

The Biogeography of Microbial Communities and Ecosystem Processes: Implications for Soil and Ecosystem Models

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3.5.1 Predicting environmental responses of soil processes

We are entering a period of rapid and pronounced environmental change. Understanding how this change will influence soil communities is essential for accurate prediction of future climate, biogeochemical cycles, and human well-being. Such reliable prediction is the fundamental test of scientific understanding (i.e. can we use knowledge of underlying mechanisms to predict accurately how phenomena change across space and time). Predicting how soils respond to environmental change will be central to adaptive management of ecosystems, given our reliance on soils for sustained food production, water purification, carbon storage, and nutrient retention. This ability to predict with certainty how environmental change will influence soil processes requires mechanistic understanding of how soils work. Developing this mechanistic understanding is perhaps the “Grand Challenge” for soil ecologists if we are to advance our basic understanding of soils and apply this knowledge to effective environmental management.

Mechanistic understanding improves our confidence in predictions of the future that extrapolate observed relationships between regulatory variables (e.g. temperature) and process rates (e.g. soil respiration) (Reynolds *et al.* 2001). Perhaps paradoxically, there may be much less agreement in predicted outcomes between ecosystem models when more mechanistic understanding is included.

Although we might have “faith” that the true ecosystem response lies somewhere within the predictions from the models, predictions from mathematical models that rely on empirical (or statistical) relationships may be much more similar. Empirical models comprise the majority of ecosystem models used to predict soil biogeochemical processes (see Box 3.5.1). Our confidence in the predictions by empirical models of future ecosystem response relies on the assumption that observations of regulatory variable-process rate relationships hold across space and time (Reynolds *et al.* 2001). So, we are faced with a dilemma. Do we develop and employ mechanistic models that may be more accurate but also more uncertain or do we follow the more traditional approach, relying on empirical models that may predict ecosystem processes with more certainty but less accuracy? There is likely no single right answer to this question when developing models to predict how ecosystems will respond to environmental change. A family of models that covers this continuum of approach—between empiricism and mechanism—will permit us to determine where model predictions agree. Where they disagree likely indicates the greatest uncertainty in model predictions, and it is in addressing these disagreements that future research might yield most insight.

The soil ecology community predominately relies on more empirical models and this reliance has repercussions beyond the discipline and can influence global policy. For example, the soil submodels

Box 3.5.1 Comparison of mechanistic and empirical models

Most commonly it is the perspective of an individual, not model structure, which determines whether a model is classed as mechanistic or empirical. In reality, these two terms distinguish opposite ends of a continuum. Mechanistic models are designed to explain outcomes with formulations that represent actual physical, chemical, and biological processes, such as increased catalytic rates of respiratory enzymes as temperature increases. Empirical models are often referred to as “correlative or statistical models” and are designed to predict—as opposed to explain—outcomes. To enable this prediction, formulations are used that best describe relationships between two measured variables, such as temperature and soil respiration rates, with no necessary regard for the underlying mechanism. Empirical models are typically parameterized—at least in the

ecological and biogeochemical sciences—using regression relationships derived from data. When we extrapolate these relationships we are assuming they are robust across space and time, even if the physical, chemical, and biological conditions under which the data were collected differ markedly to those in the new location or time for which we make the prediction. With mechanistic models the argument is that—if we understand and represent the underlying mechanisms accurately in the model formulations—then we can make robust predictions for other locations and times. The challenges with mechanistic models are thus twofold: we have to both understand the mechanisms and then be able to represent them accurately when formulating models. These challenges are not trivial, and may delimit the very edges of our understanding of soils.

embedded within the coupled atmosphere–biosphere carbon cycle models used by the Intergovernmental Panel on Climate Change (IPCC) to predict future climate are largely empirical. The IPCC has high uncertainty in some of the assumptions inherent to the embedded soil models, and this leads to uncertainty in climate prediction. For example, there is marked uncertainty as to whether warmer temperatures will lead to the net loss of soil carbon that then generates a positive feedback to global warming (Denman *et al.* 2007). Given the vast published literature on this topic (e.g. Davidson & Janssens 2006; Bradford *et al.* 2008; Allison *et al.* 2010), it is unsettling that we—the soil ecology community—cannot reach agreement on the question of how soil carbon stocks will respond to temperature change, especially given the societal need for resolution. One plausible reason for this disagreement is that biological and ecological mechanisms are typically represented implicitly—not explicitly—in soil models (Bahn *et al.* 2010).

