Chapter 7
Biogeochemistry in the Scales

S.A.F. Bonnett, P.J. Maxfield, A.A. Hill, and M.D.F. Ellwood

Abstract Global environmental change is challenging our understanding of how communities as a whole interact with their physical environment. Ideally, we would model the impacts of global environmental change at a global level. However, in order to mathematically model the sheer functional diversity of Earth's dynamic ecosystems, we need to integrate the scales at which these processes operate. Traditionally, studies of ecosystem function have focused on singular ecological, evolutionary or biogeochemical process within an environment. Such studies have contributed much more to the development of our understanding of ecosystem function than those focused on the interactions between biotic and abiotic factors. Ultimately, the productivity of most ecosystems is controlled by the concentration, molecular form and stoichiometry of the macronutrients thereby highlighting the importance of biogeochemical modelling for dynamic ecosystem models across molecular, habitat, landscape and global scales. But as we face unprecedented rates of habitat degradation and species extinctions, few traditional theories can predict in detail how ecosystems will respond to perturbations such as environmental disturbance or shifting weather patterns. To be both statistically and ecologically informative, future ecosystem and biogeochemical models must address complex interactions from atoms to ecosystems. Unless ecological processes are modelled explicitly, significant feedbacks, thresholds and constraints will be missed. The aim of this chapter is to review the state of the art in the use of such models, and suggest new approaches for ecologists, biogeochemists and mathematicians to work together to model the inputs and outputs of entire ecosystems rather than as a series of individual interactions.

Keywords Biogeochemistry • Modelling • Ecosystems • Scales • Global environmental change • Functional diversity

S.A.F. Bonnett (✉) • P.J. Maxfield • A.A. Hill • M.D.F. Ellwood
Department of Applied Sciences, University of the West of England,
Frenchay Campus, Bristol BS16 1QY, UK
e-mail: sam.bonnett@uwe.ac.uk

7.1 Introduction

Biogeochemistry is a multidisciplinary subject dealing with chemical, physical, geological and biological processes that drive the flow of matter and energy within the Earth system. In particular, the biogeochemical cycling of water, carbon (C), nitrogen (N) and phosphorus (P) between abiotic and biotic pools are considered essential to the sustainability of ecosystem functions and the biosphere as a whole. That productivity of most ecosystems is in part controlled by the concentration, molecular form and stoichiometry of the macronutrients highlights the importance of biogeochemical modelling for dynamic ecosystem models across molecular, habitat, landscape and global scales.

Global environmental change is challenging our understanding of how communities as a whole interact with their physical environment. Soils, plants and microbial communities respond to global change perturbations through coupled, non-linear interactions (Sistla et al. 2014) that complicate projecting how global change disturbances will influence ecosystem processes, such as carbon (C) storage and greenhouse gas climate feedback loops. Ideally, we would model the impacts of global environmental change at a global level. However, in order to mathematically model the sheer functional diversity of Earth's dynamic ecosystems, we need to integrate the scales at which these processes operate. Biogeochemical cycles operate at a landscape or global scale but are composed of countless microbial functions that have been experimentally examined using an array of distinct laboratory and field-based experiments at differing scales with differing degrees of explanatory power and system representativeness. Issues of scale are also apparent in mathematical models of complex systems that rely on either a top-down or bottom-up approach. Top-down models can detect general trends at a larger scale but cannot produce specific, detailed predictions such as stability of ecological systems. Bottom-up models require detailed micro-scale process equations that have been evaluated through empirical studies and are therefore inherently complex and impractical for ecological systems. Most models therefore incorporate both top-down and bottom-up into what is known as Middle-out modelling. However, this approach still lacks the resolution from a true 'bottom-up' approach. In ecology, natural microcosms are used as model communities for testing links between biodiversity and ecosystem function. Issues in this field range from a lack of standardization between models, or artificiality in experiments using laboratory-assembled communities, to problems of complexity with experiments based on entire ecosystems. However, carefully chosen natural microcosms offer ecologists a way forward. To be both statistically and ecologically informative, future ecosystem and biogeochemical models must address complex interactions from atoms to ecosystems. Unless ecological processes are modelled explicitly, significant feedbacks, thresholds and constraints will be missed.

The aim of this chapter is to review the state of the art in the use of such models, and suggest new approaches for ecologists, biogeochemists and mathematicians to work together to model the inputs and outputs of entire ecosystems across scales

rather than as a series of individual interactions. Problems of scale in biogeochemistry are similar to those in ecology and mathematics. In this chapter, we will use examples from disciplines where scale has been more fully addressed to the field of biogeochemistry.

7.2 Loose Definitions and the Problems of Scale

7.2.1 Views of Experimental Scale Across Scientific Disciplines

The most accurate way to parameterize a biogeochemical process is to study it at its most irreducible scale. Biogeochemical cycles at the micro-scale are driven by microbial functions (see Sect. 7.3.2), and the establishment of microcosm experiments to investigate the environmental controls over specific biogeochemical processes offer significant explanatory power. Due to the sheer number of different micro-scale processes that are operating within just one biogeochemical cycle, and the vast range of microcosm experiments that have been established to study these processes, it is beyond the scope of this chapter to give a comprehensive overview of the range of studies that have been performed. Some of the most significant microcosms that have been utilized in biogeochemical modelling are discussed below. It should be noted that whilst this approach is most accurate it is by no means necessarily the most effective, as the heterogeneity of the environment can render microcosm manipulation experiments meaningless if sufficient care is not taken to embed them within a wider scientific context. Furthermore, the isolation of microcosms from the wider environment can cause significant problems when interpreting and re-integrating experimental results into their wider context.

Within certain disciplines, mesocosms are favoured as more representative experimental systems. It is difficult to clearly differentiate between microcosms and mesocosms based on a simple definition as there are differences of opinion on what constitutes a microcosm or a mesocosm. A range of different criteria have been used to differentiate mesocosms from microcosms. The three main factors include size, location (field vs. laboratory) and isolation (whether the system is open or closed to external exchange). In addition, these definitions can vary greatly between different scientific areas of study from a definition based purely on scale (e.g. freshwater hydrology) (Cooper and Barmuta 1993) to a definition that also incorporates experimental setting (e.g. soil ecology) and as such, many experimental systems labelled as microcosms in certain scientific disciplines would be considered as mesocosms in other areas of research. A good example is that under certain definitions the Biosphere 2 project in the Arizona desert during the 1980s, which explored the potential use of closed biospheres for Mars colonization, has been categorized as a microcosm despite its size as it was a fully enclosed system (Odum 1984). In the field of soil ecology, Kampichler et al. (2001)

