1 Introduction

Edward A. Johnson and Yvonne E. Martin

The concept of *ecosystem*, like many ecological concepts that have come down to us from the early developments in ecology, has a rather elusive meaning. A. G. Tansley's (1935) original definition of ecosystem states: "the more fundamental conception is 'as it seems to me' the whole system (in the sense of physics) including not only the organism complex but the whole complex of physical factors we call the environment of the biome—the habitat factors in the widest sense." However, "system" is never defined or further discussed so it is unclear what Tansley and his contemporaries understood it to mean. Did he mean simply that the abiotic and biotic were to be considered together as a unit unlike the more biologically focused concepts of community and biome? Or did he mean a more process-based approach, as in the physics of coupled systems of partial differential equations (i.e., coupled processes)? If the latter, how was this to be accomplished with no governing equations, such as the Navier–Stokes equations based on the conservation of three basic qualities – mass, energy, and momentum? Whatever Tansley meant initially, the ecosystem concept was subsequently used both as a classification of communities, biomes, and their habitat in terms of environmental factors and as nutrient cycles and energy flows through food webs (McIntosh, 1985). Thus, we are left with an incomplete understanding of how the environment is to be connected as a "system" to organisms, populations, communities, and ecosystems.

Recent decades have seen several advances that are contributing to the beginning of this synthesis (e.g., Nealson and Ghiorse, 2001; Hedin *et al.*, 2002). One of the most interesting developments in ecology has been the Metabolic Theory of Ecology (MTE). This theory (West *et al.*, 1997; 1999; Brown *et al.*, 2004; Enquist *et al.*, 2003; 2007) argues that mass conservation, biological mechanics, hydraulics, heat budgets, and thermodynamics can be used to explain the flux of energy, water, and nutrients from cells to ecosystems. This, in turn, explains the empirical scaling evidence for $B = B_o M^{3/4}$ where B is an organism's metabolic rate, B_o is a normalization constant independent of an organism's mass, and M is an organism's mass (West *et al.*, 1997). MTE assumes a hierarchical, self-similar network that delivers energy and nutrients to every organelle in a cell. The final branch of the network is the same size in all organisms and thus defines the branching of the rest of the network. The network is designed to approximate minimum energy dissipation. An individual's metabolic rate is the sum of the fluxes of energy from the chloroplasts and water and nutrients from the roots.

At carrying capacity, Enquist *et al.* (1998) and Savage *et al.* (2004) show that population density is proportional to the inverse of biomass and proportional to individual biomass raised to the $-3/4$ power multiplied by a Boltzmann–Arrhenius function of the form $\exp(-E_p/kT)$ where T is absolute temperature, k is the Boltzmann constant, and $E_p{\sim}0.32$ eV. All of this is, in turn, proportional to the supply rate of limiting resources in the environment. Thus, when holding size and temperature constant, abundance increases proportional to resource supply.

MTE gives a way to connect individual organisms, and thus populations and ecosystems, to the geosciences since the delivery of resources from the environment to individuals involves transport systems in the landscape and atmosphere. Individual organisms are at the nexus of two transport systems: the individual's metabolic (vascular) system delivers nutrients and complex carbon to cells and the geoscience system delivers water, nutrients, and heat to the organism, populations, communities, and ecosystem from the earth's surface and atmosphere. In essence, the two delivery systems provide a means to accomplish Tansley's notion of the ecosystem incorporating both the organisms and their environment.

Ecological stoichiometry (Sterner and Elser, 2002; Frost *et al.*, 2005), in turn, looks specifically at the relative availability of elements at different levels from genes to ecosystems and how changes regulate growth by the Law of Definite Proportions. Element composition is flexible between autotrophs and heterotrophs but most research has been, not surprisingly, directed at the biology. However, the structure of the geophysical processes and their delivery to the organisms, particularly autotrophs and detritivores, is an important part of biogeoscience.

Equally, there have been major advances in hydrology, geomorphology, meteorology, and climatology. Hydrology has a quantitative understanding of the flux equations (e.g., the Richards equation) for subsurface water movement, Penman for evaporation, Penman–Monteith for transpiration, and Manning and Chezy, Darcy, Fick, and others for surface water flow. Eagleson (2002) has developed integrated models that couple energy and water with plant density and vegetation type using a natural selection-type process that leads to optimal vegetation growth and reproduction. Others have attempted similar approaches (e.g., Rodriguez-Iturbe, 2000). Of these, perhaps the most influential has been the development of TOPMODEL by Beven and Kirkby (1979) and its many variations and derivations. This distributed model approach has been influential because it shows how the water budget and flow can be organized and can capture the convergence and divergence in a watershed. The use of a similarity index either as a topographic index or as a wetness index has inspired a large amount of research. These indices have proved to be useful in describing the distribution of plants in a watershed and providing a process-based understanding of why the terrain organization explains the importance of moisture and nutrient gradients in the distribution and composition of vegetation at the watershed scale.

