On Theory in Ecology

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We argue for expanding the role of theory in ecology to accelerate scientific progress, enhance the ability to address environmental challenges, foster the development of synthesis and unification, and improve the design of experiments and large-scale environmental-monitoring programs. To achieve these goals, it is essential to foster the development of what we call efficient theories, which have several key attributes. Efficient theories are grounded in first principles, are usually expressed in the language of mathematics, make few assumptions and generate a large number of predictions per free parameter, are approximate, and entail predictions that provide well-understood standards for comparison with empirical data. We contend that the development and successive refinement of efficient theories provide a solid foundation for advancing environmental science in the era of big data.

Keywords: theory unification, metabolic theory, neutral theory of biodiversity, maximum entropy theory of ecology, big data

> The grand aim of all science is to cover the greatest number of empirical facts by logical deduction from the smallest number of hypotheses or axioms. (Albert Einstein)

Science is intended to deepen our understanding of the natural world. Progress in science arises from the tension between induction and deduction, empiricism and theory. Data gathered through observation and experimentation provide clues about the structure and function of the natural world, and theory organizes existing data and new ideas into a cohesive conceptual framework to both explain existing observations and make novel predictions. Theory reduces the apparent complexity of the natural world, because it captures essential features of a system, provides abstracted characterizations, and makes predictions for as-yet unobserved phenomena that additional data can be used to test.

There are many ideas about the nature of theory in science and in philosophy (Nagel 1961, NRC 2008). In ecology, there is currently no consensus regarding the definition, role, and generality of theories, which is discussed in several essays (e.g., Pickett et al. 1994, Scheiner and Willig 2011). It is not surprising that ecologists use the label *theory* to refer to many things. Meanings of *theory* range from highly specific to very general, from hypotheses (e.g., the hypothesis of clutch overlap or the intermediate disturbance hypothesis) to conceptual frameworks for complete fields or research programs (e.g., macroecology, conservation biology). A survey of the ecological literature finds reference to 78 theories (see supplemental table S1), almost half of which have been mentioned in more than two publications (figure 1, table S1), which suggests that ecology is awash with theories. But is ecology theory rich? Are there different types of theories in ecology, with different precepts and goals? What theories constitute a foundational conceptual framework for building a more predictive, quantitative, and useful science of ecology? A field with a large and diverse number of theories may be a healthy one, but this can also hamper progress; stifle innovation; and lead to inadequate policy to manage, mitigate, and adapt to undesirable environmental impacts. A discussion of the different types of theories in ecology is a timely and necessary exercise.

Here, we define a *theory* as a hierarchical framework that contains clearly formulated postulates, based on a minimal set of assumptions, from which a set of predictions logically follows. Theory is inherently deductive. Advances in data stimulate theory, and new theory refines, expands, and replaces old theory, thereby correcting flaws and explaining and predicting phenomena in the domain in which they apply. As such, the evolution of a successful theory is for it to become more general, through the development of detailed models that apply the theory to a wider class of phenomena.

Is ecology theory rich?

The richness of theories in ecology is, to some degree, illusory. As was mentioned above, several "theories" (see table S1) are actually specific hypotheses or models. Ecologists and other scientists often use the terms *model* and *theory* indistinguishably (e.g., Leijonhufvud 1997, Ginzburg and Jensen 2004), but they are fundamentally different. *Models* are

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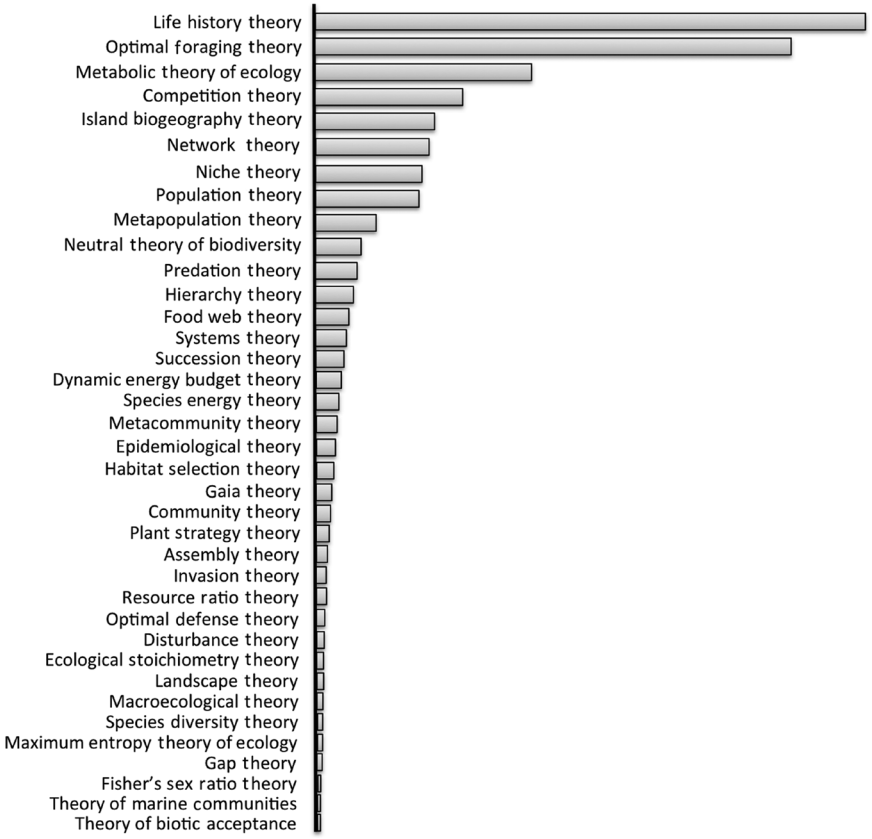


Figure 1. Examples of theories in ecology that have been named so in the Thomson Reuters Web of Knowledge database and based on queries specified in supplemental table S2. The bars are proportional to the number of times each theory has been mentioned.

usually intended to increase our understanding or solve a particular problem in a particular domain (e.g., the role of nutrient additions to lake ecosystems) or to explore the consequences of relaxing one or more assumptions of a theory (e.g., inclusion of Allee effects in metapopulation theory). "Since models are simplified, partial statements of theories, several models may belong to the same theory, designed to elucidate different aspects of it" (Leijonhufvud 1997, p. 194) Some models, if they are repeatedly tested and supported, can eventually give way to a theory, but they are not theories, themselves.