attempted to clarify the definition of mesocosms as systems within the realm of microcosms or 'enclosed model ecosystems' that were a special type of microcosm which allowed for controlled exchange between the model system and the wider environment (Fig. 7.1a). As such mesocosms are therefore the type of microcosm that was most representative of the real world (or macrocosm). One problem with this definition is that it negates the effect of the size of a model system; for example, the interaction between invertebrates and two different plant species within a greenhouse could be considered a mesocosm, whereas the entire greenhouse
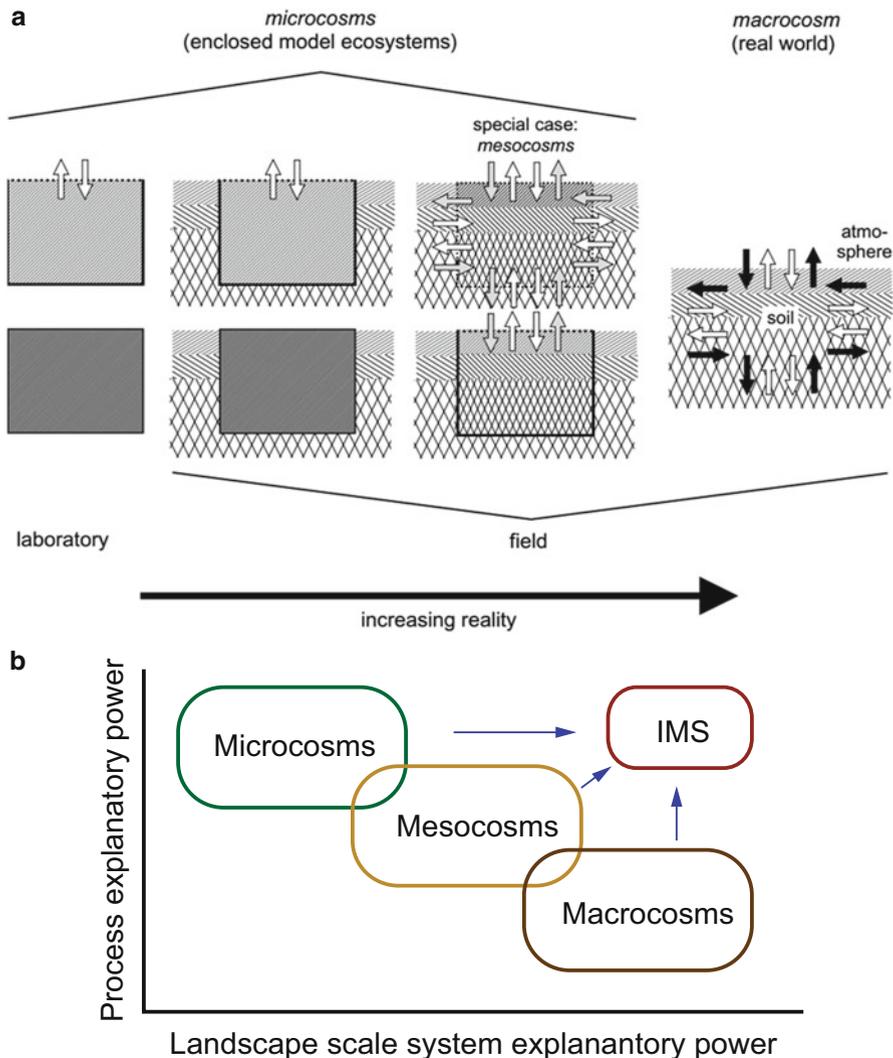
Fig. 7.1 (**a**) Mesocosms as systems. (**b**) Explanatory power of an Idealized Model System

would be classified as a microcosm. In reality, despite attempts to clarify the definition of a mesocosm, the term is used very loosely and is often applied to model systems that are larger in size than those classified as microcosms.

As indicated by the above proposal, a macrocosm is representative of the real-world system and as such is not enclosed and places no restriction on the free movement of nutrients and organisms (as would be the case with microcosms, and to a degree mesocosms). In terms of scale, experimental results from macrocosm experiments are far easier to relate to global biogeochemical cycles. However, in terms of explanatory power, the precision of macrocosm experiments to explain changes to discreet processes within complex systems can be limited, a fact not clearly recognized by Kampichler et al. (2001).

Figure 7.1a shows mesocosms as systems within the realm of microcosms or 'enclosed model ecosystems' that are a special type of microcosm which allows for controlled exchange between the model system and the wider environment (Kampichler et al. 2001); Fig. 7.1b shows the explanatory power of an idealized model system (IMS).

7.2.2 Problems of Experimental Scale

Irrespective of the precise definition of microcosm, mesocosm and macrocosm, it is apparent that manipulation experiments within microcosms offer the highest degree of explanatory power for discreet biogeochemical processes, whereas experimental macrocosms are far more powerful and representative of biogeochemical cycles at the landscape scale. Thus, an idealized model system (IMS) would encapsulate the explanatory power of both of these experimental settings (Fig. 7.1b).

The challenge is to identify ideal model systems (whether micro-, meso- or macrocosms) that can best bridge the gap between accurately explaining specific biogeochemical processes, whilst encapsulating these within a broader suite of interconnected processes that is more representative of the operation of a biogeochemical cycle at the landscape scale.

7.3 Mathematical Modelling Approaches

7.3.1 Top-Down and Bottom-Up Modelling

Traditionally, two alternative modelling methodologies based on the top-down and bottom-up approaches, respectively, have been used in describing complex systems cf. Noble (2003). In the top-down methodology, the approach begins with a high-level functional model of the entire system and then successively replaces each functional block with a model of the mechanism that implements it. The obvious

advantage of this approach is the ability to detect general trends in the system at every stage without requiring every possible interaction to be modelled. In the context of ecosystems, this had been a widely implemented approach that has led to a substantial increase in our understanding of the spatial and temporal scales of biophysical interaction at both global and regional scales, e.g. Moore et al. (2004), Soberón (2010). Mathematical modelling on an ecological macro-scale usually relies on modern and stochastic control theory (Astrom 2006), optimization theory (Lasdon 2011) and parameter estimation (Aster 2011). In essence, these approaches attempt to encapsulate a generalized system through macro-scale data, where the exact model is not known. However, due to its inherent 'black box' approach which averages out the mechanisms of lower level components, a top-down methodology does not tend to produce specific, detailed predictions. Another potential issue lies in its ability to accurately model the stability of ecological systems in a changing environment as a top-down approach tends to create a self-regulating model which relies heavily on recreating macro-scale data, and thus tends to focus on stability to environmental perturbation, removing the effects of potential destabilizing lower level components.