Geomorphology has followed a similar path of development, often closely connected to hydrology because of their common interest in water flow. Geomorphology, in concert with hydrological principles, has developed sediment transport processes and put these together into landscape development (evolution) models based on a general agreement of an Exner-type equation of mass transport of sediments (Paola and Voller, 2005). The fundamental equation simply states that change in landscape height is a function of any tectonic uplift minus the convergence and divergence of different transport equations across the landscape. This approach has been used at the landscape, hillslope, and riparian level, with appropriate modifications depending on the temporal and spatial scales being considered (Martin and Church, 2004).

The success of geomorphology, hydrology, and MTE has been the use of processes (mechanisms) approaches that are understood to be the causes of how a particular phenomenon or set of phenomena operate. These processes can be coupled with or forced by other processes. Coupling here means that one process affects another and vice versa. Forcing refers to a one-directional effect. It is these couplings that ecologists call interactions and that produce the nonlinearity seen in most biogeoscience systems. Furthermore, they use transport or flow rates put together in a conservation equation.

Biogeoscience is by definition interdisciplinary, but it overcomes the common impediment to successful interdisciplinary studies by having an explicit model that requires specific input and understanding of the processes of all disciplines involved. The model is not just a set of boxes with arrows connecting them. The model is the logical calculus that assembles and directs the flow of mass, energy, information, and momentum.

Despite the advancements discussed previously, as of yet there is no agreement as to how to produce a formal biogeoscience viewpoint. For example, molecular biology, in its early stages, adopted a set of viewpoints that came to be called, unfortunately, the “central dogma.” This has always been one of the principal problems of interdisciplinary fields in that they are often asymmetric in viewpoint. For example, landscape development models in geomorphology have incorporated biotic components in the creep, shallow landslide and soil production function. They may even add in a biotic component such as ecological population dynamics or biotic productivity processes but the overall viewpoint is still landscape form, and the problem is considered at the relevant geoscience spatial and temporal scale. The same concern can be laid out for ecological models that incorporate geoscience components.

Consequently, this book is a challenge to develop biogeoscience as the discipline that creates a new combination of disciplines and offers deeper insight into the organization and principles that operate in biotic and abiotic systems. The underlying idea in several of the chapters in this book, often implicitly, is the coevolution of biotic and abiotic processes. This is an old idea put forth in 1913 by Lawrence Henderson in a non-metaphysical approach as the fitness of the environment for life.

The book is divided into four parts. Part I, **Connecting Ecosystem and Geoscience Processes,** gives an in-depth introduction to recent approaches in ecology that provide a rigorous and empirically founded approach that can be used to couple the physical environment and ecology in a system as Tansley might have wished. Part II, **Transport Processes and Conservation Budgets in Biogeoscience** gives the conceptual ideas and basic mathematics of two conservation laws and transport processes that form the basis of many models in the forthcoming chapters. There is also a discussion of how to implement these models using numerical methods. Specifically, there is a

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discussion of continuity, systems, and control volume approaches, differential element approaches, and processes, particularly heat and transport processes. This is followed by Part III**, Coupling Hillslope Geomorphology, Soils, Hydrology, and Ecosystems.** Here the movement of nutrient ions is traced through geochemical and geophysical systems into plants to explain the principal processes and transport equations. This is a slightly different view from the approach to nutrient cycling presented in many terrestrial ecology texts by focusing the discussion within the physical setting and defining the transport rate equations rather than simply showing arrows in box diagrams. Finally, Part IV**, Coupling Fluvial and Aeolian Geomorphology, Hydrology/Hydraulics, and Ecosystems** provides strategies for incorporating current understandings of some physical processes and their connection to ecosystem processes.

References

Beven, K. J. and Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Bulletin*, **24**(1), 43–69, doi:10.1080/02626667909491834.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, **85**, 1771–89.

Eagleson, P. S. (2002). *Ecohydrology: Darwinian Expression of Vegetation Form and Function*. Cambridge: Cambridge University Press.

Enquist, B. J., Brown, J. H. and West, G. B. (1998). Allometric scaling of plant energetics and population dynamics. *Nature*, **395**, 163–5, doi:10.1038/25977.

Enquist, B. J., Economo, E. P., Huxman, T. E. *et al.* (2003). Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–42.

