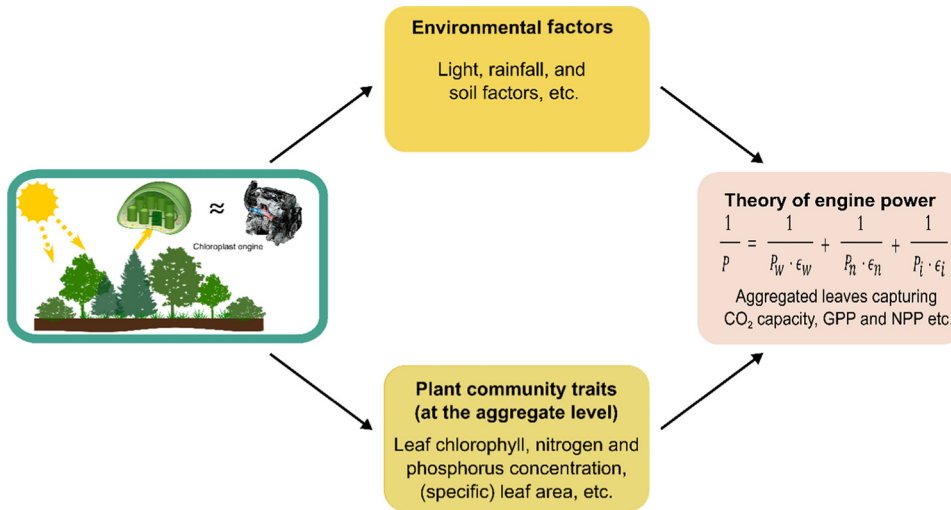
$$SLA_{CWM} = \sum_{i=1}^n SLA_i \times \frac{B_i}{\sum_{i=1}^n B_i} = \sum_{i=1}^n \left(\frac{LA_i}{M_i} \times \frac{M_i}{\sum_{i=1}^n M_i} \right) = \frac{\sum_{i=1}^n LA_i}{\sum_{i=1}^n M_i} \quad [III]$$

$$SLA_{ecosystem} = \sum_{i=1}^n LA_i / \sum_{i=1}^n M_i = SLA_{CWM} \quad [IV]$$

where $Trait_i$ represents a specific trait of the i th species; B_i , LA_i , and M_i represent, respectively, the biomass, leaf area, and leaf mass of all individuals of the species i in the community; and n is the total number of species present in the community. Thus, when $Trait_{ecosystem}$ is a ratio of other traits (e.g., SLA, N:P ratio, etc.), it is equivalent to the $Trait_{cwm}$. The above formula is similar to the derivation of traits from species to community-aggregated level, which is logically consistent [8].

plant communities are far more complex than mechanical engines, yet this analogy is applicable to the scaling of productivity from the traits of individual plants and species to the ecosystem (Figure 2). Indeed, this analogy is formalized in the production ecology equation [63–66]: Production = Resource supply \times Proportion of supply captured \times Production efficiency, which has also been applied in agriculture as the ‘harvest equation’ [67,68]: $W_h = \epsilon_c \times \epsilon_i \times S_i$, in which the accumulation of energy in plant biomass (W_h) is determined by the ‘use efficiency’ that intercepted radiation is converted to biomass energy (ϵ_c), the efficiency of light interception by the canopy (ϵ_i), and total incident solar radiation (S_i). Yet, a weakness of these simple formulations is that the ‘use efficiency’ term masks many interacting physiological effects. Production is often strongly co-limited by multiple resources, of which the most important across the world’s dominant ecosystems are light, water, and soil nutrients, and given traits will often influence the acquisition and retention of different resources. Thus, a new generation of approaches is needed to estimate trait-based productivity (TBP), enabling the prediction and partitioning of ecosystem or community productivity with respect to plant community traits in addition to climate factors and nutrient inputs (Figures 2 and 3). To illustrate an approach for considering productivity as a function of multiple limitations, we provide a simple model-based analysis in which these limitations are approximately separable from one another [69], the ‘inverse production equation’:

$$\frac{1}{\bar{P}} = \frac{1}{P_w \cdot \epsilon_w} + \frac{1}{P_n \cdot \epsilon_n} + \frac{1}{P_i \cdot \epsilon_i} \quad [1]$$



