

Bridging the gap between micro - and macro-scale perspectives on the role of microbial communities in global change ecology

T. C. Balser · K. D. McMahon · D. Bart ·
D. Bronson · D. R. Coyle · N. Craig · M. L. Flores-Mangual ·
K. Forshay · S. E. Jones · A. E. Kent · A. L. Shade

Received: 8 February 2006 / Accepted: 16 August 2006
© Springer Science+Business Media B.V. 2006

Abstract In order to understand the role microbial communities play in mediating ecosystem response to disturbances it is essential to address the methodological and conceptual gap that exists between micro- and macro-scale perspectives in ecology. While there is little doubt microorganisms play a central role in ecosystem functioning and therefore in ecosystem response to global change-induced disturbance, our ability

to investigate the exact nature of that role is limited by disciplinary and methodological differences among microbial and ecosystem ecologists. In this paper we present results from an interdisciplinary graduate-level seminar class focused on this topic. Through the medium of case studies in global change ecology (soil respiration, nitrogen cycling, plant species invasion and land use/cover change) we highlight differences in our respective approach to ecology and give examples where disciplinary perspective influences our interpretation of the system under study. Finally, we suggest a model for integrating perspectives that may lead to greater interdisciplinary collaboration and enhanced conceptual and mechanistic modeling of ecosystem response to disturbance.

T. C. Balser (✉) · D. Bart · M. L. Flores-Mangual
Department of Soil Science, University of Wisconsin,
Madison, WI 53706, USA
e-mail: tcbalser@wisc.edu

N. Craig · T. C. Balser
Gaylord Nelson Institute for Environmental Studies,
University of Wisconsin, Madison, WI 53706, USA

K. D. McMahon · S. E. Jones · A. E. Kent ·
A. L. Shade
Department of Civil and Environmental Engineering,
University of Wisconsin, Madison, WI 53706, USA

D. Bronson
Department of Forest Ecology and Management,
University of Wisconsin, Madison, WI 53706, USA

D. R. Coyle
Department of Entomology, University of Wisconsin,
Madison, WI 53706, USA

K. Forshay
Department of Zoology, University of Wisconsin,
Madison, WI 53706, USA

Keywords Ecosystem ecology · Global change ecology · Interdisciplinary research · Land use change · Microbial ecology · Nitrogen cycling · Plant species invasion · Soil respiration

Introduction

Microorganisms play a central role in ecosystem functioning and therefore in ecosystem response to disturbance. However, our ability to investigate the exact nature of that role is often limited by disciplinary differences among microbial and ecosystem ecologists. For many years a schism has

existed between micro- and macro-ecological theory, epistemology, and attitudes. Micro- and macro-scale ecologists are trained in different schools of thought, speak different scientific languages, use contrasting approaches to experimental design, and have different comfort levels with uncertainty. Most modern microbial ecologists choose to study patterns in microbial community composition across various environmental gradients in an effort to understand the forces driving change in community structure while macro-scale ecologists have traditionally taken a broader perspective—focusing on processes at the watershed or landscape-scale. These differences in perspective likely arise from differences in our cultural, conceptual and methodological approaches, compounded by the incongruent ranges of spatial and temporal scale between the two types of ecology (Fig. 1; Ettema and Wardle 2002). Further, the advent of “cultivation independent” (i.e. gene-based) approaches to studying microbial species distribution (Forney et al. 2004) has led to a move away from traditional ecology-focused methods of microbial study (e.g. selective culturing) and toward a more molecular biology-based approach. While the resulting new