Enquist, B. J., Kerkhoff, A. J., Stark, S. C. *et al.* (2007). A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, **449**, 218–22.

Frost, P. C., Cross, W. F. and Benstead, J. P. (2005). Ecological stoichiometry in freshwater benthic ecosystems: an introduction. *Freshwater Biology*, **50**(11), 1781–5.

Hedin, L., Chadwick, O., Schimel, J. and Torn, M. (2002). *Linking Ecological Biology and Geoscience*. Report to the National Science Foundation 4 April. Workshop at Annual Meeting of the Ecological Society of America August 2001, Madison, WI.

Henderson, L. J. (1913). *The Fitness of the Environment: An Inquiry into the Biological Significance of the Properties of Matter*. New York: The MacMillan Co.

Martin, Y. and Church, M. (2004). Numerical modelling of landscape evolution: geomorphological perspectives. *Progress in Physical Geography*, **28**(3), 317–39, doi:10.1191/0309133304pp412ra.

McIntosh, R. P. (1985). *The Background of Ecology: Concept and Theory*. Cambridge: Cambridge University Press.

Nealson, K. and Ghiorse, W. (2001). *Geobiology. Exploring the Interface between the Biosphere and the Geosphere. A report from the American Academy of Microbiology*. Available at http://academy.asm.org/images/stories/documents/12.GeobiologyReport.pdf.

Paola, C. and Voller, V. R. (2005). A generalized Exner equation for sediment mass balance. *Journal of Geophysical Research*, **110**, F04014, doi:10.1029/2004JF000274.

Rodriguez-Iturbe, I. (2000). Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research*, **36**, 3–9.

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B. and Charnov, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, **163**(3), doi:10.1086/381872.

Sterner, R. W. and Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton University Press.

Tansley, A. G. (1935). The use and abuse of vegetation concepts and terms. *Ecology*, **16**(3), 284–30.

West, G. B., Brown, J. H. and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–6.

West, G. B., Brown, J. H. and Enquist, B. J. (1999). A general model for the structure and allometry of plant vascular systems. *Nature*, **400**, 664–7.

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Part I

Connecting Ecosystem and Geoscience Processes

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2 Toward a General Scaling Theory for Linking Traits, Stoichiometry, and Body Size to Ecosystem Function

Brian J. Enquist, Sean T. Michaletz, and Andrew J. Kerkhoff

2.1 Introduction

> *[W]ithout theory, we have only phenomenology and correlation, and we lose the opportunity to yoke the complexity of ecological systems using simple, quantitative principles.*
>
> Marquet *et al.* (2014)

Scaling has been heralded as one of the major challenges of ecology for more than two decades (Levin, 1992; Ehleringer and Field, 1993). Here, in the spirit of Marquet *et al.* (2014), we provide an overview of a general theory for scaling based on simple quantitative principles. We argue that a focus on scaling also presents some of the more powerful scientific tools available to ecologists facing problems that are unprecedented in both their scope and their stakes. Indeed, one of the central challenges of ecosystem science is to scale up from measurements on individual traits, organisms, and locations to predict the carbon and nutrient pools and fluxes of entire ecosystems.

In terrestrial ecosystems, this challenge requires us to integrate the physiological functioning of plants (e.g., leaf-level photosynthesis) across a collection of heterogeneous individuals (e.g., plants of different species) to understand the functioning of the entire ensemble (e.g., primary productivity) (Ehleringer and Field, 1993; Chapin, 2003). In order to better predict the future of plant communities and ecosystem functioning in response to rising CO_2 and enhanced nitrogen (N) deposition with changes in climate (temperature and precipitation), this sort of understanding must be extended to connect simultaneous changes in multiple biogeochemical cycles.

2.1.1 Why a General Allometric and Metabolic Theory of Ecosystems Is Needed

Recent re-evaluations of global change models indicate that they could greatly benefit from incorporating allometry and ecosystem scaling. Specifically, global change models used to understand how ecosystems respond to climate change frequently do not produce realistic biomass and allometries, which suggests the need for better models of plant growth, nutrient uptake, and mortality (Wolf *et al.*, 2011). Metabolic scaling provides a bridge between leaf-, plant-, and stand-level measurements and the biogeochemical and thermodynamic processes that drive global change models.

In this chapter, we focus on the powerful control that plant size and functional traits exert on ecosystem pattern and process. We use recent insights from the Metabolic Scaling Theory (MST) to scale up from individual plant metabolism, nutrient stoichiometry, and functional traits to ecosystem-level pools and fluxes. The resulting suite of models predicts the scaling of many structural and functional characteristics of plants and whole plant communities that underlie and drive the functioning of terrestrial ecosystems.