Trends in Plant Science

Figure 2. The theoretical basis for the use of plant community traits to predict ecosystem productivity in natural ecosystems by analogy to an engine. Different from the complex process model [82], we adopt an emergent approach to view the entire ecosystem as a whole based on the plant community traits [9] and apply the production ecology equation [63] or harvest equation [68] to formulate the trait-based productivity (TBP) theory, which can be conceptualized by analogy to an engine. In the formula, P_w , P_n , and P_i represent maximum production limited only by water, nitrogen, and irradiance, respectively, that is, potential production in the absence of other limitations (e.g., P_w is the maximum production possible when nitrogen and light are available in infinite supply, and water uptake and transport and stomatal resistance do not limit the acquisition and use of water for production). ϵ_w , ϵ_n , and ϵ_i represent resource acquisition efficiencies – the fractions of each available resource actually captured by the plant community.

Where P is production (i.e., GPP or NPP or another production-related variable); P_w , P_n , and P_i represent maximum production limited only by water, nitrogen, and irradiance, respectively (i.e., potential production in the absence of other limitations; e.g., P_w is the maximum production possible when nitrogen and light are available in infinite supply); and ϵ_w , ϵ_n , and ϵ_i represent resource acquisition efficiencies, that is, the fractions of each available resource actually captured by the plant community. The inverse production function can be derived from a model of photosynthesis and gas exchange, with some minor simplifications, providing insights into how traits will influence productivity (see Appendix 1 in Supplementary Materials in the supplemental information online).

$$\frac{1}{P} = \frac{1}{c_a - \Gamma} \left(\frac{1.6D}{E_o} \left(\frac{E_o}{K(\psi_{soil} - \psi_{leaf})} \right) + (rc_a + M) \left(\frac{1}{\chi N_o} \left(\frac{N_o}{N} \right) + \frac{1}{\phi i_o} \left(\frac{1}{f_{par}} \right) \right) \right), \quad [2]$$

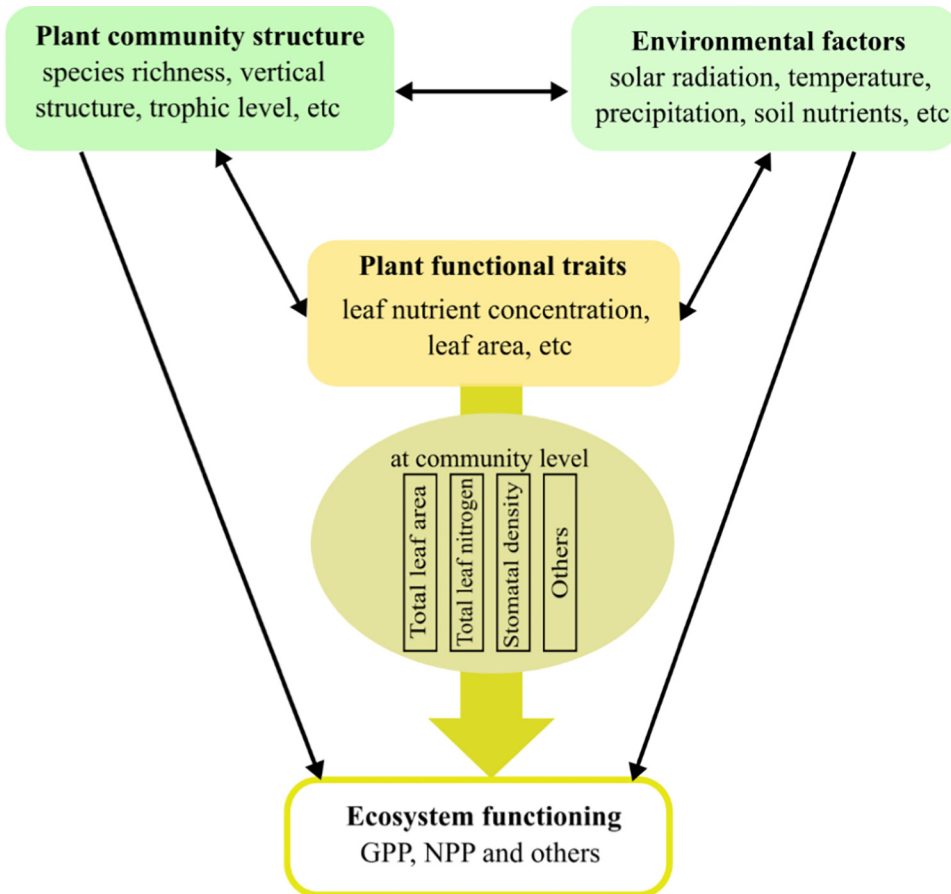
which is Equation 1, but where the terms on the right-hand side are expressed in relation to underlying environmental variables or plant traits:

$$P_w = \frac{E_o(c_a - \Gamma)}{1.6D}, \quad \epsilon_w = \frac{K(\psi_{soil} - \psi_{leaf})}{E_o}, \quad [3]$$

$$P_n = \left(\frac{c_a - \Gamma}{rc_a + M} \right) \chi N_o, \quad \epsilon_n = \frac{N}{N_o}, \quad [4]$$

$$P_i = \left(\frac{c_a - \Gamma}{rc_a + M} \right) \phi i_o, \quad \epsilon_i = f_{par}. \quad [5]$$

where c_a is ambient CO₂ molar fraction, Γ is the photosynthetic CO₂ compensation point, D is the leaf-to-air water vapor molar fraction difference, E_o is precipitation, K is plant hydraulic conductance,



Trends in Plant Science

Figure 3. Integrating plant traits into the prediction of ecosystem functioning. Plant community traits are drivers of productivity in the trait-based productivity theory. Abiotic factors, such as light, temperature, precipitation, and soil nutrients, and biotic factors, such as herbivory, would not only directly affect productivity but also interact with traits and, in addition, influence traits and thus take on an additional indirect influence on the gross primary productivity (GPP) and net primary productivity (NPP).

ψ_{soil} is soil water potential, ψ_{leaf} is leaf water potential, r is the average ratio of intercellular to ambient CO_2 concentrations (about 0.7 for C3 plants and 0.4 for C4 plants [70]). M is an effective average Michaelis constant for the effect of CO_2 on photosynthetic rate, N_o is total ecosystem nitrogen, N is total plant nitrogen, ϕ is the quantum yield of electrons, i_o is the irradiance above the canopy, and f_{par} is the fraction of i_o that is absorbed by the canopy.

This illustrative heuristic model shows how the essential simplicity of the traditional production-function approach can be retained yet can integrate separate influences of multiple environmental and endogenous factors. Importantly, this formulation addresses the major weakness of the traditional approach, that is, its focus on a single resource (commonly light) – and resulting conflation of several different limitations in the ‘use efficiency’ term – by separating the three dominant photosynthetic resource limitations using a process-based framework based on ‘acquisition efficiencies’. Acquisition efficiencies, as defined here, are the fractions of each resource actually captured by the plant community; for example, ε_w is the ratio of actual transpiration rate [$K(\psi_{\text{soil}} - \psi_{\text{leaf}})$] to the maximum transpiration rate theoretically possible (the rate of water inputs or precipitation, E_o). Most important, because the production potentials

(P_w , P_n , and P_i) and acquisition efficiencies are traceable to a simple process-based model, they offer clear logical hypotheses regarding where in the model to incorporate data for various traits. For example, hydraulic traits would affect ε_w , light-interception traits would affect ε_i , and nutrient-capture traits would affect ε_n . The role of acquisition efficiencies highlights the importance of plant structural traits scaled to the ecosystem. For example, f_{par} is determined largely by leaf area index, N/N_o by belowground carbon investment, and K by investment in below- and aboveground water transport. Many key leaf traits that regulate photosynthesis and determine ecosystem productivity can be incorporated by considering their influence on equation parameters, including leaf chlorophyll and nutrient concentrations, leaf size, specific leaf area, and many more. Notably, the parameters of Equation 1, including the environmental input variables, will all differ, depending on time scales and could in principle be defined for durations ranging from minutes to hours, to growing seasons, to years.