In the bottom-up methodology, the global state of all the components is assumed to be impossible to obtain, so the approach begins with the properties of the component parts and their interactions, and higher level processes are constructed by assembling these detailed components. Micro-scale modelling relies heavily on mean-field techniques such as statistical mechanics, master equations and dynamical systems theory (Gaspard 2005). In essence, these approaches recreate individual physical interactions through well-defined models (i.e. basic first principles), and then combine them to attempt to encapsulate higher level interactions. Although it is clear that this approach has the potential to include all interactions of a system, it is usually impractical to manage the computational complexity of a fully encompassing, bottom-up approach for most ecological systems.

7.3.2 Middle-Out Modelling

Mathematical modelling on the meso-scale adopts a 'middle-out' approach, which starts at an intermediate level of scale and reaches out to link with larger and smaller scale components. This can be implemented using a combination of mathematical approaches form both top-up and bottom-down methodologies and can potentially encapsulate the lower level effects of a system, without suffering from over generality, see e.g. Allen and Fulton (2010), Creutzig et al. (2012).

At any scale, whether macro, micro or meso, mathematical models rely on conceptually derived equations, which are parameterized and evaluated through empirical studies. Intuitively, to maximize the effectiveness of a model in addressing the hypothesis being tested, it should be constructed at an appropriate level of complexity and data availability to support it, cf. Noble (2003). Existing models can certainly be used (in any of the approaches), but they should always be

assessed as to their usefulness in their current state, and be pliable to revision. 'Therefore rather than slaving ourselves to a single approach, we should consider a balanced combination of all three (top-down, bottom-up and middle out) approaches and focus on the following criteria; a good model should be, descriptive (represents the available data), integrative (demonstrate how elements interact), explanatory (provide biological insight)' (Allen and Fulton 2010).

It is important to note that to develop a truly representative mathematical model of any ecological system, the dialogue between the modellers and practitioners needs to be substantial. Without context and statistical data for verification, any model would have no validity, and similarly, without modelling expertise to construct a model at the most applicable level, context and statistical data will provide limited predictive benefits.

7.3.3 Example of Biogeochemical Integration of Top-Down, Bottom-Up and Middle-Out Modelling

Peatland C dynamics are a subject of great current interest as they are intrinsically linked with the atmospheric concentration of methane (CH_4), a potent greenhouse gas. Due to the heterogeneity and widespread distribution of natural wetlands, accurately modelling C fluxes from peatlands has been problematic. Net soil C flux is predominantly controlled by soil hydrology, and thus approaches to integrate and model the global impact of peatland C emissions have been based on a top-down modelling approach linked with the soil hydrological cycle.

Whilst this approach has proven effective at integrating global C flux, there are a number of uncertainties linked with a lack of knowledge of the geographical distribution and interannual variability of CH_4 emissions from natural wetland ecosystems. Unfortunately, many of the processes governing CH_4 exchange between ecosystems and the atmosphere are poorly constrained on the global scale. Measurements of localized C emissions have indicated a number of both temporal and areal discrepancies with observations. There are a range of reasons for these inaccuracies, but one major factor is the lack of accurate vegetational model components, which are not captured by top-down approaches. Typically, biogeo-chemical processes linked with CH_4 exchange have been considered as one process linked with wetland emissions, when in reality a number of processes contribute to the net flux and estimates of global emissions, which have only been calculated from simple parameterizations (e.g. Kaplan (2002)).

Bottom-up or inversion modelling approaches have been far more widely applied in dynamic global vegetational models, which provide a versatile platform for studying the interactions between vegetation and C cycling. In recent years, attempts have been made to formulate similar 'bottom-up' emission models for natural wetlands (Zhuang et al. 2004; Wania et al. 2010), incorporating soil thermal dynamics, peatland hydrology, and peatland-specific plant functional types into a

dynamic global vegetation model. It is hoped that the development of these models will increase the explanatory power of global models of peatland C flux, but many are still at a relatively early developmental stage.

Spahni and co-workers (2011) have attempted an intermediate model of global wetlands through combining a 'bottom-up' model of the biogeochemical cycle of the land biosphere with two 'top-down' models of atmospheric inversions, incorporating atmospheric chemistry and CH_4 emission transport. To constrain this 'middle-out' approach, both local emissions (flux data) and global observations (satellite data) were incorporated and estimated outputs correlated with real-world observations (Spahni et al. 2011). Whilst this approach offers improvements over previous estimates, which have broadly characterized all natural terrestrial CH_4 sources as 'wetlands', the model still lacks the necessary resolution that would be obtained from a true 'bottom-up' approach.

7.4 How Do We Model Complex Ecosystems?

7.4.1 Biodiversity

Biodiversity is also a multidisciplinary subject, dealing with many species, a wide range of evolutionary relationships, and a multitude of ecological interactions. Ecologists attempting to study biodiversity must therefore by definition consider more than one species at a time. To do this, ecologists often use natural microcosms (Srivastava et al. 2004) as model communities for testing the effects of metacommunity theory or the links between biodiversity and ecosystem function (Ellwood and Foster 2004). Such microcosm studies combine the advantages of small size, short generation times, contained structure and hierarchical spatial arrangement with the authenticity of field studies: natural environmental variance, and realistic species combinations with shared evolutionary histories (Srivastava et al. 2004). An important distinction between biology and ecology is that—for ecologists—the model system is often the environment, or the community, rather than a specific organism.

Biologists make extensive use of organisms as model systems. Classic examples include the bacteria *Escherichia coli* for molecular biology, the pipid frog *Xenopus* for developmental biology, the fruit fly *Drosophila melanogaster* for animal genetics and the thale cress *Arabidopsis thaliana* for plant genetics. Such biological models have proven to be powerful research tools because they are tractable, general and realistic (Levins 1984). With the notable exceptions of *Tribolium* beetles for population ecology, or Darwin's finches for evolutionary ecology, ecologists have overcome their lack of model systems by developing their own model ecological communities by using natural microcosms. Ecologists have also had to overcome the problem of many of their model systems meeting some but not all of the criteria necessary for future experiments to effectively standardize and

utilize previous results. For example, laboratory-assembled communities of protozoa which enable rapid, precise and replicated experiments (Lawler 1998; Jessup et al. 2004) have been criticized for their artificiality (Carpenter 1996). Experiments based on entire ecosystems represent the other extreme: whilst entire natural communities are highly realistic, their large size and vague dimensions usually necessitate poorly replicated, long duration, overly simplified studies. This has led to heated debate among ecologists focused on the issue of replication versus realism (Schindler 1998). However, carefully chosen natural microcosms offer ecologists a way forward; in other words, natural microcosms allow ecologists to study biodiversity in a similar manner to the way biologists study genetics or developmental biology using model organisms. However, ecological model systems (natural microcosms) must satisfy the same criteria as model organisms which, although they do not correspond completely to the systems that they represent, must be similar enough to be useful. For example, the nematode *Caenorhabditis elegans* is clearly different from humans. However, both have eukaryotic genomes, meaning that the small nematode genome could be a useful model for understanding how the larger human genome functions. Again this raises the issue of scale: in biology, where model systems are used for theory testing and development, the theory may need to be parameterized for other systems (e.g. evolution theory developed based on experiments with *Drosophila* needs to be adjusted for selection coefficients and modes of inheritance before it can be applied to other organisms (Srivastava et al. 2004)). Likewise, rates and processes observed in ecological model systems may need to be scaled up to describe the natural ecosystem.