Our approach is to develop a zeroth-order efficient theory of ecosystem scaling. Specifically, the theory is grounded in first principles, and makes relatively few assumptions in order to generate a large number of predictions per free parameter (Marquet *et al.*, 2014). Our goal is to provide a baseline for comparison with empirical data and for further theoretical elaboration. We contend that the development and successive refinement of the theory provides a solid foundation for advancing environmental science. Our chapter details the key assumptions and derivations that are necessary for scaling from organisms to ecosystems. While we mainly focus on scaling in plants and autotrophic components of ecosystems, our approach is general and could also be applied to heterotrophs and other ecosystem processes. Further, we show how our framework provides a basis to recast and quantify concepts such as succession and ecosystem resilience.

Here we synthesize this work to provide a more integrated view of MST applied to ecosystems. Recently, several papers have together outlined a general scaling theory for linking functional traits and organism size to ecosystem pattern and process. Our chapter contribution overviews and builds specifically upon the work of West *et al.* (1997), Enquist *et al.* (1998), Kerkhoff *et al.* (2005), Kerkhoff and Enquist (2006, 2007), Enquist *et al.* (2007, 2009), Allen and Gillooly (2009), Elser *et al.* (2010), and Michaletz *et al.* (2014). The resulting synthesis provides a “relatively simple” framework for “scaling up” trait and size measurements, and points to the importance of functional traits, size distributions, and the processes that influence them as fundamental drivers of ecosystem processes. We show that together, this work enables us to connect integrated organismal phenotypes to the structure and function of ecosystems and even provide a basis for concepts such as ecosystem resilience and stability via the lens of scaling.

2.2 Overview of Metabolic Scaling Theory (MST)

An overview of MST for linking traits, stoichiometry, and body size to ecosystem function is given in Figure 2.1. Figure 2.1 shows the key inputs, assumptions, and optimization steps to scale from traits to ecosystems. There are eight key components to the theory, which are discussed in the sections that follow.

2.2.1 The Allometry of Individuals is Central to “Scale Up” from Traits to Ecosystems

As is highlighted throughout this chapter, organismal size is a key variable influencing the magnitude of fluxes and sizes of pools of carbon and nutrients within and across ecosystems. Arguably, body size is one of the most important organismal traits in