We note that this illustrative formulation is one of many possibilities, emphasizing mechanistic processes. Phenomenological approaches may also be used to scale from traits to productivity; for example, Bayesian models of tree growth have considered that a species' trait values may modulate the coefficients of the growth responses to environmental variables [71,72], an approach that may also be extended to considering ecosystem productivity.

Implications and future perspectives of TBP

We propose that efforts to integrate increasing numbers of plant traits to explain and predict GPP, NPP, and other ecosystem-scale parameters will streamline the current theory and provide novel applications in ecology and earth system science, including better constrained and parameterized dynamic vegetation models, and greater resolution of the influence of vegetation change on fluxes under climate change (Figures 2 and 3). Notably, environmental factors such as irradiance, temperature, precipitation, and soil nutrients not only directly influence productivity but their influence also may interact with that of traits. Furthermore, over longer time scales, environmental factors influence ecosystem structure and plant traits, thus taking on a further indirect influence on productivity. Statistical methods, such as structural equation modeling, can be used to probe indirect effects and further refine the TBP framework in future studies. Furthermore, taxonomic, phylogenetic, and functional diversity may influence ecosystem productivity by optimizing resource uptake efficiencies, a hypothesis to be tested in the future and, if supported, integrated into the TBP framework.

Notably, the role of ecosystem structure is fundamental in influencing productivity, given that plant community traits are determined by the species and the structure of the ecosystem (Figure 3). For incorporation into predictive equations such as Equation 1, the CWM for leaf traits is multiplied by measures of stand structural density, that is, the leaf area index (LAI), defined as the total one-sided area of leaf tissue per unit land surface area, equivalent to the numbers of layers of leaves [73,74] or the leaf mass index, that is, the leaf dry matter mass per unit land area (LMI; Box 2). Previous analyses of variation across ecosystems in productivity per unit land area have often focused on LAI, which is a key driver of biogeochemical cycles in ecosystems, as it influences the within- and below-canopy microclimate and the interception of light and water and carbon gas exchange [75]. Mass-based leaf traits can be multiplied by the LMI to predict productivity per unit land area (Box 2). Similar logic can be extended for traits in other plant organs, such as roots. In addition, intraspecific variation can also be included in the derivation of plant community traits by considering in their estimation different trait values for the individuals of given species. Furthermore, tissue-level traits can vary with tissue and plant age [76], and these dynamics would scale up to ecosystem-level traits, and thereby ecosystem productivity, an avenue for future research.

Concluding remarks and future perspectives

Traditional analyses have shown that physiological productivity correlates with traits at the cellular and leaf levels, but recent work shows that the concept of ‘traits per unit land area’ should be considered when scaling up to canopy or ecosystem carbon fluxes. The TBP framework provides a novel approach to explain ecosystem productivity according to its influence by plant traits and climate, including their direct and indirect effects. The TBP approach can be further developed in several key ways. First, the approach can be informed by the increasingly large amount of trait data available, through rapid assessment of CWMs of leaf functional traits [77–79], especially given the standardization of trait measurement protocols. Second, TBP theory may be integrated into ecological models to replace the widespread use of plant functional types in ecological models. Unlike the traditional big-leaf and multilayer models that directly scale up from cell and individual-leaf level traits to predict processes occurring at the level of groups of leaves or canopies [75,80,81], the TBP approach matches traits to canopy or landscape-scale processes. The range of applications of TBP will expand our ability to explain and predict the responses of these terrestrial ecosystems to global change at the wide range of spatial and temporal scales (see [Outstanding questions](#)).

Acknowledgments

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (2019QZKK060602), the CAS Project for Young Scientists in Basic Research (YSBR-037), the National Natural Science Foundation of China (42141004, 31988102), the National Science and Technology Basic Resources Survey Program of China (2019FY101304), the National Science Foundation (Awards 1457279 and 1951244), and the US Department of Agriculture National Institute of Food and Agriculture (Hatch Project 1016439).