3.5.2 Misplaced physics envy in soil models

Soils are not merely physical and chemical entities, yet we generally model soil processes by assuming they can be represented simply as a product of physics and chemistry. This assumption is not

actually at odds with the fact the models are usually also implicitly rooted in fundamental biological understanding. But what it does mean is that we assume we can omit biology (and within “biology” we include ecology) from the models as a force that could shape responses of soil processes to perturbation. That is, we assume physicochemical controls on soil processes are unaffected by phenotypic or genotypic changes in biota, and biotic interactions, across time and space. Yet at the same time we’re aware that soil organisms—at least in part—mediate many soil processes (e.g. respiration and nitrification). The omission of biology from soil models is perhaps best illustrated through example. Take the approach of using a single, first-order decay equation to estimate how the rate of soil carbon decomposition varies with temperature (e.g. Kirschbaum 2004; Knorr *et al.* 2005). The equations are typically parameterized by data collected across a large range in one or more controlling factors, in this case temperature. Variation in temperature is generated by use of broad spatial gradients (e.g. elevation, latitude) or short temporal changes (e.g. incubators, daily variation). Using these statistical relationships to project how soil carbon decomposition responds to environmental change assumes that the biology is invariant across space and time. In other words, understanding of biological mechanism is

unnecessary for accurately predicting how soil processes will respond to environmental change.

Social scientists are well aware of the shortcomings of using principles from classical physics to predict response of human (and hence biological) systems to perturbation (for an excellent commentary see Bernstein *et al.* 2000). Application of principles such as 1) invariance, 2) probability, and 3) simplicity “promise” a level of certainty in prediction that will not be realized where biological processes influence outcomes. With invariance (1) we assume that history does not matter, with responses a fixed function of controlling variables. In human systems, we can understand that “experience” influences decision-making, so outcomes of perturbations differ if a person is naïve or familiar with the event. Soil organisms may not exhibit higher learning but directional selection in gene frequencies provides a mechanism whereby history and past conditions can influence outcomes of perturbations. For example, the development of resistance of microbial populations chronically exposed to antibiotics influences whether populations are extirpated when antibiotics are applied in acute doses. Likewise, microbial communities that have developed under conditions of moisture stress are likely to have accumulated osmoregulants and other physiological strategies to cope better with future drought events.

With probability (2) the assumption is that all individuals are equally likely to respond identically—hence we can predict rates of radioactive decay even if we can’t predict which atom actually undergoes decay. Yet we know that soil organisms sort out along an r to K life-history continuum (Fierer *et al.* 2007)—or at least exhibit metabolically alert strategies—so whereas r -selected individuals might rapidly increase their intrinsic population growth rates if resources are made available, K -selected organisms will display a lagged response. In practice this could mean that, for example, the decomposition of labile versus more recalcitrant carbon pools could exhibit different temperature responses if microbes with r versus K strategies, respectively, decompose these different carbon pools. Admittedly, there is burgeoning debate about whether we can assume—at least when explaining species abundance distributions—that species

exhibit identical life-history strategies (e.g. Clark 2009; Rosindell *et al.* 2010). Yet recent work highlights that those patterns attributed to this assumption of identical strategies can equally well be explained by statistical artefact introduced when dealing with large data sets, and that the same data sets used to make this “probability argument” can actually only have arisen through complex (i.e. ecological niche) processes (Warren *et al.* 2011). In other words, the assumption of probability might accurately predict patterns (or process rates) that we observe, but for the wrong mechanistic reasons.