The discovery of new empirical statistical patterns and statistical relationships often leads to theoretical advances. However, the inductively revealed patterns do not, themselves, constitute a theory, and neither do statistical representations of data or model-fitting exercises. Some ecologists consider a statistical regression model a theoretical construct (e.g., Peters 1991), but regression fails to meet our definition of *theory*. Although regression can test a theory by evaluating predicted relationships among variables, it does not constitute theory in itself. Statistical analyses may lead to the creation and refinement of theory; however, theory goes further to provide understanding of the processes that give rise to the relationships, independent of the statistical fit.

Notwithstanding the apparent richness of theories in ecology (figure 1, table S1), there seems to be a general trend that the use and importance of theory is declining in biology as a whole (NRC 2008). Biologists appear to increasingly underappreciate the role that theory can play. The fact that so called "model organisms" are used in the majority of research in molecular biology and biomedicine implies that biologists are searching for general trends and unified principles, but there is seemingly little motivation to organize new findings into a rigorous hierarchical framework expressed in the language of mathematics. This may be, in part, because we are overwhelmed and overly impressed by the vast amount of data that can be obtained from the natural world. The era of big data, or data deluge (e.g., Bollier and Firestone 2010), has fostered the proliferation of giant databases, data mining, machine learning, and other inductive approaches. Some have suggested that theories are irrelevant in the big data era—that correlations are sufficient to build a vigorous science (Anderson 2008).

We disagree. We argue that data are fundamentally necessary and important but not sufficient; healthy productive science needs both theory and data to feed the continuous interplay between induction and deduction. No matter how much data one can obtain from social, biological, and ecological systems, the multiplicity of entities and interactions among them means that we will never be able to predict many salient features of their structures and dynamics. To discover the underlying principles, mechanisms, and organization of complex adaptive systems and to develop a quantitative, predictive, conceptual framework ultimately requires the close integration of both theory and data.

Are there different types of theories in ecology?

Many of the theories listed in figure 1 comply with the definition of *theory* given above, but some theories are more efficient than others. To understand the importance of efficiency, it is instructive to revisit the remarks of the British statistician George E. P. Box (Box 1976), who said, "Since all models are wrong, the scientist cannot obtain a 'correct' one by excessive elaboration. On the contrary, following William of Occam, he should seek an economical description of natural phenomena" (p. 792). We claim that the same is true for evaluating alternative theories that purport to explain the same phenomena. As was pointed out by the philosopher of science Larry Laudan, the evaluation of theories is a comparative matter (Laudan 1977), and one important criterion

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for comparison is efficiency. A theory is more *efficient* than its rivals if it can make more and better explanations and predictions with the same number of free parameters or constructs (Laudan 1977).

Here, we describe our emerging strategy for developing efficient theories in ecology. Our strategy is not normative. Specifically, we do not imply that this is the only way to advance ecological understanding, especially under a postmodern scientific framework (Funtowicz and Ravetz 1993, Allen TFH et al. 2001). In the following discussion, it is useful to bear in mind that *theory*, etymologically, comes from the ancient Greek *theōria*, which means "contemplation" or "a viewing." In that sense, a theory is a way of looking at the world and not necessarily a way of knowing how the world is. Our main claim is that efficient theories provide a particular way of looking at the world that can be particularly insightful and useful. Building efficient theories is of fundamental importance, because we think it will allow for a faster advancement of our field.

We do not suggest that all ecologists should be theoreticians. We recognize the value of pluralistic approaches. We do believe that a healthy and advancing science of ecology needs some appropriate balance between empiricists and theoreticians. Such a balanced science will not only contribute to the development of a quantitative and predictive science of ecology, it will also contribute to the application of ecological science in addressing pressing climate, societal, and health challenges. We hope that our reflections will contribute to better understanding of the role of theory in ecology and explain why we think the development of theory in ecology is such an important pursuit.

In what follows, we provide a detailed account of what we think the salient characteristics of efficient theories are in ecology.

What constitutes an efficient theory?

Efficient theories should be built, as much as is possible, on first principles. *First principles* are the bedrock of science—that is, quantitative law-like postulates about processes underlying a given class of phenomena in the natural world with well-established validity, both theoretical and empirical (i.e., core knowledge). They are not just descriptions of observed phenomena (see Scheiner and Willig 2008). First principles are the building blocks of efficient theories. They serve two functions. First, they allow unifying connections across the entire realm of science—for example, between ecology and chemical stoichiometry or thermodynamics. Second, their application and consequences, which are articulated by the theory, lead logically to the structure of the theory and to a priori predictions.

The language of mathematics usually (but not always) expresses efficient theories. Mathematically formulated theories are generally preferable, because the logic is more transparent, less subject to alternative interpretations, and more amenable to rigorous empirical testing. Increasing the number of imprecise, qualitative terms and meanings will do little to advance ecology, but using mathematics to reduce ambiguity will. Nevertheless, we are not denying the importance of verbal theories. Darwin and Wallace, for example, clearly articulated the foundational idea of modern biological theory—evolution by natural selection—in words only. However, verbal theories can be enriched by mathematical formulation, as is the case of Darwin's theory of evolution by means of natural selection, which was further refined through the mathematical formulation of the process of evolution and adaptation as expressed in Fisher's fundamental theorem and Sewall Wright's adaptive landscapes. Given the role of mathematical formulations in efficient theories, it is likely that their role in biological sciences will increase (e.g., Cohen 2004, Krakauer et al. 2011) and become as important in biology as they were for physics during the last century (Wigner 1960). Mathematics is indeed the salient feature of twentieth-century science and the appropriate vehicle to generate knowledge of things in the world a *mente concipere* according to Heidegger (1977). To understand its role in the generation of scientific knowledge, one must bear in mind the Greek notion of mathematics, which comes from ta mathēmata, or "what can be learned" and, at the same time, "what can be taught" (Heidegger 1977). Mathematics as the driver of learning and teaching about the world helps reduce ambiguity in communication and prediction.