Declaration of interests

There are no conflicts of interest to declare.

Supplemental information

Supplemental information associated with this article can be found at <https://doi.org/10.1016/j.tplants.2022.08.015>.

References

1. Violle, C. *et al.* (2007) Let the concept of trait be functional. *Oikos* 116, 882–892
2. McGill, B.J. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
3. Levine, J.M. (2016) A trail map for trait-based studies. *Nature* 529, 163–164
4. Mittelbach, G.G. and McGill, B.J. (2019) *Community Ecology*. Oxford University Press
5. Sack, L. *et al.* (2013) How do leaf veins influence the worldwide leaf economic spectrum? Review and synthesis. *J. Exp. Bot.* 64, 4053–4080
6. Garnier, E. *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637
7. Garnier, E. *et al.* (2016) *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford University Press
8. Shipley, B. (2010) *From Plant Traits to Vegetation Structure: Chance and Selection in the Assembly of Ecological Communities*. Cambridge University Press
9. He, N.P. *et al.* (2019) Ecosystem traits linking functional traits to macroecology. *Trends Ecol. Evol.* 34, 200–210
10. Reich, P.B. *et al.* (1997) From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U. S. A.* 94, 13730–13734
11. Sack, L. *et al.* (2012) Developmentally based scaling of leaf venation architecture explains global ecological patterns. *Nat. Commun.* 3, 837
12. Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556
13. Chapin III, F.S. *et al.* (2000) Consequences of changing biodiversity. *Nature* 405, 234–242
14. Lieth, H. and Whittaker, R.H. (1975) *Primary Productivity of the Biosphere*. Springer-Verlag
15. Violle, C. *et al.* (2014) The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci. U. S. A.* 111, 13690–13696
16. Chapin III, F.S. (2003) Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Ann. Bot.* 91, 455–463
17. Reich, P.B. (2012) Key canopy traits drive forest productivity. *Proc. Biol. Sci.* 279, 2128–2134
18. Peng, Y. *et al.* (2020) A theory of plant function helps to explain leaf-trait and productivity responses to elevation. *New Phytol.* 226, 1274–1284
19. Fyllas, N.M. *et al.* (2017) Solar radiation and functional traits explain the decline of forest primary productivity along a tropical elevation gradient. *Ecol. Lett.* 20, 730–740
20. Bahar, N.H.A. *et al.* (2017) Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation Andean tropical moist forests of Peru. *New Phytol.* 214, 1002–1018
21. Wang, H. *et al.* (2017) Photosynthetic responses to altitude: an explanation based on optimality principles. *New Phytol.* 213, 976–982
22. Barry, K.E. *et al.* (2021) A graphical null model for scaling biodiversity–ecosystem functioning relationships. *J. Ecol.* 109, 1549–1560
23. Šimová, I. and Storch, D. (2017) The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship. *Ecography* 40, 239–252

Outstanding questions

What is the relationship between the maximum productivity of an ecosystem and its actual productivity under the combined constraints imposed by multiple environmental factors, such as water, nutrients, and radiation?

To what extent do plant community traits affect the key parameters of resource acquisition efficiencies, and how do these differ across ecosystems?

What role in determining ecosystem productivity can be attributed environmental factors, including climate, relative to plant community traits?

How do different types of traits, such as economic traits and size traits, modulate ecosystem productivity, and do their roles shift with changing climate?