Finally, with simplicity (3) the assumption is that only a few variables influence outcomes and that these variables can be measured with accuracy. Yet even if simplicity holds then phenomena that should be predictable from deterministic parameters can be inherently unpredictable because of spatial complexity. For example, Bernstein *et al.* (2000) observe that the arrangement of balls on a pool table, following their break, should be predictable from a few physical laws. Yet, when we introduce spatial complexity across different pool tables, such as in the exact lay of the table, the nap of the felt, the curvature of each ball, and so on, we introduce fine-scale complexity that means the resulting distribution of the balls is unpredictable (approximating one that is random). The development of the sub-field of “spatial soil ecology” is testament to the fact that rates of biogeochemical processes in soils are influenced—at least to some degree—by spatial complexity (Ettema & Wardle 2002). For example, the presence of anaerobic microsites may not be captured in models with insufficient spatial complexity, meaning that denitrification might be observed but not predicted for soils that are, on average, aerobic.

No soil ecologist would argue that soils follow the rules of invariance, probability, or simplicity. When we assume these rules apply (i.e. through our modeling efforts that “black box” the biology) we recognize that we are abstracting reality. There are two primary reasons for such an abstraction. The first is pragmatic; you have to start somewhere and the best place to start is with simplifying assumptions. Mathematical models force us to formalize our understanding, highlighting to us the assumptions we make, the evidence supporting these

Box 3.5.2 Messages soil ecologists can communicate when we “black box” soil communities

When we, as a community of soil ecologists, submit mathematical models of soil biogeochemical processes to the wider scientific and policy community we communicate important information about the state-of-the-art of our understanding of how soil communities influence ecosystem function. The majority of our models “black box” soil communities and, in doing so, they do not account for how changes in soil communities across time or space might influence biogeochemical pools and fluxes. These models are embedded in management and policy efforts of global significance, such as projections of future climate. It is therefore imperative that we make a statement concerning how the wider scientific community should interpret the black boxing of soil communities. We consider we have three main options and that numbers two and three likely best represent the state of our science:

1. Black boxing is valid because the effect of soil communities on ecosystem function aggregates to a common, invariant response across environmental variation (e.g. temperature) in time and space. You can have high certainty in the projections of our models.
2. We black box because the complexity of how soil communities influence function is beyond our current modeling capabilities. This is the best we have, so be skeptical of the certainty of our model projections.
3. We black box because it is the simplest assumption we can make, and we recognize the need for research to test this assumption robustly because it might be wrong. This is the best we have, so be skeptical of the certainty of our model projections.

assumptions, and the need for empirical research to test them. In this regard they provide the most effective tool for integration of theory and empirical research to advance basic understanding. They also permit us to make predictions that can inform policy and adaptive management. Even though we are aware of limitations in our knowledge and measurements, such modeling efforts must be favored over inaction. What we have to be careful with is the message we present to those outside of the soil ecology community—i.e. do we wish to communicate that we recognize our abstraction is likely wrong, or that we think the abstraction is a fair generalization (see Box 3.5.2)? If the latter then this gives us the second reason for abstracting the biology in soil models: we believe the abstraction is valid. That is, we can reliably predict how ecosystem processes will respond to a perturbation because biological phenomena aggregate to a common, invariant response (e.g. Rosindell *et al.* 2010). This is the rationale often invoked for black boxing the biology in soil and ecosystem models, and the rationale is presented under the hypotheses of functional redundancy, similarity, and equivalence. Although these hypotheses have been applied to soil communities in an inclusive framework encompassing both animals and microorganisms (e.g.

Andrén & Balandreau 1999), we restrict our discussion to bacteria and fungi (collectively “microbes”). This is not to minimize the potential role of animals in shaping ecosystem processes (e.g. Schmitz 2008) but because in modeling soil and ecosystem processes, we typically discuss the microbes as the primary agents of biogeochemical transformations.

3.5.3 Functional redundancy, similarity, equivalence, and biogeography

Terms in ecology are often used to convey multiple meaning (e.g. consider “niche” when used by Grinnell vs. Hutchinson), which creates confusion. The terms functional redundancy, similarity, and equivalence are applied interchangeably in ecology to comparisons between species, between communities, and as properties of a community (Reserits & Chalcraft 2007; Allison & Martiny 2008; Strickland *et al.* 2009). Following Allison and Martiny (2008), “functional redundancy” is the ability of one microbial taxon to carry out a process at the same rate as another under the same environmental conditions. Species loss can occur without change in function if a community has many taxa that are functionally redundant (Fig. 3.5.1). The same can even be true where taxa are not functionally redundant but their