Efficient theories entail as few assumptions and free parameters as possible. Theories come in all guises in ecology; they differ in how many assumptions they make, how many free parameters they have, and how many predictions they make. A *free parameter* is a number that usually cannot be derived from the theory but whose value is required to make predictions. The best theories are those that explain or unify the greatest number of phenomena and generate the most predictions on the basis of the fewest assumptions and free parameters. If a theory needed to account for all the details of a system to yield predictions about its future behavior, gathering sufficient data to evaluate its predictions would require an inordinate amount of work. Such a theory would be *inefficient* and as complex as the system it was attempting to describe. Theories should yield a compressed description of the system or phenomenon under study, thereby reducing its complexity. The property of reducing complexity through theory compression is an important and often neglected attribute of good (i.e., efficient) theory.

A theory does not have to be a precise, faithful description of the phenomenon under study: We should value approximations. In physics, there are many approximate theories that make approximate predictions, which are essential to the refinement of the theory and progress in our efforts to understand the nature of the phenomenon under analysis. The examples include Newtonian mechanics and Newtonian gravity, which are now thought of as approximations of special and general relativity, respectively. In turn, many physicists expect general relativity and the field theories that describe particle physics to be approximations of a more fundamental, unified theory, the details of which are the subject

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of ongoing research. This iterative procedure is essential for evaluating what approximate theories can and cannot explain and for exposing where we might appropriately focus new work. It is common in ecology to claim that a theory is wrong because a specific observation disagrees with the theory. However, when empirical observations deviate from theory predictions, we are alerted to the possibility that we have not taken other important processes into account.

Efficient theories in ecology provide a known standard against which to measure natural phenomena. By a *standard*, we mean a prediction of how the world would work if only the first principles of the theory are at work; they are true by definition and do not need to be tested, because they follow logically from the action of first principles. Without standards, no deviations or gaps in knowledge would be apparent, so there would be no need for theory refinement and increasing understanding, which would lead to scientific stagnation. A historical example will help to clarify this point. In 1908, R. C. Punnett was invited to read a paper at the Royal Society of Medicine, where he presented evidence on the importance of Mendelian inheritance for understanding human diseases such as brachydactyly. During the discussion that this paper engendered, the British statistician Udny Yule objected to the importance of Mendelian inheritance in brachydactyly, stating that if it were a dominant character, it would tend to increase in the human population. The same year, the great British mathematician G. H. Hardy, in a letter to the editor of *Science*, showed that Yule's statement was groundless, because, under the assumption of random mating, there is not a tendency for dominant characters to increase or for recessive ones to die out in populations, because they remain fixed after one generation. This is the well-known Hardy–Weinberg principle. When alleles occur in frequencies different from Hardy–Weinberg expectations, we do not conclude that the this principle is falsified; rather, we conclude that other processes, such as drift and selection, as well as nonrandom mating also influence the between-generation gene frequencies. The Hardy–Weinberg principle is akin to a neutral model showing us what to expect in the absence of drift, mutation, or selection. It provides a standard against which patterns in nature can be compared, unexplained deviations identified, and whose explanation would require refinement and further testing. The end result would be an increase in our understanding of the phenomenon under study. Furthermore, as was seen in this example, the fact that Mendel's theory of inheritance was amenable to mathematical analyses led to the discovery of the Hardy–Weinberg principle, which, in turn, increased our understanding of factors affecting microevolutionary change, thus furthering theory development.

Some examples of efficient theories

Several deductive frameworks that fit our description of *efficient theory* have emerged in ecology and evolutionary ecology. In this section, we review and compare some of these theories to orient readers to key characteristics of deductive theory that we consider highly efficient and useful. From these comparisons, we argue that efficient theory in ecology is simple, parsimonious, derived from first principles, quantitative, and mathematical, with few inputs and many predictions.

Fisher's sex ratio theory. The argument behind Fisher's sex ratio theory is that the relative reproductive value to parents of sons (rather than daughters) is equal to the relative selection pressure favoring the production of sons. Theory includes the assumption that parents determine the sex of their offspring and a definition of *reproductive value*. Fisher (1930) defined *reproductive value* in the context of populations with age structure, such that, given that an individual survives to age x, its expected reproduction from age x onward is v_x. This quantity is calculated in the discrete case as $\Sigma_{y=x}\, l_y m_y/R$ and in the continuous case as $\int_{y=x} l_y m_y\, dy/R$, where l_x is the probability of surviving from age 0 to age x, m_x is the average number of offspring produced by an individual of age x and R is the net reproductive rate of the population. Fisher's canonical example assumed a nongrowing population of a species in which each offspring had a mother and a father. In this case, the predicted equilibrium sex ratio is parity. When we observe deviations from a one-to-one sex ratio in species with two parents, we do not claim to have falsified Fisher's theory. Rather, we ask whether the reproductive value of daughters and sons is indeed equal. Therefore, a failure of predictions to match observations suggests follow-up hypotheses about sources of differential reproductive value of each sex of offspring (e.g., Gowaty and Lennartz 1985).