24. Zhang, Y. *et al.* (2021) Advances in hyperspectral remote sensing of vegetation traits and functions. *Remote Sens. Environ.* 252, 112121
25. He, L. *et al.* (2019) Diverse photosynthetic capacity of global ecosystems mapped by satellite chlorophyll fluorescence measurements. *Remote Sens. Environ.* 232, 111344
26. Genung, M.A. *et al.* (2020) Species loss drives ecosystem function in experiments, but in nature the importance of species loss depends on dominance. *Glob. Ecol. Biogeogr.* 29, 1531–1541
27. Elser, J. *et al.* (2003) Growth rate–stoichiometry couplings in diverse biota. *Ecol. Lett.* 6, 936–943
28. Elser, J.J. *et al.* (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142
29. Tian, D. *et al.* (2018) Global leaf nitrogen and phosphorus stoichiometry and their scaling exponent. *Natl. Sci. Rev.* 5, 728–739
30. McGill, B.J. (2019) The world, how and why of doing macroecology. *Glob. Ecol. Biogeogr.* 28, 6–17
31. Reich, P.B. (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
32. Reich, P.B. *et al.* (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* 80, 1955–1969
33. Field, C. and Mooney, H. (1986) Photosynthesis – nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function: Proceedings of the Sixth Maria Moors Cabot Symposium, Evolutionary Constraints on Primary Productivity, Adaptive Patterns of Energy Capture in Plants, Harvard Forest, August 1983*, Cambridge University Press
34. Kull, O. and Jarvis, P.G. (1995) The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant Cell Environ.* 18, 1174–1182
35. Farquhar, G.D. (1989) Models of integrated photosynthesis of cells and leaves. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 323, 357–367
36. Luo, X. *et al.* (2018) Comparison of big-leaf, two-big-leaf, and two-leaf upscaling schemes for evapotranspiration estimation using coupled carbon-water modeling. *J. Geophys. Res. Biogeosci.* 123, 207–225
37. Huang, M. *et al.* (2019) Air temperature optima of vegetation productivity across global biomes. *Nat. Ecol. Evol.* 3, 772–779
38. Malhi, Y. *et al.* (2017) The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytol.* 214, 1019–1032
39. McGill, B.J. (2010) Matters of scale. *Science* 328, 575
40. Harfoot, M.B. *et al.* (2014) Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biol.* 12, e1001841
41. Li, Y. *et al.* (2020) Leaf size of woody dicots predicts ecosystem primary productivity. *Ecol. Lett.* 23, 1003–1013
42. Wright, S.J. *et al.* (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91, 3664–3674
43. Yang, J. *et al.* (2018) Why functional traits do not predict tree demographic rates. *Trends Ecol. Evol.* 33, 326–336
44. Rubio, V.E. *et al.* (2021) Improving predictions of tropical tree survival and growth by incorporating measurements of whole leaf allocation. *J. Ecol.* 109, 1331–1343
45. Lohbeck, M. *et al.* (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96, 1242–1252
46. Prado-Junior, J.A. *et al.* (2016) Conservative species drive biomass productivity in tropical dry forests. *J. Ecol.* 104, 817–827
47. Heckman, R.W. *et al.* (2020) Plant biomass, not plant economics traits, determines responses of soil CO₂ efflux to precipitation in the C4 grass *Panicum virgatum*. *J. Ecol.* 108, 2095–2106
48. Enquist, B.J. *et al.* (2007) A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature* 449, 218–222
49. He, N.P. *et al.* (2018) Variation in leaf anatomical traits from tropical to cold-temperate forests and linkage to ecosystem functions. *Funct. Ecol.* 32, 10–19
50. Suding, K.N. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob. Chang. Biol.* 14, 1125–1140
51. Van Cleemput, E. *et al.* (2018) The functional characterization of grass- and shrubland ecosystems using hyperspectral remote sensing: trends, accuracy and moderating variables. *Remote Sens. Environ.* 209, 747–763
52. Liu, X. *et al.* (2019) Downscaling of solar-induced chlorophyll fluorescence from canopy level to photosystem level using a random forest model. *Remote Sens. Environ.* 231, 110772
53. Meacham-Hensold, K. *et al.* (2019) High-throughput field phenotyping using hyperspectral reflectance and partial least squares regression (PLSR) reveals genetic modifications to photosynthetic capacity. *Remote Sens. Environ.* 231, 111176
54. Kattge, J. *et al.* (2020) TRY plant trait database – enhanced coverage and open access. *Glob. Chang. Biol.* 26, 119–188