7.4.2 Biogeochemistry

Terrestrial ecosystem biogeochemistry models have been used to simulate the productivity and carbon storage of a diversity of ecosystems (Baisden and Amundson 2003). Models have been used to evaluate ecosystem management (Riley and Matson 2000) and to predict or understand the response of ecosystems to global changes including nitrogen deposition (Holland et al. 1997), CO_2 fertilization (Paustian et al. 1996), land-use change (Parton et al. 1996) and global climate change (Schimel et al. 1996). Traditionally, process-based and data-driven biogeochemical models have been conceptualized, parameterized, calibrated and validated using datasets from monitoring and experimental networks (e.g. Rothamsted Experimental Station established in 1843, the International Biological Program (1970–1975), Hubbard Brook Ecosystem Study began in 1964, Long Term Ecological Research Network (LTER) started in 1980, the global network of flux towers (FluxNet) (Evrendilek 2012)). The related literature contains numerous process-based (mechanistic) biogeochemical models such as BIOME-BGC (BioGeochemistry Cycles) (Running and Hunt 1993), CENTURY (Parton et al. 1987), TEM (Terrestrial Ecosystem Model) (Raich et al. 1991) and DNDC (Denitrification-Decomposition) (Li et al. 1992) as well as data-driven (empirical)

models such as multiple regression models, artificial neural networks and geostatistical models. The Global Change and Terrestrial Ecosystems Soil Organic Matter Network (GCTE-SOMNET) database (online at http://saffron.rothamsted.bbsrc.ac.uk/cgi-bin/somnet/) contains metadata on over 30 current operational soil organic matter (SOM) models (see Falloon and Smith 2009).

An SOM model simulates either the decomposition of SOM as whole or as soil organic carbon (SOC), N or other nutrient and may be part of a larger model package, e.g. RothC (Coleman et al. 1997) and CENTURY models (Falloon and Smith 2009). Most models are process based as they focus on the processes mediating the movement and transformations of matter or energy and usually assume first-order rate kinetics (Falloon and Smith 2009). Food web models simulate C and N transfers through a food web of soil organisms (Falloon and Smith 2009) explicitly accounting for different trophic levels or functional groups of biota in the soil. Many studies have used SOM models to assess SOM dynamics at the regional, national and global scales such as in the post-Kyoto Protocol debate on the ability of terrestrial biosphere to store carbon (IPCC 2000). The RothC SOM model is concerned only with soil processes and is therefore not linked to plant production. The CENTURY SOM model, however, is part of a larger ecosystem model that simulates crop, grass and tree growth and the effects of different management practices on both plant production and SOM (Falloon and Smith 2009). Both models have been adapted to simulate N and S dynamics, but only CENTURY simulates P dynamics. RothC has been applied to databases of soil and land use and climate in the UK (Falloon et al. 2006). Upscaling the results from process-based soil–plant models to assess regional SOC change and sequestration potential is a great challenge due to the lack of detailed spatial information, particularly soil properties (Luo et al. 2013). Meta-modelling can be used to simplify and summarize process-based models and significantly reduce the demand for input data and thus could be easily applied on regional scales. For example, Luo et al. (2013) used the pre-validated Agricultural Production Systems SIMulator (APSIM) to simulate the impact of climate, soil and management on SOC at reference sites across Australia's cereal-growing regions under a continuous wheat system. They developed a simple meta-model to link the APSIM-modelled SOC change to primary drivers and used the meta-model to assess SOC sequestration potential and the uncertainty associated with the variability of soil characteristics. Sistla et al. (2014) provide an example of an ecosystem-scale model (SCAMPS—Stoichiometrically Coupled, Acclimating Microbe–Plant–Soil model) that simulates the dynamic feedbacks between above-ground and below-ground communities that affect their shared soil environment. This model has shown that incorporating dynamically interacting microbial and plant communities into ecosystem models might increase the ability to link ongoing global change field observations with macro-scale projections of ecosystem biogeochemical cycling in systems under change.

7.4.3 Potential Solutions (Principle of Model Systems in Ecology)

Whilst ecological model systems (natural microcosms) may not always represent direct analogues of other ecological systems, in the way that *C. elegans* can model the human genome, they can serve as scaled analogues (Petersen et al. 2003; Schneider 2001). In this approach, rates are scaled to system size: for example, marine ecologists have derived empirical relationships relating productivity to mesocosm size. When scaled up to coastal systems, the mesocosms provide remarkably good predictions for productivity (Petersen et al. 2003). Natural microcosms may also be used for screening potential hypotheses before resources are committed to experiments in larger, slower systems such as forests or lakes. To this end, only rough concordance between the model and target systems is needed, such that effects seen in the model system (e.g. rock pools, pitcher plants or epiphytes) are likely to be worth investigating in the target system (e.g. lakes or forests). However, as well as screening hypotheses, natural microcosms have been used extensively as systems for testing and developing theory.

7.5 A Way Forward for Integrating Biogeochemical and Ecosystem Models Using Natural Microcosms

7.5.1 Mathematical Models

The key issue when modelling complex ecosystems is not necessarily the number of components to be modelled, but how they interact. Systems which can be successfully modelled by considering averaged effects can be entirely represented using a bottom-up approach. However, most ecosystems contain non-linear interactions, making it impossible to simply reduce the system's behaviour to the sum of its parts (combining separately modelled biogeochemical processes for example). Feedback loops can play a significant role in these non-linear interactions (Kell and Knowles 2006), where the outputs of the system impact onto its inputs. An understanding of such loops and their effects is central to building and understanding models of complex systems (Milo et al. 2002).