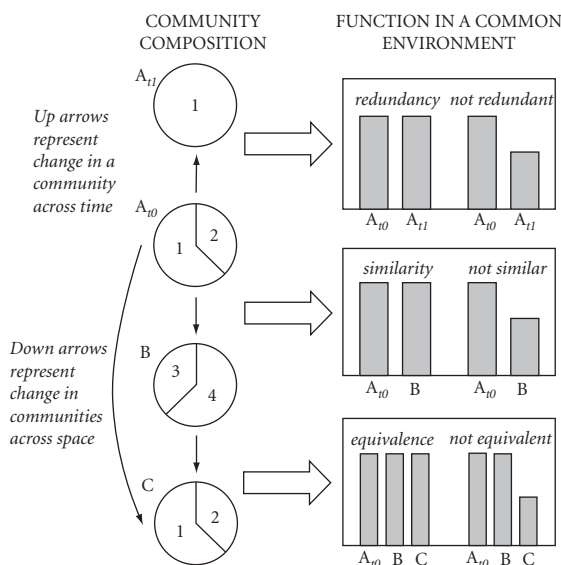


Figure 3.5.1 Organization across space and time of the terms functional redundancy, similarity, and equivalence when applied to the biogeochemical processes performed by soil microbial communities. Circles represent communities. Shown within each community is the abundance of each taxon (denoted by the numbers 1–4). For community A, a perturbation that shifts the community composition from time zero to time one (through the loss of taxon 2) but does not alter function—in a common environment—supports the hypothesis of redundancy. In comparing different communities (i.e. across space), the hypothesis of similarity is supported when a change in community composition does not alter function; again assuming the comparison is made in a common environment. The hypothesis of equivalence is less restrictive: there is no burden on the investigator to demonstrate a difference in richness, relative abundance, or phylogenetic structure of taxa in an assemblage (collectively referred to as “composition”) to falsify the hypothesis of equivalence, as there is with redundancy and similarity. Instead, a change in for example phenotypic abundance or physiology within a community—without a necessary change in composition—that alters function in a common environment disproves the hypothesis of functional equivalence. Note that in the figure community C can be classed as functionally non-equivalent to both communities A₀ and B, despite having the same composition as A₀.

collective positive and negative responses to disturbance sum to zero net change in aggregate community function: a so-called “portfolio effect.” Allison and Martiny (2008) define “functional similarity” as the ability of two microbial communities to carry out a function at a similar rate under the same environmental conditions, regardless of differences in community composition. The same criterion of common environmental conditions applies to the definition of functional equivalence (sensu Strickland *et al.* 2009), which is the ability of two microbial communities to carry out a functional process at a similar rate, regardless of differences in community composition, physiology, and/or interaction strengths (see Fig. 3.5.1). In this regard, mechanisms underlying functional similarity are a subset of the mechanisms that might drive functional equivalence. That is, similarity refers to the functional effects of shifts in the taxonomic or phylogenetic

composition of communities, whereas equivalence includes the effects of these shifts and/or 1) changes in the phenotypes (including physiology) of the members of a community, and 2) interactions between individuals. Indeed, Allison and Martiny (2008) restrict use of the terms redundancy and similarity to differences in microbial community composition—where they define “composition” as the richness, relative abundance, and phylogenetic structure of taxa in an assemblage. The definition of functional equivalence is much less restrictive.

Here we focus on functional equivalence because we argue “equivalence” (as opposed to redundancy or similarity per se) is the assumption that is made when using soil models, that black box microbial communities, to predict ecosystem process rates. This is best illustrated by example. Imagine two identical communities: one maintained at a constant temperature and one to which we apply a step

increase in temperature. With temperature increase we would expect enhanced physiological rates (e.g. respiration) because of the positive effect of temperature on the rate of enzyme-mediated reactions. Although physiological rates increase, there is not necessarily a change in organismal physiology and if temperature is returned to control conditions then both communities function equivalently. If the temperature treatment alters community composition, then functional redundancy and similarity are only falsified if the compositional change elicits functional differences when control conditions are restored. If functional differences are observed, say through altered physiology (e.g. shifts in enzyme expression), but there is no measurable change in composition, then there is no evidence to reject the redundancy and similarity hypotheses. However, functional equivalence is falsified. Allison *et al.* (2010) incorporate microbial physiology in a soil model and show that by doing so respiration rates in warmed soils, that are returned to ambient conditions on reaching steady-state, are lower than in control soils given the role of physiological response in reducing microbial biomass and extracellular enzyme abundance.