Optimal foraging theory. Optimal foraging theory (OFT) is concerned with understanding the decisions that individuals make while foraging in heterogeneous environments (e.g., MacArthur and Pianka 1966, Charnov 1976). This theory has been around for more than 50 years and continues to be refined and expanded (e.g., Beckerman et al. 2006). OFT is intended to explain the foraging behavior of animals by means of a quantitative theory based on the first principles of energy and mass balance and natural selection. By assuming that natural selection has molded the behavior of organisms so as to maximize fitness, it yields predictions on a variety of phenomena, including optimal diets, patch choice, and how much time to spend foraging in a patch, as well as movement and visiting rates (e.g., Pyke 1984). One fundamental mathematical theorem within OFT is the marginal value theorem (Charnov 1976), which states that the time a forager will stay in patch i, T_i, depends on the marginal rate of net energy intake, $g_i(T_i)$, associated with the patch, and the average energy intake of the entire habitat, E_n, through the following relationship:

$$\frac{\partial g_i(T_i)}{\partial T_i} = E_n.$$

According to this theorem, a forager should leave a patch when the rate of energy intake drops below the average

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for the habitat. Departures from predicted patch residence times, rather than being taken as a reason to reject the theory, have paved the way to understanding the effects of other processes constraining energy intake and foraging decisions, such as predation risk, competing activities (e.g., the search for mates), and physiological state (e.g., Pyke 1984, Nonacs 2001). We know that the activities of animals in the natural world can be suboptimal, the same as we know that species are not equal on a per capita basis and that demographic processes are not purely stochastic, as is assumed in neutral theory (Hubbell 2001). However, the mathematics of optimality and neutrality allow us to derive precise predictions that can be tested against data. The result of this confrontation of theory and data leads to the refinement of the theory and the prediction of new phenomena, guides data collection, and increases our understanding of the natural world.

The metabolic theory of ecology. The metabolic theory of ecology (MTE) is focused on understanding how the interplay among physiological, ecological, and evolutionary processes both affect and are affected by individual metabolic rate (Brown et al. 2004, West and Brown 2005, Sibly et al. 2012). An underlying premise of the theory is that metabolic rate is fundamental to ecology, because it is through metabolism that organisms interact with their environments. Over the last 10 years, the MTE has yielded two general classes of models. The first predicts how two variables—body size and temperature—affect the metabolic rates of organisms (e.g., Spatz 1991, West et al. 1997, Gillooly et al. 2001). This focus on size and temperature is based on early work demonstrating that these variables are each primary determinants of metabolic rate across the diversity of life (Arrhenius 1889, Kleiber 1961, Robinson et al. 1983). The second class of models explores the consequences of metabolic rate at different levels of biological organization, from genomes to ecosystems. Empirical data are generally consistent with predictions of the MTE that size and temperature constrain diverse rate processes, including DNA evolution (e.g., Gillooly et al. 2005), population growth (e.g., Savage et al. 2004), and ecosystem carbon flux (Enquist et al. 2003, Allen AP et al. 2005, López-Urrutia et al. 2006), through their effects on metabolic rate. Since the MTE yields predictions for these diverse phenomena, given only two parameters—body size and temperature—it represents an efficient theory in ecology. Importantly, however, the variance left unexplained by MTE models can be substantial, as has been noted in some critiques (e.g., Tilman et al. 2004). This variation probably reflects the effects of other traits or determinants of metabolic rate and of other ecological and evolutionary processes (e.g., Marquet et al. 2004, Enquist et al. 2007, Rüger and Condit 2012, Lin et al. 2013). Therefore, deviations of data from MTE predictions provide benchmarks for assessing the importance of variables other than body size and temperature in influencing biological rate processes (Enquist et al. 2009).

The MTE provides a common frame of reference to make comparisons among organisms that, notwithstanding their different evolutionary histories and ecological settings, obey the same first principles linked to metabolism, size, and temperature. This is exemplified in the application of the MTE to understanding variation in ontogenetic growth rates (figure 2a; West et al. 2001). Specifically, the MTE predicts a universal growth trajectory that all organisms obey—or collapse to—once they are put into the same reference frame (rescaled time and size), which is provided by the theory.

The maximum entropy theory of ecology. Information theory in the form of the MaxEnt inference procedure (Jaynes 1982) provides the foundation for the maximum entropy theory of ecology (METE), which predicts realistic functions describing major patterns in macroecology. The predictions of the METE include the species–abundance distribution, the spatial distribution of individuals within species, the species–area and endemics–area relationships, and the distribution of metabolic rates over the individuals within and among species (Harte et al. 2008, 2009, Harte 2011). In analogy with thermodynamics, in which the state variables pressure, volume, temperature, and particle number characterize a system, in the METE, knowledge of the state variables S_0 (the number of species), N_0 (the number of individuals), E_0 (the metabolic rate summed over individuals), and A_0 (the area of the system) provide the constraints that are used to derive predictions, and with the additional state variable L_0 (the number of trophic links in a network), MaxEnt predicts link distributions (Williams 2010). A noteworthy prediction of the theory is a universal scale collapse of all species–area curves onto a universal curve (Harte et al. 2009). Specifically, if the local slope of the log(species richness) and the log(area) curve is plotted as a function of the ratio of the average total abundance at that scale to average species richness at that scale, the METE predicts that all the data fall on a single declining curve (figure 2b). This validated prediction is dramatically different from power-law behavior, in which different species–area relationships would show up as horizontal lines, with intercepts varying from one ecosystem to another. Although tests of the METE using census data for plants, birds, and arthropods from a variety of habitats and over spatial scales ranging from square meters to thousands of square kilometers indicate that the theory predicts observed patterns without any adjustable parameters, some systematic discrepancies are noted for communities that are relatively rapidly changing—for example, following a disturbance (Harte 2011). Patterns in the deviation from theory of rapidly changing systems may allow extension of the METE from a static theory to a dynamic theory.