The potential way forward to address this crucial issue for the mathematical modelling of ecosystems is to explore natural microcosms as a simulation for the larger system. By modelling a microcosm, for which the inputs and outputs can be controlled experimentally, an understanding of its interaction mechanisms can be developed. The possibility of experimental control allows for the significant testing of model accuracy, which would not be possible in larger uncontrollable systems. Once a model is constructed, substantial hypothesis testing can then be performed, allowing one to analyse the effects of manipulating experimental conditions in the model without having to perform multiple experiments. Even if the microcosm is a

Table 7.1 Modelling considerations for simulating microcosms

| Dimension or feature	Possible choices	Comments
Stochastic or deterministic	*Stochastic*: Monte Carlo methods, or statistical distributions	Phenomena are not of themselves either stochastic or deterministic; large-scale, linear systems can be modelled deterministically, whilst a stochastic model is often more appropriate when nonlinearity is present
	Deterministic: equations, e.g. ordinary differential equations (ODEs), partial differential equations (PDEs)	
Fully quantitative versus partially quantitative versus qualitative	*Qualitative*: direction of change modelled only, or on/off states (Boolean network)	Reducing the quantitative accuracy of the model can reduce complexity greatly and many phenomena may still be modelled adequately
	Partially quantitative: fuzzy models	
	Fully quantitative: ODEs, PDEs	
Predictive versus exploratory/ explanatory	*Predictive*: specify every variable that could affect outcome	If a model is being used for precise prediction or forecasting of a future event, all variables need to be considered. The exploratory approach can be less precise but should be more flexible, e.g. allowing different control scenarios to be tested
	Exploratory: only consider some variables of interest	

heavily idealized version of the larger ecosystem, it can suggest areas of investigation (such as regions of instability) that would not have been predictable utilizing a system which is uncontrollable experimentally.

When deciding on the type of mathematical model for the microcosm, there are several strategic choices to be made when deciding what may be most appropriate to simulate the physical system. Table 7.1 (based on Table (1.2) of Kell and Knowles (2006)) suggests the three main mathematical considerations which should be made for this simulation.

When applying these approaches to complex systems, the key factor is a model system that enables the delineation of specific interactive processes in order that the interactions can be characterized. We will consider the possibilities through examples taken from ecological and biogeochemical studies.

7.5.2 Ecology Models

Natural microcosms, the model systems of ecology, are small, discrete habitats containing natural communities of organisms (Srivastava et al. 2004). Examples include the animal communities of aquatic *Phytotelmata* (e.g. pitcher plants, bromeliads) and of non-aquatic epiphytes such as birds nest ferns (Ellwood and Foster 2004; Fig. 7.2). Other natural microcosms include the microarthropod communities of moss patches and crustacean communities in rock pools. Natural
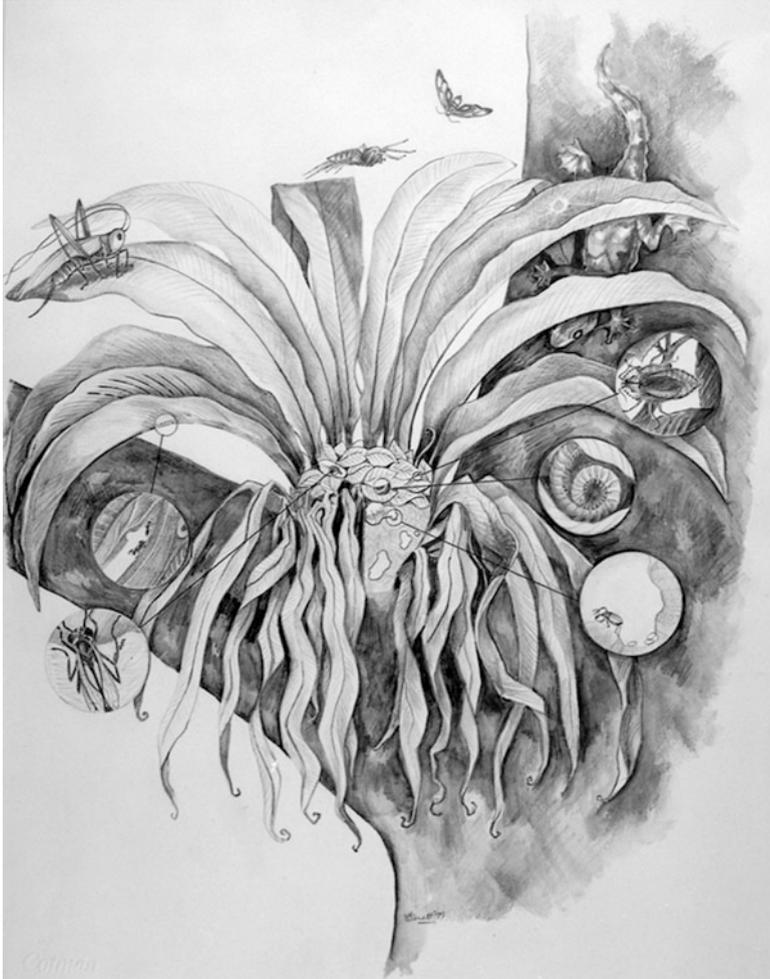
Fig. 7.2 Bird's nest ferns are islands of biodiversity in a sea of canopy

microcosms are, by definition, small habitats, facilitating replicated experimentation and allowing for robust statistical analysis. Another feature of natural microcosms is that they are contained habitats with clearly delineated arenas for species interactions. Compared with food webs and communities in continuous habitats, natural microcosms represent ideal experimental units allowing the precise delineation of communities, without problems of artificial inclusion or exclusion of animals (Krebs 1996). On the contrary, the physical boundaries between natural microcosms and their surrounding habitat—for example, air or water—can aid in the removal or addition of species (Kneitel and Miller 2002; Fincke et al. 1997). In some cases, entire communities can be assembled from scratch (Ellwood et al. 2009; Miller et al. 2002a; Srivastava and Lawton 1998; Bengtsson 1989; Levine

2001). However, natural microcosms are not closed systems; eventually, all experimental manipulations will be altered by, for example, the emergence of adult insects, oviposition of eggs and colonization by microorganisms (Srivastava et al. 2004). However, these dispersal processes can be valuable in their own right for answering questions about metacommunity dynamics.

Owing to the relatively small size of natural microcosms, the organisms inhabiting them are also small: insects and smaller arthropods (e.g. amphipods, mites and collembola), annelids, protozoa (e.g. rotifers, ciliates and flagellates) and bacteria. Small size (<5 mm) and rapid generation times allow studies of long-term effects to be completed in a matter of weeks or months (Ellwood et al. 2009; Bengtsson 1989; Miller et al. 2002b). In contrast, even when studies are conducted over several years, experiments with larger organisms often capture only transient dynamics (Tilman 1989).