In subsuming the hypotheses of redundancy and similarity, the hypothesis of functional equivalence has broad application to the question over whether the biogeography of microorganisms can be causally linked to variation in ecosystem function. The two overarching factors that shape biogeographic patterns are environment and history. The role of environment is nicely summarized by Baas Becking's evocative paradigm that "everything is everywhere, *but*, the environment selects" (de Wit & Bouvier 2006). The mechanism underlying this hypothesis is global dispersal where propagules of all microbial taxa are ubiquitously dispersed across the globe (Martiny *et al.* 2006). Growth and survival is then determined (non-randomly) by environmental conditions and there is at least some evidence that this factor structures microbial assemblages at coarse levels of phylogenetic resolution (e.g. Fierer & Jackson 2006; Lauber *et al.* 2009). In soil models, we can reliably black box microbial communities if Baas Becking's hypothesis can be extrapolated to function and if we can identify the key environmental factors driving the microbial process of interest. Under such a scenario, we can still recognize that

microbial communities exert proximate control on ecosystem process rates. Yet, because the environment ultimately shapes the community, its role is implicit in the model when we regulate the function of the black box with environmental variables such as temperature and moisture.

We only require the second part of Baas Becking's hypothesis to hold (i.e. "the environment selects [function]") for microbial communities to exert only proximate control on ecosystem processes. This is pertinent to the "black-box debate" because evidence is accumulating that microbes are not all globally dispersed—at least not at rates that obviate the role of historical contingencies in shaping communities—even at spatial scales of only a few meters (Ramette & Tiedje 2007). Even with limited dispersal we can, however, still invoke a number of properties of microbial communities that might serve to homogenize microbial functional potentials across communities; namely high taxon abundance and diversity, rapid evolutionary adaptation, and prolific growth rates (Allison & Martiny 2008; Green *et al.* 2008). We can apply the same arguments to justify disbelief in the functional equivalence hypothesis. Under limited dispersal, these same properties of microbial communities might facilitate rapid genetic differentiation. When populations are isolated geographically, they can solve the same survival problem different ways, which might have different functional implications. Such phenomena introduce contingencies in biological systems that make them "unique" (e.g. Jacob 1977; Levin 1998). In this regard they differ fundamentally from physical and chemical entities in that the rules change (evolution) across time, making replication difficult and history fundamental to understanding their current structure and function. Arguments that we can ignore the identity of microbial taxa (e.g. Falkowski *et al.* 2008) and instead focus on the 500 or so enzyme systems underpinning biogeochemical cycling—have not considered that many enzyme systems (e.g. aerobic respiration) are conserved across the domains of life (Hochachka & Somero 2002) but yield markedly different process rates under the same environmental conditions. Indeed it is now well supported that rates of biogeochemical processes such as litter decomposition, measured in the field, are not only a product of the environment

but also adaptation/specialization of the soil community (Ayres *et al.* 2009).

The question that remains is how to test the hypothesis of functional equivalence if we are to justify a microbial-explicit modeling approach. Before reviewing approaches in the next section, we justify the methodological advantage of testing for functional equivalence, as opposed to redundancy or similarity. The advantage is that to test for equivalence there is no requirement to demonstrate differences in microbial community composition. When attempting to falsify functional redundancy or similarity there is the requirement to prove shifts in the structure of microbial communities are associated with shifts in function. This is not trivial—the structure of microbial communities can be analyzed at many different levels of resolution (from the phylum to the strain level), and we do not know which level of phylogenetic resolution is most closely related to function. And with macro-organisms, such as angiosperms, we now know that different genotypes within a single population can markedly influence ecosystem process rates (Whitham *et al.* 2008). Such a genetic shift in the composition of soil communities is unlikely to be detected even with the most advanced molecular techniques available, given that the researcher—before quantifying the genotypic diversity of a population—must first identify the taxon within the many thousands present. There are numerous other issues that complicate the association of community shifts with functional shifts, including microbial dormancy (who is active and when), horizontal gene transfer, and the fact that we often lack a fundamental understanding of which taxa are likely responsible for a specific process. So, if we follow philosophical arguments that a scientific hypothesis must be falsifiable, the methodological issue of being able to demonstrate difference in composition could be used to question the validity of even posing the hypotheses of functional redundancy and similarity for soil communities.