55. Maitner, B.S. *et al.* (2018) The bien r package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol. Evol.* 9, 373–379
56. Wright, I.J. *et al.* (2004) The worldwide leaf economics spectrum. *Nature* 428, 821–827
57. Ordóñez, J.C. *et al.* (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Glob. Ecol. Biogeogr.* 18, 137–149
58. Diaz, S. *et al.* (2015) The global spectrum of plant form and function. *Nature* 529, 167–171
59. Meyer, C. *et al.* (2016) Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecol. Lett.* 19, 992–1006
60. Meyer, C. *et al.* (2016) Range geometry and socio-economics dominate species-level biases in occurrence information. *Glob. Ecol. Biogeogr.* 25, 1181–1193
61. Meyer, C. *et al.* (2015) Global priorities for an effective information basis of biodiversity distributions. *Nat. Commun.* 6, 8221
62. Cordlandwehr, V. *et al.* (2013) Do plant traits retrieved from a database accurately predict on-site measurements? *J. Ecol.* 101, 662–670
63. Monteith, J.L. (1977) Climate and the efficiency of crop production in Britain. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 281, 277–294
64. Linder, S. (1985) Potential and actual production in Australian forest stands. *Res. For. Manag.* 11–35
65. Stape, J.L. *et al.* (2004) Eucalyptus production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. *For. Ecol. Manag.* 193, 17–31
66. Waring, R. *et al.* (2016) Tamm review: insights gained from light use and leaf growth efficiency indices. *For. Ecol. Manag.* 379, 232–242
67. Morgan, P.B. *et al.* (2005) Smaller than predicted increase in aboveground net primary production and yield of field-grown soybean under fully open-air [CO₂] elevation. *Glob. Chang. Biol.* 11, 1856–1865
68. Dermody, O. *et al.* (2008) How do elevated CO₂ and O₃ affect the interception and utilization of radiation by a soybean canopy? *Glob. Chang. Biol.* 14, 556–564
69. Nobel, P.S. (1999) *Physicochemical and Environmental Plant Physiology*. Academic Press
70. Wong, S. *et al.* (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* 282, 424–426
71. Fortunel, C. *et al.* (2018) Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. *Ecology* 99, 2272–2283
72. Feng, X. *et al.* (2018) Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling. *Glob. Chang. Biol.* 24, e213–e232
73. Watson, D.J. (1947) Comparative physiological studies on the growth of field crops: I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot.* 11, 41–76
74. Asner, G.P. *et al.* (2003) Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Glob. Ecol. Biogeogr.* 12, 191–205
75. Farquhar, G.D. *et al.* (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 species. *Planta* 149, 78–90
76. Anderegg, W.R.L. (2015) Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytol.* 205, 1008–1014
77. Brulheide, H. *et al.* (2018) Global trait–environment relationships of plant communities. *Nat. Ecol. Evol.* 2, 1906–1917
78. Moreno-Martínez, Á. *et al.* (2018) A methodology to derive global maps of leaf traits using remote sensing and climate data. *Remote Sens. Environ.* 218, 69–88
79. Šimová, I. *et al.* (2015) Shifts in trait means and variances in North American tree assemblages: species richness patterns are loosely related to the functional space. *Ecography* 38, 649–658

80. Amthor, J.S. (1994) Scaling CO₂-photosynthesis relationships from the leaf to the canopy. *Photosynth. Res.* 39, 321–350
81. Rogers, A. *et al.* (2017) A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytol.* 213, 22–42
82. Friend, A.D. (2001) Modelling canopy CO₂ fluxes: are ‘big-leaf’ simplifications justified? *Glob. Ecol. Biogeogr.* 10, 603–619
83. Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910
84. Wang, R. *et al.* (2015) Latitudinal variation of leaf stomatal traits from species to community level in forests: linkage with ecosystem productivity. *Sci. Rep.* 5, 14454
85. Mouchet, M.A. *et al.* (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876
86. Enquist, B.J. *et al.* (2015) Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. *Adv. Ecol. Res.* 52, 249–318
87. Kerkhoff, A.J. *et al.* (2005) Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Glob. Ecol. Biogeogr.* 14, 585–598
88. Brown, J.H. *et al.* (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789