Understanding the scale and importance of ecological processes is a key goal in ecology. The usefulness of natural microcosms will therefore depend on their physical, chemical and biological properties—in relation to the theoretical questions being asked. In terms of scale and process, natural microcosms are ideal for testing two very active areas of ecological theory: the effects of neighbouring communities on species richness and the effect of declining diversity on ecosystem function. It is this second area which is most relevant to the current discussion. In the face of mass extinctions and global environmental change, it is critical that we understand the effects of species loss on the stability of ecosystem functions. Previous studies have focused on manipulation of monotrophic communities such as grassland plants in 1 m^2 plots; whilst such studies are useful for developing theory, we must move beyond these singular interactions to multitrophic food webs of coevolved species experiencing real patterns of species loss (Duffy 2003; Srivastava 2002). It is here that ecology's model system (the natural microcosm) has potential to play a particularly important role in diversity–function research programmes. Local extinctions can be easily (and ethically) induced by changes in the habitat; and the effects of changes to species diversity on ecosystem function can be monitored over multiple generations and through multiple trophic levels.

An example of local extinction being experimentally induced is by the fragmentation of moss patches before tracking the effects on microarthropod biomass (Gonzalez and Chaneton 2002). This study noted a lag effect between species extinctions and declining microarthropod biomass because it was the rare microarthropod species that were the first to disappear, which had minimal impact on community biomass. Community biomass was most affected by the declining abundance of common species as they neared extinction. This highlights the fact that real extinctions can occur long before the effects are observed in the functioning of ecosystems (Gonzalez and Chaneton 2002). Rock pools offer another natural microcosm for diversity–stability studies. An open question in ecology is whether increased species diversity can reduce variability in ecosystems (Kampichler et al. 2001). By using natural variation in the faunal diversity of different rock pools, positive diversity–stability relationships have been shown at the levels of both populations and communities. These relationships were, however, only observed

when the confounding effects of environmental variation (Kaplan et al. 2002) or habitat specialization (Kell and Knowles 2006) were removed. Tropical epiphytes, another example of natural microcosms, have been used to tease apart the effects of environmental gradients and ecological succession on the relative importance of interspecific competition versus stochastic processes instructuring rainforest arthropod communities (Ellwood et al. 2009). In all of these examples, natural microcosms have provided genuine ecosystems in which to test theory developed from mathematical models or synthetic communities, revealing how theory can be modified to incorporate real patterns in extinctions or community assembly.

Possibly, the ecology of natural microcosms will be dominated by non-equilibrium dynamics caused by dispersal, local extinction and spatial structure. For example, drought and treefalls have catastrophic effects on the fauna of individual treeholes (Kneitel and Miller 2002) but minor effects on the larger forest ecosystem. Diurnal variation in the temperature of rock pools exceeds that in large bodies of water (Krebs 1996). However, such processes are important in all communities, regardless of size, and most taxa in natural microcosms have short generation times. Once disturbance and dispersal are scaled by generation times, there may be little difference between natural microcosms and larger systems (Lawler 1998). Spatial effects could similarly be scaled by body size of organisms. This type of biological scaling has rarely been attempted but is a fertile area for future research (Srivastava et al. 2004).

7.5.3   Biogeochemical Models

Whilst biological model systems are relatively widespread, model systems have received less emphasis in ecological and biogeochemical studies. As discussed above, a 'model system' is a system—which could be a gene and its regulators, an organism or an ecosystem—that displays a general process or property of interest, in a way that makes it understandable. Oceanic islands are a good example of such a system that is relatively large in scale. They are useful as analogues of model systems as they are identical to natural ecosystems in many ways but are (naturally) clearly bounded and therefore simpler than other similar systems. Even though oceanic islands are not as controllable as would be in an ideal model system, islands can be used a scaled analogue of the wider ecosystem, similar to the way *C. Elegans* can represent a scale analogue of the human genome (as discussed in Sect. 7.3.1). Thus, an island is an integrated, natural example of a larger complex system where the natural functioning of the island ecosystem can shed light on the functioning of much more complicated systems, whilst retaining a full suite of natural functions. Whilst islands simplify the wider natural environment (similarly to a microcosm), realistic processes and dynamics are retained because they are complete, real systems. In contrast, artificial microcosms are not always authentic as they can fail to include many ecosystem processes. Furthermore, the use of

Fig. 7.3 Hawaiian archipelago

islands as analogues of model systems is that their unique setting can isolate specific variables, which can enable unique insights to be made.

One of the most well-known island systems used in biogeochemical models is the Hawaiian archipelago (Fig. 7.3). A range of ecological studies within these bounded tropical forests have revealed a number of scientific principles that are also relevant to larger comparative ecosystems, which can commonly be hidden by the added complexity of larger systems. The main factors that ensure Hawaii is an effective model system include unique geographical isolation, and the constancy and predictability of a number of environmental variables. In the case of Hawaii, a well-studied aspect of the island's geological setting is the effect that substrate age (from 300 to 4.1 Myr) has on the island's ecology and habitats. Thus, process studies in this environment offer the rare opportunity for naturally isolating and characterizing specific biogeochemical processes within a real complex ecosystem setting. Vitousek (2002) used this approach to identify the crucial limiting nutrients within the system, and the inputs and potential influence of external nutrient sources including marine aerosols and of Aeolian dust transported from central Asia. Crucially, it is not that Hawaii uniquely receives more of these external inputs than other tropical forests, but that the model system allows a much clearer characterization of specific phenomena within an ecosystem that inform in general settings much more widely (e.g. old, deeply leached soils depend on arid ecosystems hundreds to thousands of miles away for nutrient inputs).

The approach ecologists have taken (see previous section) for modelling biodiversity across landscapes using natural mesocosms is a good example for biogeochemists to follow. Benton et al. (2007) recently argued that small-scale experiments using 'model organisms' in microcosms or mesocosms can be a useful approach for apparently intractable global problems, such as ecosystem responses to climate change or managing biodiversity through the design of nature reserves.

Increasing evidence from microcosm studies suggest that both the rate and magnitude of important below-ground processes, such as decomposition of organic matter and resulting nutrient release, depend not only on the biomass of the decomposer community but are also influenced by the detrital food web (Setälä et al. 2005). However, evidence at the species level in microcosms and field experiments shows that there is considerable functional redundancy in soil species, suggesting little effect on rates of general decomposition processes with loss of species (Hunt and Wall 2002; Wall et al. 2005). As long as there is a functional group available to perform a particular role in a given ecosystem function, it may not matter whether there are many or a few species within the functional group. This contrasts markedly with experimental results from above-ground (plant) communities (Tilman et al. 1996). However, key species may sometimes strongly affect a range of soil-based ecosystem processes, including decomposition pathways, carbon and nutrient cycling, hydrologic pathways and the maintenance of soil structure, all of which interact in biogeochemical cycles and models (Wall et al. 2005). However, few studies exist in which the relationship between species diversity and system level process has been explicitly studied (Setälä et al. 2005). In an example of a microcosm study, Setälä and McLean (2004) manipulated the species richness of soil saprophytic fungi and showed that decomposition activity (CO_2 production) was only weakly related to the number of fungal species.