3.5.4 Experimental tests of functional equivalence

Reed and Martiny (2007) comprehensively evaluate three approaches used to test whether there is a

necessary relationship between microbial communities and ecosystem function. They focus on approaches that consider “whole communities” (i.e. those that we find extant at field sites). The three approaches have increasing power to tease out causal relationships between microbial communities and function. The first approach is long-term environmental manipulation. These types of studies identify correlative relationships between microbial communities and function, such as the predominance of more *r*-selected phylotypes under N fertilization (e.g. Ramirez *et al.* 2010). Common garden experiments, where a microbial community is manipulated through environmental treatment at a common location, permits short-term investigation of links between microbial communities and function. In the longer-term the change in the environment is considered itself to play a role in regulating biogeochemical rates (i.e. the idea of the environment as the ultimate control) meaning that as with long-term environmental manipulations, correlative and not causative relationships are evaluated. The third approach—and that approach with the most power to identify causation—is the use of reciprocal transplants where the transplant is the community (e.g. a soil monolith) and the environment is considered common to the location where the different communities are brought together. Reed and Martiny (2007) highlight that even with this approach caveats include the fact that the environment of the transplanted units may not fully equilibrate with the new environment. We might ask how long it would take for a soil core transplanted from a pine to an oak forest to assume the environment of the oak forest. For example, total soil carbon and soil texture are parameters that are unlikely to change in such an instance, and even if controlled for there is likely to be immigration from the surrounding community which obscures clear relationships between microbial communities and function that are separate from the environmental conditions.

All three of the approaches evaluated by Reed and Martiny (2007) reduced—to at least some extent—the issue we have in field observation where it is not possible to move beyond correlation (to causation) between microbial communities and function, given the confounding issue of

environmental variation. Admittedly, observations are the classical starting point for scientific investigation—and such approaches can identify potentially important environmental and microbial factors that might regulate biogeochemistry (e.g. Strickland *et al.* 2010). Yet to link microbial community composition unquestionably to function requires tightly controlled experiments. These are provided in the form of experimental assemblies of known isolates. Strict control of environmental conditions (e.g. in a bioreactor) permits identification of ultimate causation through the microbial community in terms of regulating process rates. Such studies unambiguously show that microbial composition and diversity influence productivity and nutrient cycling (Bell *et al.* 2005). Where the environment is slightly more realistic (e.g. wood disks), studies with natural isolates have even shown that the assembly history of the community influences decomposition and carbon release rates (Fukami *et al.* 2010). The major limitation of these approaches is, of course, the difficulties associated with assembling the complex communities found in the field. If we assume that a gram of soil may contain as many as 10,000 taxa, the drastic simplification of the experimental assemblages (~10 taxa) is certainly not representative of the enormous taxon diversity in natural microbial communities. This means that mechanisms—such as the portfolio effect and functional redundancy—are strongly selected against in isolate experiments as agents creating functional equivalence. In addition, if ~1% of taxa are culturable and these taxa likely represent more *r*-selected organisms, then experiments with isolates select for a narrow slice of the ecological strategies observed in natural communities.

Strickland *et al.* (2009) present an experimental approach for testing functional equivalence that is a compromise between whole community and cultured isolate approaches. Recognizing the joint needs of establishing a highly diverse microbial community and to have a common but realistic environment, they established experimental microcosms with milled and sterilized leaf litter (the environment), and inoculated these with whole communities through introduction of a small mass of soil. They combined common garden (a single leaf litter) with reciprocal transplant (litters and soils

crossed from multiple sites) approaches and measured carbon mineralization rates from the microcosms across 300 days. The microbial community inocula explained as much as 86% of the variation in mineralization rates, providing strong support for the hypothesis that functional dissimilarity, not functional equivalence, can be important and biogeochemically-relevant in soil communities.