The neutral theory of biodiversity. The neutral theory of biodiversity (NTB) is focused on understanding the role of stochastic demographic processes in controlling the structure and dynamics of communities at ecological to macroevolutionary timescales (Hubbell 2001). The theory yields a rich set of predictions on diverse phenomena, including the frequency distribution of species abundance, species–area relationships,

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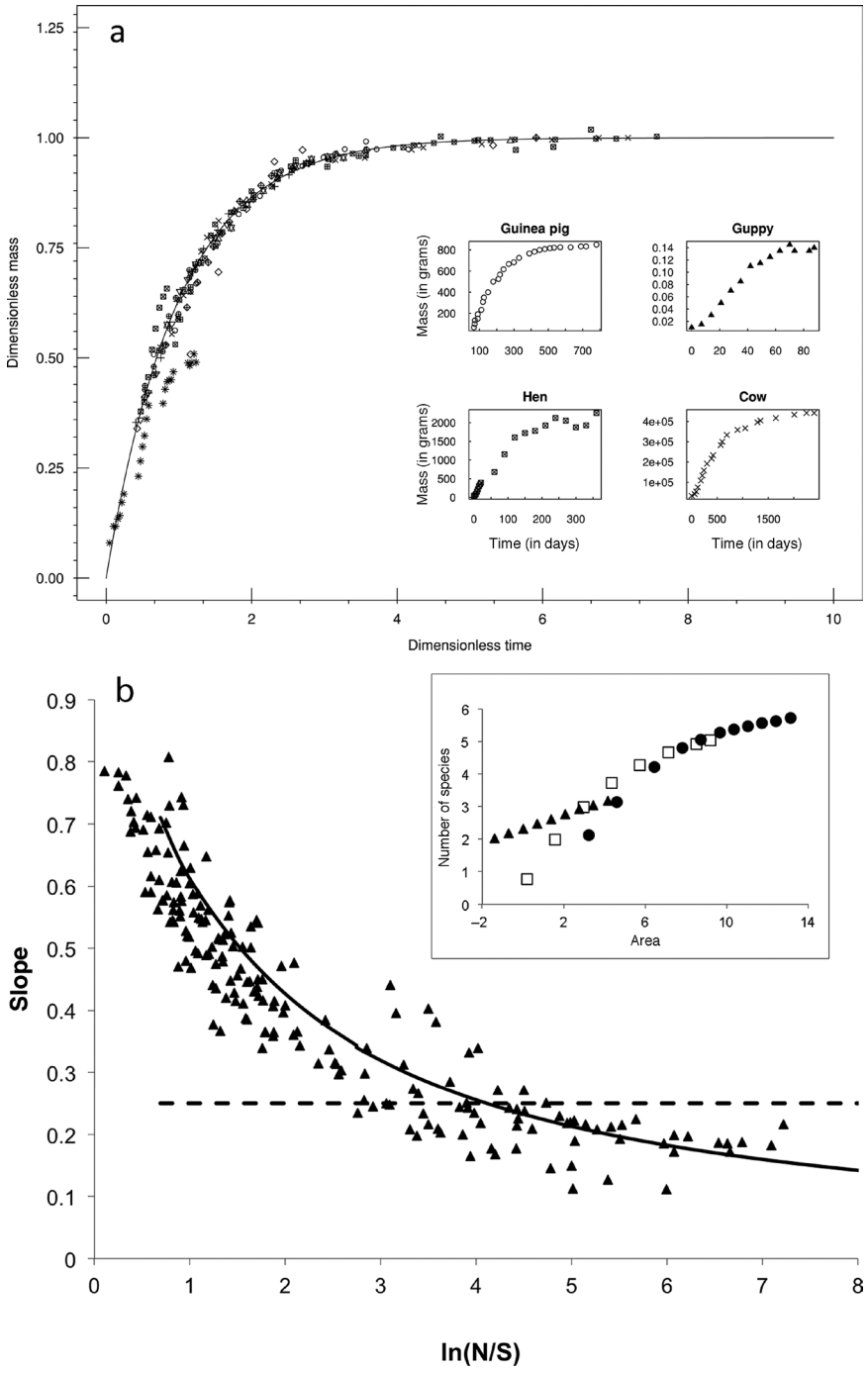


Figure 2. Scale collapse in ontogenetic growth trajectories (a) and species–area curves (b) as predicted by the metabolic theory of ecology (a) and the maximum entropy theory of ecology (b) (after West et al. 2001 and Harte et al. 2009, respectively). Scale collapse means that when different systems are brought into the same frame of reference, which is accomplished by rescaling, different realizations of the same phenomenon (the insets) can be shown to obey the same universal relationship predicted by a theory. In panel (a), the theory allows for a rescaling of time and size into dimensionless variables, which shows that ontogenetic trajectories corresponding to 13 different species, identified by different symbols, follow the same general law. Four of these species are plotted in the inset. In panel (b), the plot shows how the slope of different species–area curves change as a function of the ratio of the total number of individuals (N) and species richness (S) observed at a particular area. The inset shows three particular cases of how the number of species changes with area.

phylogenetic-tree structure, and the relationship of species richness to the macroevolutionary rates of speciation and extinction (Hubbell 2001). Moreover, it does so using remarkably few parameters, by assuming demographic equivalence among species with respect to per capita (i.e., individual-level) rates of speciation, birth, death, and dispersal (Volkov et al. 2005). Therefore, the NTB represents an efficient theory. It demonstrates how variation among species in relative abundance can arise solely from simple, stochastic rules that apply to all species composing a community and thus provides a useful baseline against which to compare empirical data (Hubbell 2001, Leigh 2007). This focus on species similarities rather than species differences represents a major challenge to the niche paradigm, which has predominated in community ecology since the 1960s. Despite the simplicity of NTB models, they often exhibit remarkably good fits to species-abundance data (Volkov et al. 2005) and other ecological patterns (e.g., Rosindell and Cornell 2009, Halley and Iwasa 2011), although deviations from model predictions are also frequently observed (e.g., Gilbert and Lechowicz 2004). However, we would argue that the ability to falsify the NTB represents a virtue of this theory—and of efficient ecological theories in general—because it paves the way for more-realistic models and a deeper understanding of ecological systems based on underlying dynamical processes. When efficient theories fail, they do so in informative ways. As Bateson (1908) said,

> Treasure your exceptions! When there are none, the work gets so dull that no one cares to carry it further. Keep them always uncovered and in sight. Exceptions are like the rough brickwork of a growing building which tells that there is more to come and shows where the next construction is to be. (p. 19)

We contend that first and foremost, exceptions to efficient theories help the purpose of advancing scientific knowledge on firm ground.