Whilst there is evidence suggesting the fundamental importance of structural complexity and diversity of detrital food webs in affecting below-ground processes, and ultimately, net primary production, species diversity per se may not be a significant factor controlling soil processes and plant growth. Most ecosystem-level models ignore microbial community dynamics, yet still do an adequate job of describing large-scale flows of carbon and nitrogen (Schimel 2001). Estimates indicate that less than 5 % of microbial species or less than 1 % of operational taxonomic units (OTUs) in soils are described, and we are therefore only beginning to connect identity to function (Wall et al. 2005). Indeed, an individual species may have an identifiable effect on function in microcosm experiments but at the mesocosm or macrocosm scale, species richness results in multiple indirect interactions making observations impossible. Evidence of significant horizontal gene transfer between prokaryotes has brought into question the definition and existence of bacterial species (O'Donnell et al. 2005). Horizontal gene transfer in prokaryotes and eukaryotes is correlated with gene function with marked differences in observed transfer frequencies between 'informational genes' (e.g. the 16S rRNA signature molecule for diversity) and 'operational genes' (e.g. those involved in amino acid synthesis). This 'complexity hypothesis' implies that sequence data from 'informational genes' may not be truly representative for studying diversity–function relationships in soil where function (phenotype expression) is largely coded for by operational genes (O'Donnell et al. 2005). However, the advent of next-generation sequencing, microarrays and other environmental genomic, metabolomic and proteomic technologies is improving our understanding of diversity and function relationships. A better understanding of functional redundancy in natural mesocosms could lead to simplification and advancement of complex landscape and global biogeochemical models.

7.6 Summary

Ecosystems are in part controlled by the concentration, molecular form and stoichiometry of the macronutrients, highlighting the importance of biogeochemical modelling for dynamic ecosystem models across molecular, habitat, landscape and global scales. Global environmental change is challenging our understanding of how communities as a whole interact with their physical environment. In order to mathematically model the functional diversity of Earth's dynamic ecosystems, we need to integrate the scales at which these processes operate. Microbial functions have been experimentally examined using an array of distinct micro, meso and macrocosm laboratory and field-based experiments with differing degrees of explanatory power and system representativeness for given scales. Issues of scale are also apparent in mathematical models of complex systems that rely on either a top-down or bottom-up approach. In ecology, natural microcosms are used as model communities for testing links between biodiversity and ecosystem function but through careful selection, natural mesocosms may offer a new way forward for biogeochemical modelling as scaled analogues or mathematical simulations that can also be used for testing and developing theory. In conclusion, the natural microcosm has potential to play a particularly important role in diversity–function research programmes linking biogeochemistry, ecology and mathematics across multiple scales.

References

Allen JJ, Fulton EA (2010) Top-down, bottom-up or middle-out? Avoiding extraneous detail and over-generality in marine ecosystem models. Progr Oceanogr 84:129–133

Aster R (2011) Parameter estimation and inverse problems. Academic, Waltham

Astrom KJ (2006) Introduction to stochastic control theory. Dover, New York

Baisden WT, Amundson R (2003) An analytical approach to ecosystem biogeochemistry modelling. Ecol Appl 13:649–663

Bengtsson J (1989) Interspecific competition increases local extinction rate in a metapopulation system. Nature 340:713–715

Benton TG, Solan M, Travis JMJ, Sait SM (2007) Micocosm experiments can inform global ecological problems. Trends Ecol Evol 22:516–521

Carpenter SR (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680

Coleman K, Jenkinson DS, Crocker GJ et al (1997) Simulating trends in soil organic carbon in long-term experiments using RothC-26.3. Geoderma 81:29–44

Cooper SD, Barmuta LA (1993) Field experiments in biomonitoring. In: Rosenberg DM, Resh VH (eds) Freshwater biomonitoring and Benthic macroinvertebrates. Chapman & Hall, New York, pp 399–441

Creutzig F, Popp A, Plevin R, Luderer G, Minx J, Edenhofer O (2012) Reconciling top-down and bottom-up modelling on future bioenergy deployment. Nat Clim Change 2:320–327

Duffy JE (2003) Biodiversity loss, trophic skew and ecosystem functioning. Ecol Lett 6:680–687

Ellwood MDF, Foster WA (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature 429:549–551. doi:10.1038/nature02560

Ellwood MDF, Manica A, Foster WA (2009) Stochastic and deterministic processes jointly structure tropical arthropod communities. Ecol Lett 12:277–284. doi:10.1111/j.1461-0248.2009.01284.x

Evrendilek F (2012) Modeling of spatiotemporal dynamics of biogeochemical cycles in a changing global environment. J Ecosyst Ecogr 2, e113. doi:10.4172/2157-7625.1000e113

Falloon P, Smith P (2009) Modelling soil carbon dynamics. In: Kutsch WL, Bahn M, Heinemeyer A (eds) Soil carbon dynamics. Cambridge University Press, Cambridge

Falloon P, Smith P, Bradley RI et al (2006) RothC UK: a dynamic modelling system for estimating changes in soil C at 1-km resolution in the UK. Soil Use Manag 22:274–288

Fincke OM, Yanoviak SP, Hanschu RD (1997) Predation by odonates depresses mosquito abundance in water-filled tree holes in Panama. Oecologia 112:244–253

Gaspard P (2005) Chaos, scattering and statistical mechanics. Cambridge University Press, Cambridge

Gonzalez A, Chaneton EJ (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. J Anim Ecol 71:594–602

Holland EA, Braswell BH, Lamarque JF, Townsend A, Suleman J, Muller JF, Denterer F, Brasseur G, Levy H, Penner JE, Roelofs GJ (1997) Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. J Geophys Res Atmos 102(D13):15849–15866

Hunt HW, Wall DH (2002) Modelling the effects of loss of soil biodiversity on ecosystem function. Glob Chang Biol 8:33–50

IPCC (2000) Land use, land-use change, and forestry. A special report of the IPCC. Cambridge University Press, Cambridge

Jessup CM, Kassen R, Forde SE, Kerr B, Buckling A, Rainy PB, Bohannan BJM (2004) Big questions, small worlds: microbial model systems in ecology. Trends Ecol Evol 19:189–197

Kampichler C, Bruckner A, Kandeler E (2001) Use of enclosed model ecosystems in soil ecology: a bias towards laboratory research. Soil Biol Biochem 33:269–275