The common caveat to tests of functional equivalence is that we expect the community to modify the environment as the experiment progresses which, in turn, modifies the community. The crux here is modification of the environment. We only falsify equivalence if microbial community effects are compared “under common environmental conditions.” This need to hold the environment constant explicitly recognizes that functional rates vary directly as environmental factors change. Indeed, covariation between functional rates and controlling factors is central to all soil models, whether they treat the microbial community as a black box or not. To identify microbial communities as ultimate controllers of biogeochemical process rates requires differences under constant environmental conditions. In Strickland *et al.* (2009) there was high certainty that the initial environments were essentially the same, but with time the environments diverged as decomposition proceeded and the communities shaped the environmental conditions (e.g. the carbon pools available, nutrient levels, pH, etc.). It then leaves us with the conclusion that initial functional differences in the community led to overall differences in function that themselves might have been a product of the community and/or altered environment. Separation of the effects of community composition and the environment is challenging, and clearly we need the suite of experimental approaches outlined in this section to robustly challenge the hypothesis of functional equivalence. Criticism of one approach to support another fails to recognize the advantages each brings to the discourse (e.g. Fukami *et al.* 2010) and will only reinforce the hypothesis in the absence of appropriate falsification. Given the common assumption of the functional equivalence hypothesis in ecosystem modeling there is a scientific and societal need to test it appropriately. If we do so we will advance basic understanding of soil ecology

and permit reliable evaluation of modeled ecosystem responses and feedbacks to environmental change.

3.5.5 Putting ecology into soil models

The soil (and ecosystem) models applied widely to address questions related to feedbacks to global warming, carbon stocks across regional gradients, and nitrogen dynamics across agricultural management regimes, all “black box” the microbial community. They assume functional equivalence in their parameterization, validation, and prediction. Indeed, we often parameterize ecosystem models using data collected across space, and then apply these parameterizations to make predictions across time for a system. This approach assumes microbial communities do not ultimately influence biogeochemical cycling either in time or space. So what happens when we construct models that open up the black box and permit the identity of taxa, their physiology, and biomass to influence ecosystem process rates? An in-depth model evaluation and review is beyond the scope of this chapter, but below we present a brief discussion to identify future modeling needs by highlighting the implications of relaxing the “black box” assumption.

Using multi-pool, soil organic carbon (SOC) models—which black box soil communities—Kirschbaum (2004) and Knorr *et al.* (2005) showed that depletion of labile SOC pools could explain the ephemeral augmentation of soil respiration under simulated warming. Once the warmed systems reached a steady-state—i.e. the labile pools had been depleted to a constant value—respiration rates matched carbon input rates, which were unchanged from pre-warming conditions. That inputs equal outputs is expected for any steady-state system. Yet the studies demonstrated that the conventional way we model soil carbon can predict observed respiration responses to soil warming. Indeed, there is empirical support for this substrate-depletion mechanism (Bradford *et al.* 2008). However, at the same site, there is also empirical support that the microbial communities adjust to the thermal regime in a manner that influences respiration rates (Bradford *et al.* 2008). So where the conclusions of Kirschbaum (2004) and Knorr *et al.* (2005) went too far was

in arguing that by finding evidence for the substrate-depletion hypothesis they had falsified alternate hypotheses that microbial community responses explained observed patterns of respiration to warming. Demonstrating that one mechanism can explain an observed pattern does not falsify alternate mechanisms that might equally recreate the same pattern (i.e. the absence of evidence is not evidence of absence). To evaluate the competing hypotheses of functional equivalence and redundancy, we require soil models that open-up the black box by explicitly modeling microbial dynamics to evaluate the role of microbes in driving biogeochemical processes.