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Some examples of inefficient theories

For the sake of clarity, we think it useful to highlight some theories that are not efficient. We do not imply that they should be dismissed as of limited value, but they do not fit some of the characteristics used to define efficient theories.

R* or resource-ratio theory. The body of work represented by R* or the resource-ratio theory, which has stimulated an enormous amount of research, was first proposed by MacArthur and Levins (1964), then expanded by Tilman (1982) to yield predictions on competition among consumer species for limiting resources. Under competition for a single homogenously distributed limiting nutrient, R* theory predicts the winner to be the species that maintains a positive population growth rate at the lowest concentration of the limiting nutrient. It also predicts coexistence of two species when the growth rate of each species is limited by a different nutrient. When resources are heterogeneously distributed, the number of species can be larger than the number of limiting resources, thereby resolving Hutchinson's paradox of the plankton. R* theory is a conceptual advance over previous phenomenological-competition theories, such as the Lotka–Volterra predator–prey model, because it predicts the outcome of competition experiments before they are performed. However, it has proven difficult to test, because it has a large number of free parameters (a minimum of three parameters per species–resource combination, in addition to death rates and resource supply rates), which must all be measured to yield predictions. This explains why most of the tests have been restricted to laboratory or experimental microcosms, using species with short generation times (usually primary producers in freshwater ecosystems; Miller et al. 2005). Although the theory is based on the first principles relating population growth to resource supply and consumption, it is not efficient because of its large number of free parameters, which restricts it scope of application and the possibility of field testing. Nonetheless, it has proven to have heuristic value, which has given rise to several extensions (Leibold 1995, Daufresne and Hedin 2005).

Dynamic energy budget theory. The dynamic energy budget theory (DEB) is intended to explain the life history of organisms in an environment with a given amount of resources on the basis of a mathematical description of the rates at which individuals assimilate and use energy and materials from resources to sustain the processes of maintenance, growth, reproduction, and development. DEB is based on the first principles dictated by the kinetics and thermodynamic of energy and material fluxes but is data demanding and rich in free parameters (see Kooijman 2000). According to Nisbet and colleagues (2000), to apply the theory to a growing organism requires estimating 15 parameters; DEB, like the R* theory, is rich in parameters, and most of them are species specific, which hinders the generation of general predictions.

Throughout the present article, we have emphasized the importance of theory in the inductive–deductive cycle. There are situations, however, in which the complexity of the system under study and the lack of adequate theories hinder progress in understanding. In this situation, the use of simulations or individual (agent) based models (e.g., Railsback and Grimm 2012) can be the only tool at hand. Agent-based models, which are parameter rich and rest on massive simulations, can be powerful in generating hypotheses and in helping to test alternative ones for patterns seen in nature (e.g., Arim et al. 2010), especially when field or laboratory tests are not an option (but see May 2004). However, we see this approach only as a stage in the process of understanding that may lead to the identification of first principles and, eventually, to the development of efficient theories.

On theory synthesis and unification

Deductive, quantitative theories based on first principles continually expand and, in doing so, may come close to or overlap with the domains of other theories, thereby increasing the potential for synthesis and unification. Although understanding biodiversity from a theoretical perspective clearly represents a formidable challenge (e.g., Simberloff 2004), we are optimistic that significant progress can be made using simple quantitative, predictive theories grounded in first principles.

Efficient theories based on first principles foster synthesis and unification. For example, although the MTE and the NTB are focused on different aspects of ecological complexity—energy and stochasticity, respectively—they share a fundamental point of contact that affords opportunities for synthesis. Specifically, each theory postulates that ecosystems are governed by universal principles and processes that operate at the level of the individual organism and, therefore, transcend species identities in shaping patterns of biodiversity. The MTE, for example, yields predictions on the size dependence of metabolic rate by assuming that organisms are constrained by generic properties of biological distribution networks (West et al. 1997). Similarly, the NTB derives predictions on the frequency distribution of species abundance by assuming demographic equivalence among species with respect to per capita rates of speciation, birth, death, and dispersal (Volkov et al. 2005).

There are several ways in which the potential for unification among these theories could be realized. For example, one of the key assumptions of the NTB is that all individuals have identical demographic rates, independent of their size. This assumption is biologically unrealistic and contrary to the predictions of the MTE but may be relaxed by integrating the effects of demographic stochasticity with size-dependent demographic rates (O'Dwyer et al. 2009). The size dependence of birth, mortality, and growth rates may then be taken as inputs from the MTE (Savage et al. 2004), and the resulting range of intertwined predictions is much broader than those of either the NTB or the MTE alone. For example, the integration of the two theories allows for the prediction of alternative-currency distributions, such as the species biomass distribution (e.g., Morlon

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et al. 2009), alongside the traditional species abundance distribution.

Conclusions

Advances in science are largely due to the iterative process of induction and deduction, prediction and testing. We believe that greater recognition of the positive role of this interplay in discovery will significantly enhance scientific progress in biology—and in ecology, in particular. Fifty years ago, John Platt (1964) embraced the interplay between induction and deduction and enjoined scientists to pursue a program that he dubbed *strong inference*, which directly links data acquisition to well-posed hypotheses. Strong inference entails following a simple but rigorous protocol of experimental science, efficiently designed to falsify alternative hypotheses. Platt's (1964) paper had a tremendous impact on the practice of experimental science and, more recently, in modeling (e.g., Beard and Kushmerick 2009, Railsback and Grimm 2012, Gowaty and Hubbell 2013). A clarifying discussion of theory types and their roles in discovery, as we have attempted here, may have a similar effect on ecology.