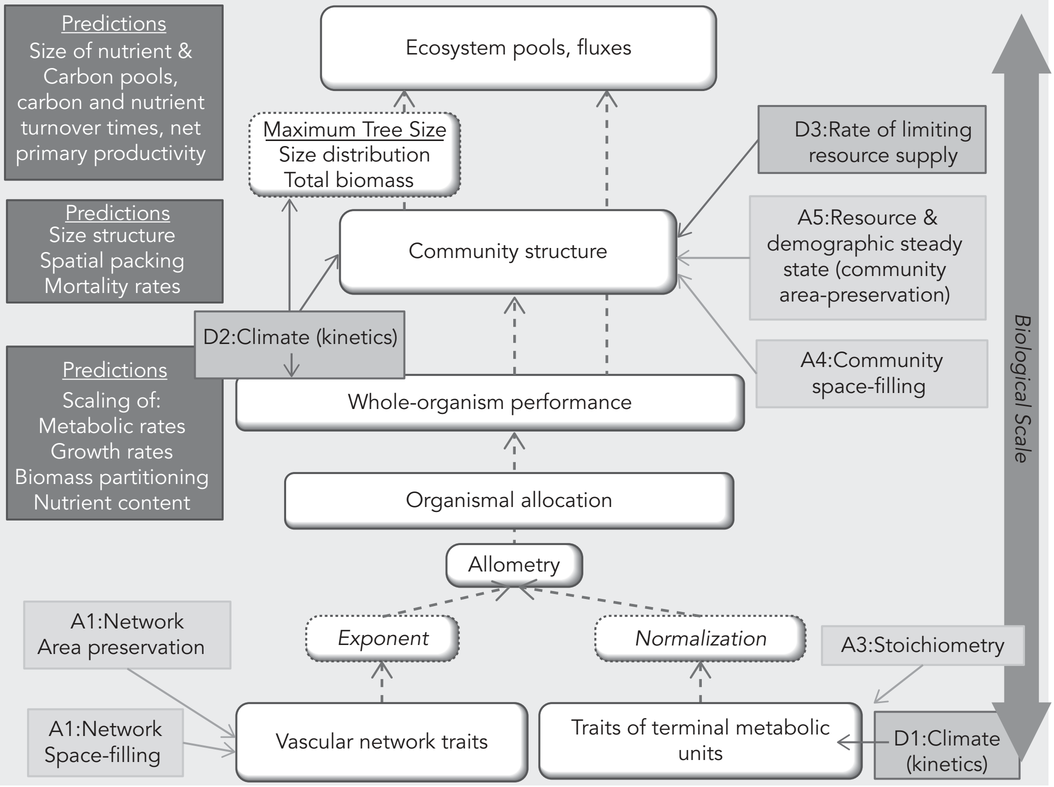

Figure 2.1 Overview of Metabolic Scaling Theory linking traits to ecosystems. The chain of white boxes highlights the central biological focus points of the theory that spans a range of biological scales. The key principles or assumptions of the theory are detailed in the boxes A1-A5. The influence of the abiotic environment and how they enter into the theory are given by boxes D1-D3. Together, the theory generates a series of predictions shown in the 'Predictions' boxes. The central predictions for metabolic scaling theory are from the organismal, community, and ecosystem levels. The dotted boxes are key allometric inputs of the theory that they link pattern and process at different biological scales via the dashed arrows. Note, allometric scaling of individuals links variation in traits all the way to the scaling of ecosystem pools and fluxes.

biology. It influences nearly all aspects of structure and function via scaling relationships with numerous other traits (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Most size-related variation within a defined taxonomic group can be characterized by allometric scaling relationships of the form:

$$Y = Y_0 m^{\alpha} \tag{2.1}$$

where Y is the variable or trait of interest, Y_0 is a normalization constant that may vary across taxa and environments, m is body mass (kg), and α is a mass-scaling exponent. An allometric approach has been a part of the botanical literature for nearly a century (Murray, 1927; Pearsall, 1927). As will be discussed, the allometric approach is currently the subject

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of vigorous and renewed interest stemming primarily from recent advances in mechanistic theory for the origin of *both* scaling exponents α and normalization constants Y_0.

2.2.2 The Origin of Allometric Scaling Exponents Stems from Vascular Network Traits: The West, Brown, and Enquist Model

MST starts with the core theory proposed by West, Brown, and Enquist (1997; West *et al.*, 1999a), the WBE model. The authors of this model argue that organisms have been selected to maximize fitness by maximizing metabolic capacity. They argue that selection has acted to maximize the scaling of whole-organism metabolic rate, B, and that B is limited by the geometry and scaling behavior of the total effective surface area, a, across which nutrients and energy are exchanged with the external or internal environment. Examples include the total leaf area of plants, the area of absorptive gut or capillary surface area of animals, and the total area of mitochondrial inner membranes within cells (West *et al.*, 1999a). West *et al.* (1997) showed that one solution to maximize the scaling of effective surface areas relies on the hierarchical fractal-like nature of resource distribution networks. Examples include the macroscopic branching vascular networks of plants and animals.

There are three core assumptions of the 1997 WBE network model, each of which builds on earlier botanical theories and insights (Enquist and Bentley, 2012). First, at the heart of the model is the hypothesis that the scaling of metabolism is primarily influenced by the geometry of vascular networks that control the scaling of effective surface areas where resources are exchanged with the environment. These surface areas control the transport of resources to metabolizing tissue (West *et al.*, 1997). Second, it is assumed that the normalization (Y_0 of Equation 2.1) is influenced by traits that define the metabolic demand of “terminal metabolic units” (i.e., leaves, capillaries, etc.). Third, it is assumed that the scaling of metabolism and several associated allometric relationships are shaped via natural selection on the scaling and cost of resource uptake (West *et al.*, 1999a). In sum, the core hypothesis of the WBE model is that the scaling of many organismal, anatomical, and physiological traits (e.g., whole-plant carbon assimilation, vascular fluid flow rate, and the number and mass of leaves) is mechanistically determined by natural selection on external branching network geometries (see West *et al.*, 1997).

In addition to the three core assumptions, there are several secondary assumptions that simplify the theory for allometrically ideal plants (Enquist, 2002; Price *et al.*, 2010; Bentley *et al.*, 2013). These include an assumed hierarchical, symmetrical network in which branch radii r (m) and lengths l (m) within a branching level k are assumed identical. At each branching node, a parent branch (level k) splits into n daughter branches (level $k + 1$). All parent branches (N_k) are assumed to have the same number of daughter branches ($N_k + 1$), yielding a constant branching ratio $n_k = N_{k+1}/N_k$ throughout the network. Under this framework, two branching traits govern allometric scaling within plants: the branch radii ratio β (dimensionless) and the branch length ratio γ (dimensionless). The branch radii ratio is defined by a scaling exponent a

$$\beta = \frac{r_{k+1}}{r_k} \equiv n_k^{-a} \tag{2.2}$$