Allison *et al.* (2010) present one of an emerging family of microbe-explicit models (e.g. Lawrence *et al.* 2009). They compare conventional multi-pool, SOC models to an enzyme-based approach that represents solubilization of SOC by extracellular enzymes, microbial assimilation of dissolved organic carbon compounds, and the expected negative relationship between temperature and microbial growth efficiencies. Model predictions were most sensitive to this latter parameter. In response to sustained warming, microbial biomass was reduced because less of the carbon assimilated by the microbes was allocated to growth. This served to decrease the abundance of microbial extracellular enzymes that solubilize SOC, creating a negative feedback to warming-induced losses of SOC. By explicitly modeling the microbial dynamics they found no evidence for positive feedback to climate warming through loss of SOC to the atmosphere, a finding contrary to most black box soil models. The finding is significant because when we relax the assumption of functional equivalence, model predictions that influence policy may well differ from those derived from more conventional modeling approaches.

Soil models that relax the assumption of functional equivalence are not a recent phenomenon (e.g. Hunt *et al.* 1987) but, like their earlier counterparts, they have not yet been incorporated into modeling efforts that might influence policy and practice on environmental issues such as global climate change and carbon emissions (e.g. those models used in Denman *et al.* 2007). They are also deterministic, and so do not permit context-

dependent histories that are likely essential to generating functional dissimilarity to shape functional outcomes that are not fully reversible. For example, in the Allison *et al.* (2010) model returning the system to a pre-warming state will eventually permit microbial biomass, extracellular enzyme abundance, and carbon stocks to recover to pre-warming conditions. Given context-dependent histories, we rarely expect changes in ecological systems to be fully reversible upon restoration of original environmental conditions (Levin 1998). Maybe such context-dependency is too difficult to incorporate into current modeling efforts. However, the tractability of including microbial dynamics in deterministic soil models has been demonstrated (e.g. Lawrence *et al.* 2009; Allison *et al.* 2010) and provides a likely productive direction for exploring the implications of assuming functional equivalence vs. dissimilarity when projecting biogeochemical response and feedbacks to environmental change.

3.5.6 Revisiting the functional paradigm in soil ecology

Soil models—including those used in the coupled carbon cycle models to project climate change—typically assume that soil communities are functionally equivalent. To put this in colloquial terms, “it doesn’t matter who is there, nor in what form, number, or location,” because every soil community is essentially a black box that functions the same way under the same environmental conditions when we look across space or time (see Schimel 2001). Application of this hypothesis assumes that functional responses to a disturbance (e.g. temperature change) can be described with a single, mathematical equation. In making this assumption “history”—in its broadest sense—is disregarded as a force that influences the functioning of microbial communities through changes in biomass, composition, or the physiology of soil taxa. For example, even the decrease in total microbial biomass observed by Allison *et al.* (2010)—when they warmed a system and assumed a negative effect of temperature on microbial growth efficiencies—would fail to elicit an initial difference in respiration rates between a system pre and post a warming disturbance if we assume functional

equivalence. Few ecosystem ecologists would argue—if we held composition and the environment constant—that microbial biomass was irrelevant to ecosystem process rates in soils (nor would any plant ecologist dare argue that plant biomass and community type are irrelevant to predicting photosynthetic rates). Yet we have to accept that as soil ecologists the dominant paradigm we espouse through our ecosystem modeling is that soil microbial communities are homogeneously functioning units across space and time, which exhibit invariant functional responses to changes in controlling factors such as temperature, even where microbial biomass differs.

Recent models (e.g. Lawrence *et al.* 2009; Allison *et al.* 2010) challenging the functional equivalence paradigm have not yet been coupled with efforts that provide the scientific basis for policy to mitigate and adapt to environmental problems (e.g. Denman *et al.* 2007). Even within academic circles, soil biology appears to have had little influence in shaping general ecological knowledge (Barot *et al.* 2007). If our field is to advance knowledge and application outside of its own perimeters, then we must take a fresh look at the paradigms of functional redundancy, similarity, and equivalence and—and if we find them lacking—challenge application of these paradigms where soil ecological knowledge is applied outside of our field. This includes application in areas of high societal importance, such as the coupled atmosphere-biosphere carbon cycle models for projecting feedbacks to climate change (Denman *et al.* 2007). Plant ecologists have engaged with atmospheric modelers in these realms, and soil ecologists must now do the same if we wish to make a robust claim that soil biology need be considered when managing ecosystems and climate in the face of environmental change.

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