The preeminence of inductive approaches in biology—and in ecology, in particular—is reflected in the fascination with gathering information about the world, as if we were to find understanding in its accumulation. This trend is becoming even more acute in recent times because of technological breakthroughs that are providing unprecedented quantities and varieties of information about organisms, from microbes to trees, and about environments, from local to global scales. The emergence of new subdisciplines, such as bioinformatics and ecoinformatics, along with monumental scientific efforts currently under way, such as the sequencing of complete genomes and metagenomes and the establishment of large-scale and long-term ecological monitoring networks (e.g., the National Ecological Observatory Network), clearly represent important and valuable scientific progress. However, we believe that for such efforts to fully bear fruit, they will need to be both guided by and more directly coupled to the development of efficient theory. Data is of great importance, but without theory, we have only phenomenology and correlation, and we lose the opportunity to yoke the complexity of ecological systems using simple, quantitative principles; as was suggested by Harte (2002), we need a better integration of Newtonian and Darwinian worldviews. With efficient theories, we can harness the potential of empirical data to make more-effective progress in our discipline and provide more-informed answers to the pressing problems facing humanity, such as understanding health, disease, and dysfunction in humans (West 2012). As was clearly stated by the Nobel laureate Sydney Brenner,

> Biological research is in crisis…. Technology gives us the tools to analyze organisms at all scales, but we are drowning in a sea of data and thirsting for some theoretical framework with which to understand it. Although many believe that more is better, history tells us that least is best. We need theory and a firm grasp on the nature of the objects we study to predict the rest. (Brenner 2012, p. 461)

In a similar vein, it can be said that "big data without a big theory to go with it loses much of its potency and usefulness" (West 2013, p. 14).

Understanding biodiversity from a theoretical perspective clearly represents a formidable challenge, but we are optimistic that, by aiming at developing efficient theories, significant progress can be made. We think that efficient theories provide a solid foundation for advancing science in the big data era.

In this article, we argued for clarifying and expanding the role of theory in ecology to accelerate scientific progress, enhance our ability to address environmental challenges, and foster the development of synthesis and theory unification. We focused on the need for developing more-efficient theories in ecology and for the application of such theories to inform experimental design and large-scale environmental-monitoring programs. Our primary goal was to identify characteristics of ecological theories that lead to more-rapid advancement. We showed that more-efficient theories tend to make fewer, simpler, and more-fundamental assumptions and generate a greater number of testable predictions per free parameter than do less-efficient theories. Finally, we argued that ecology will advance much faster if ecologists embrace efficient, approximate theories and improve on them through a process of successive refinements. The development of efficient theories, we contend, provides a robust epistemological framework to foster progress and synthesis in ecology.

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References cited

Allen AP, Gillooly JF, Brown JH. 2005. Linking the global carbon cycle to individual metabolism. Functional Ecology 19: 202–213.

Allen TFH, Tainter JA, Pires JC, Hoekstra TW. 2001. Dragnet ecology—"Just the Facts, Ma'am": The privilege of science in a postmodern world. BioScience 51: 475–485.

Anderson C. 2008. The end of theory: The data deluge makes the scientific method obsolete. Wired (16.07). (5 June 2014; *www.wired.com/science/discoveries/magazine/16-07/pb_theory*)

Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA. 2010. Food web structure and body size: Trophic position and resource acquisition. Oikos 119: 147–153.

Arrhenius S. 1889. Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Säuren. Zeitschrift für physikalische Chemie 4: 226–248.

Bateson W. 1908. The Methods and Scope of Genetics: An Inaugural Lecture Delivered 23 October 1908. Cambridge University Press.

Beard DA, Kushmerick MJ. 2009. Strong inference for systems biology. PLOS Computational Biology 5 (art. e1000459).

Beckerman AP, Petchey OL, Warren PH. 2006. Foraging biology predicts food web complexity. Proceedings of the National Academy of Sciences 103: 13745–13749.

Bollier D. Firestone CM. 2010. The Promise and Peril of Big Data. Aspen Institute.

Box GE. 1976. Science and statistics. Journal of the American Statistical Association 71: 791–799.

Brenner S. 2012. Turing centenary: Life's code script. Nature 482: 461.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85: 1771–1789.

Charnov EL. 1976. Optimal foraging: The marginal value theorem. Theoretical Population Biology 9: 129–136.

Cohen JE. 2004. Mathematics is biology's next microscope only better; Biology is mathematics' next physics, only better. PLOS Biology 2 (art. e439).

Daufresne T, Hedin LO. 2005. Plant coexistence depends on ecosystem nutrient cycles: extension of the resource-ratio theory. Proceedings of the National Academy of Sciences 102: 9212–9217.

Enquist BJ, Economo EP, Huxman TE, Allen AP, Ignace DD, Gillooly JF. 2003. Scaling metabolism from organisms to ecosystems. Nature 423: 639–642.

Enquist BJ, Kerkhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA. 2007. A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. Nature 449: 218–222.

Enquist BJ, West GB, Brown JH. 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. Proceedings of the National Academy of Sciences 106: 7046–7051.

Fisher RA. 1930. The Genetical Theory of Natural Selection. Clarendon Press.

Funtowicz SO, Ravetz, JR. 1993. Science for the post-normal age. Futures 25: 739–755.

Gilbert B, Lechowicz MJ. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences 101: 7651–7656.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. 2001. Effects of size and temperature on metabolic rate. Science 293: 2248–2251.

Gillooly JF, Allen AP, West GB, Brown JH. 2005. The rate of DNA evolution: Effects of body size and temperature on the molecular clock. Proceedings of the National Academy of Sciences 102: 140–145.

Ginzburg LR, Jensen CXJ. 2004. Rules of thumb for judging ecological theories. Trends in Ecology and Evolution 19: 121–126.

Gowaty PA, Hubbell SP. 2013. The evolutionary origins of mating failures and multiple mating. Entomologia Experimentalis et Applicata 146: 11–25.

Gowaty PA, Lennartz MR. 1985. Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. American Naturalist 126: 347–353.

Halley JM, Iwasa Y. 2011. Neutral theory as a predictor of avifaunal extinctions after habitat loss. Proceedings of the National Academy of Sciences 108: 2316–2321.

Harte J. 2002. Toward a synthesis of the Newtonian and Darwinian worldviews. Physics Today 55: 29–34.

———. 2011. Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and Energetics. Oxford University Press.

Harte J, Zillio T, Conlisk E, Smith AB. 2008. Maximum entropy and the state-variable approach to macroecology. Ecology 89: 2700–2711.