Kaplan JO (2002) Wetlands at the Last Glacial Maximum: distribution and methane emissions. Geophys Res Lett 29(6):3-1–3-4

Kell DB, Knowles JD (2006) The role of modeling in systems biology. In: Szallasi Z, Stelling J, Periwal V (eds) System modeling in cellular biology: from concepts to nuts and bolts. MIT Press, Cambridge, pp 3–18

Kneitel JM, Miller TE (2002) Resource and top-predator regulation in the pitcher plant (Sarracenia purpurea) inquiline community. Ecology 83:680–688

Krebs CJ (1996) Population cycles revisited. J Mammal 77:8–24

Lasdon LS (2011) Optimization theory for large systems. Dover, New York

Lawler SP (1998) Ecology in a bottle: using microcosms to test theory. In: Resetarits WJ Jr, Bernando J (eds) Experimental ecology: issues and perspectives. Oxford University Press, New York, pp 236–253

Levine JM (2001) Local interactions, dispersal, and native and exotic plant diversity along a California stream. Oikos 95:397–408

Levins R (1984) The strategy of model building in population biology. In: Sober E (ed) Conceptual issues in evolutionary biology. Cambridge University Press, Cambridge, pp 18–27

Li C, Frolking S, Frolking TA (1992) A model of nitrous oxide evolution from soil driven by rainfall events: 1. Model structure and sensitivity. J Geophys Res Atmos 97:9759–9776

Luo Z, Wang E, Bryan BA, King D, Zhao G, Pan X, Bende-Michl U (2013) Meta-modelling soil organic sequestration potential and its application at regional scale. Ecol Appl 23:408–420

Miller TE, Horth L, Reeves RH (2002a) Trophic interactions in the phytotelmata communities of the pitcher plant, Sarracenia purpurea. Community Ecol 3:109–116

Miller TE, Kneitel JM, Burns JH (2002b) Effect of community structure on invasion success and rate. Ecology 83:898–905

Milo R, Shen-Orr S, Itzkovitz S, Kashtan N, Chklovskii D, Alon U (2002) Network motifs: simple building blocks of complex networks. Science 298:824–827

Moore JK, Doney SC, Lindsay K (2004) Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. Glob Biogeochem Cycles 18:4028

Noble D (2003) The future: putting Humpty-Dumpty together again. Biochem Soc Trans 31:156–158

O'Donnell AG, Colvan SR, Malosso E, Supaphol S (2005) Twenty years of molecular analysis of bacterial communities in soils and what have we learned about function? In: Bardgett RD, Usher MB, Hopkins DW (eds) Biological diversity and function in soils. Cambridge University Press, New York, pp 44–56

Odum EP (1984) The mesocosm. BioScience 34(9):558–562

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. Soil Sci Soc Am J 51:1173–1179

Parton WJ, Ojima DS, Schimel DS (1996) Models to evaluate soil organic matter storage and dynamics. In: Carter MR, Stewart BA (eds) Structure and organic matter storage in agroecosystems. Advances in soil science. CRC, New York, pp 421–448

Paustian K, Elliott ET, Peterson GA, Killian K (1996) Modelling climate, CO_2 and management impacts on soil carbon in semi-arid agroecosystems. Plant and Soil 187:351–365

Petersen JE et al (2003) Multiscale experiments in coastal ecology: improving realism and advancing theory. Bioscience 53:1181–1197

Raich JW, Rastetter EB, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Moore B, Vörösmarty CJ (1991) Potential net primary productivity in South America: application of a global model. Ecol Appl 1:399–429

Riley WJ, Matson PA (2000) NLOSS: a mechanistic model of denitrified N_2O and N_2 evolution from soil. Soil Sci 165:237–249

Running SW, Hunt ER (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer JR, Field CB (eds) Scaling physiological processes: leaf to globe. Academic, San Diego, pp 141–158

Schimel JP (2001) Biogeochemical models: implicit vs. explicit microbiology. In: Schulze ED, Harrison SP, Heimann M et al (eds) Global biogeochemical cycles in the climate system. Academic, San Diego, pp 177–183

Schimel DS, Braswell BH, Makeown R, Ojima DS, Parton WJ, Pulliam W (1996) Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochem Cycles 10:677–692

Schindler DW (1998) Replication versus realism: the need for ecosystem-scale experiments. Ecosystems 1:323–334

Schneider DC (2001) Spatial allometry: theory and application to experimental and natural aquatic ecosystems. In: Gardner RH et al (eds) Scaling relations in experimental ecology. Columbia University Press, New York, pp 113–153

Setälä H, McLean MA (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia 139:98–107

Setälä H, Berg MP, Jones TH (2005) Trophic structure and functional redundancy in soil communities. In: Bardgett RD, Usher MB, Hopkins DW (eds) Biological diversity and function in soils. Cambridge University Press, New York, pp 236–249

Sistla SA, Rastetter EB, Schimel JP (2014) Responses of a tundra system to warming using SCAMPS: a stoichiometrically coupled, acclimating microbe-plant-soil model. Ecol Monogr 84:151–170

Soberón JM (2010) Niche and area of distribution modeling: a population ecology perspective. Ecography 33:159–167

Spahni R, Wania R, Neef L, van Weele M, Pison I, Bousque P, van Velthoven P (2011) Constraining global methane emissions and uptake by ecosystems. Biogeosciences 8 (6):1643–1665. doi:10.5194/bg-8-1643-2011

Srivastava DS (2002) The role of conservation in expanding biodiversity research. Oikos 98:351–360

Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am Nat 152:510–529

Srivastava DS, Kolasa J, Bengtsson J, Gonzalez A, Lawler SP, Miller TE, Munguia P, Romanuk T, Schneider DC, Trzcinski MK (2004) Are natural microcosms useful model systems for ecology? Trends Ecol Evol 19:379–384

Tilman D (1989) Ecological experimentation: strengths and conceptual problems. In: Likens GE (ed) Long-term studies in ecology. Springer, New York, pp 136–157

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720

Vitousek PM (2002) Oceanic islands as model systems for ecological studies. J Biogeogr 29:573–582

Wall DH, Fitter AH, Paul E (2005) Developing new perspectives from advances in soil biodiversity research. In: Bardgett RD, Usher MB, Hopkins DW (eds) Biological diversity and function in soils. Cambridge University Press, New York, pp 3–27

Wania R, Ross I, Prentice IC (2010) Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1.3.1. Geosci Model Dev 3 (2):565–584. doi:10.5194/gmd-3-565-2010

Zhuang Q, Melillo JM, Kicklighter DW, Prinn RG, McGuire AD, Steudler PA, Felzer BS, Hu S (2004) Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: a retrospective analysis with a process-based biogeochemistry model. Global Biogeochem Cycles 18, GB3010