Harte J, Smith AB, Storch D. 2009. Biodiversity scales from plots to biomes with a universal species–area curve. Ecology Letters 12: 789–797.

Heidegger M. 1977. Modern science, metaphysics, and mathematics. Pages 247–282 in Krell DF, ed. Martin Heidegger: Basic Writings. Harper and Row.

Hubbell SP. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Jaynes ET. 1982. On the rationale of maximum-entropy methods. Proceedings of the IEEE 70: 939–952.

Kleiber M. 1961. The Fire of Life: An Introduction to Animal Energetics. Wiley.

Kooijman SALM. 2000. Dynamic Energy and Mass Budgets in Biological Systems, 2nd ed. Cambridge University Press.

Krakauer DC, Collins JP, Erwin D, Flack JC, Fontana W, Laubichler MD, Prohaska SJ, West GB, Stadler PF. 2011. The challenges and scope of theoretical biology. Journal of Theoretical Biology 276: 269–276.

Laudan L. 1977. Progress and Its Problems: Towards a Theory of Scientific Growth. University of California Press.

Leibold MA. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76: 1371–1382.

Leigh EG Jr. 2007. Neutral theory: A historical perspective. Journal of Evolutionary Biology 20: 2075–2091.

Leijonhufvud A. 1997. Models and theories. Journal of Economic Methodology 4: 193–198.

Lin Y, Berger U, Grimm V, Huth F, Weiner J. 2013. Plant interactions alter the predictions of metabolic scaling theory. PLOS ONE 8 (art. e57612).

López-Urrutia A, San Martin E, Harris RP, Irigoien X. 2006. Scaling the metabolic balance of the oceans. Proceedings of the National Academy of Sciences 103: 8739–8744.

MacArthur RH, Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51: 1207–1210.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. American Naturalist 100: 603–609.

Marquet PA, Labra FA, Maurer BA. 2004. Metabolic ecology: Linking individuals to ecosystems. Ecology 85: 1794–1796.

May RM. 2004. Uses and abuses of mathematics in biology. Science 303: 790–793.

Miller TE, Burns JH, Munguia, P, Walters EL, Kneitel JM, Richards PM, Mouquet, N, Buckley HL. 2005. A critical review of twenty years' use of the resource-ratio theory. American Naturalist 165: 439–448.

Morlon H, et al. 2009. Taking species abundance distributions beyond individuals. Ecology Letters 12: 488–501.

Nagel E. 1961. The Structure of Science: Problems in the Logic of Scientific Explanation. Harcourt, Brace, and World.

Nisbet RM, Muller EB, Lika K, Kooijman SALM. 2000. From molecules to ecosystems through dynamic energy budget models. Journal of Animal Ecology 69: 913–926.

Nonacs P. 2001. State dependent behavior and the Marginal Value Theorem. Behavioral Ecology 12: 71–83.

[NRC] National Research Council. 2008. The Role of Theory in Advancing 21st-Century Biology: Catalyzing Transformative Research. National Academies Press

O'Dwyer JP, Lake JK, Ostling A, Savage VM, Green JL. 2009. An integrative framework for stochastic, size-structured community assembly. Proceedings of the National Academy of Sciences 106: 6170–6175.

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Peters RH. 1991. A Critique for Ecology. Cambridge University Press.
Pickett STA, Kolasa J, Jones CG. 1994. Ecological Understanding: The Nature of Theory and the Theory of Nature. Academic Press.
Platt JR. 1964. Strong inference. Science 146: 347–353.
Pyke GH. 1984. Optimal foraging theory: A critical review. Annual Review of Ecology, Evolution, and Systematics 15: 523–575.
Railsback SF, Grimm V. 2012. Agent-Based and Individual-Based Modeling: A Practical Introduction. Princeton University Press.
Robinson W, Peters RH, Zimmermann J. 1983. The effects of body size and temperature on metabolic rate of organisms. Canadian Journal of Zoology 61: 281–288.
Rosindell J, Cornell SJ. 2009. Species–area curves, neutral models, and long-distance dispersal. Ecology 90: 1743–1750.
Rüger N, Condit R. 2012. Testing metabolic theory with models of tree growth that include light competition. Functional Ecology 26: 759–765.
Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL. 2004. Effects of body size and temperature on population growth. American Naturalist 163: 429–441.
Scheiner SM, Willig MR. 2008. A general theory of ecology. Theoretical Ecology 1: 21–28.
———. eds. 2011. The Theory of Ecology. University of Chicago Press.
Simberloff D. 2004. Community ecology: Is it time to move on? American Naturalist 163: 787–799.
Sibly RM, Brown JH, Kodric-Brown A, eds. 2012. Metabolic Ecology: A Scaling Approach. Wiley-Blackwell.
Spatz H-C. 1991. Circulation, metabolic rate, and body size in mammals. Journal of Comparative Physiology B 161: 231–236.
Tilman D. 1982. Resource Competition and Community Structure. Princeton University Press.
Tilman D, Hille Ris Lambers J, Harpole S, Dybzinski R, Fargione J, Clark C, Lehman C. 2004. Does metabolic theory apply to community ecology? It's a matter of scale. Ecology 85: 1797–1799.
Volkov I, Banavar JR, He F, Hubbell SP, Maritan A. 2005. Density dependence explains tree species abundance and diversity in tropical forests. Nature 438: 658–661.
West GB. 2012. The importance of quantitative systemic thinking in medicine. Lancet 379: 1551–1559.
———. 2013. Wisdom in numbers. Scientific American 308: 14.
West GB, Brown JH. 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. Journal of Experimental Biology 208: 1575–1592.
West GB, Brown JH, Enquist BJ, 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122–126.
———. 2001. A general model for ontogenetic growth. Nature 413: 628–631.
Wigner EP. 1960. The unreasonable effectiveness of mathematics in the natural sciences. Communications in Pure and Applied Mathematics 13: 1–14.
Williams R. 2010. Simple MaxEnt models explain food web degree distributions. Theoretical Ecology 3: 45–52.

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