techniques and approaches have certainly fundamentally enhanced our understanding of the biodiversity and distribution of microorganisms, they have not generally led to greater understanding of the role or importance of such diversity in ecosystem nutrient cycles. In fact, it might be argued that we have drifted far from the ecological foundations of microbiology. During the past 30 years, macro-scale ecology has progressed from empiricism to the level of hypothesis testing and field-scale manipulations, while microbial ecology has remained in a largely descriptive mode. The methodological challenges associated with the small physical size of microbes, overwhelmingly large populations, rapid generation time, and morphological homogeneity have made simple census of microbial species (assuming a species concept could be agreed upon) nearly impossible. However, with the rapid rise of molecular techniques, microbial ecologists are now able to walk through the world with the equivalent of the naturalist’s “field notebook”, cataloging species distribution in an effort to identify patterns that may indicate an underlying mechanism influencing community composition and dynamics. There has been a move back toward our ecological “roots” as researchers begin (re) apply true conceptual ecological frameworks to experimental design and data analysis in microbial ecology (Horner-Devine et al. 2004a; Jessup et al. 2004). We are increasing our understanding of the nested hierarchy of drivers acting at varying spatial and temporal scales that impact microbial communities, as well as beginning to quantify the potential role of microbial community composition as an independent controlling variable in ecosystem functioning (Schimel 2004; Bardgett et al. 2005; Schimel et al. in press).

As microbiologists engage in interdisciplinary discussion with macro-scale ecologists, we are able to see not only where we can move beyond the paradigmatic concept of the microbial “black box” of ecosystem studies, but also how we can begin to generate a conceptual framework for microbial population, community, and even landscape, ecology that parallels the extant wealth of overarching ecological theories developed and challenged for macro-scale ecology at

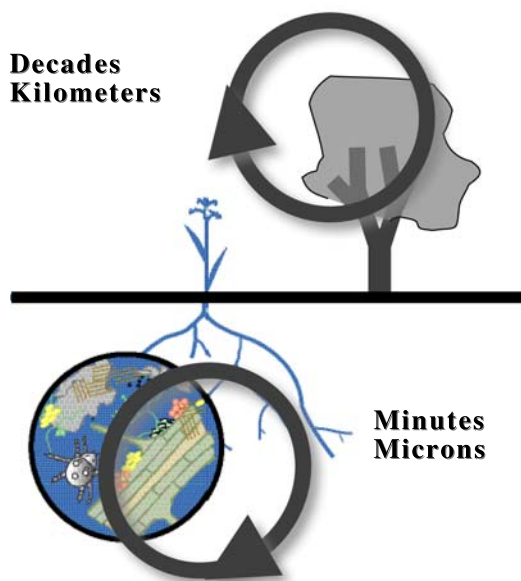


Fig. 1 Interdisciplinary collaboration among microbial and ecosystem ecologists requires addressing the different spatial and temporal scales for each

multiple spatial and temporal scales (Real and Brown 1991; Golley 1993). Examples of well-known ecological theories that have recently been applied to microbes across large spatial scales include the taxa–area relationship (Horner-Devine et al. 2004b) and island biogeography (Whitaker et al. 2003). Jiang and Morin (2004) demonstrated that microbes could be used to test large-scale ecological theories. Using aquatic microbial communities composed of “native” and “invasive” protists and rotifers they showed that large-scale environmental heterogeneity could cause a positive correlation between diversity and invasibility. These types of studies are valuable in linking micro- and macro-ecological concepts and problems as the effects of invasive species are of great concern to macro-ecologists. However, few studies have attempted to discern the effects of global-scale change on microbial community structure or function (Horz et al. 2004, Sinsabaugh et al. 2003), despite the wealth of literature available regarding macro-biota (Hooper et al. 2005). In some cases aboveground biota drive the belowground microbial activities and vice versa (Wardle et al. 2004). This is important because most activities that contribute to global change occur aboveground, but with far-reaching effects, often going through aboveground biota into belowground biota, and resulting in changes in ecosystem processes.

This paper is the result of a graduate course at the University of Wisconsin–Madison focused on how to bridge the gap between micro- and macro-scale approaches to global change studies. We argue that a mechanistic understanding of ecosystem response disturbance requires interdisciplinary synthesis between micro- and macro-scale ecologists. The course was designed to address the growing need for students and faculty specifically trained to work in teams addressing research questions that span spatial, temporal and scientific scales (Gonzalez 2001; Pellmar and Eisenberg 2000; NRC 2003; Sung et al. 2003). Course participants worked as teams to generate and present case studies in which disciplinary perspectives influence our interpretation of the system under study, and suggest a model with mechanisms for integrating perspectives that could lead to greater interdisciplinary collabora-

tion and enhanced conceptual and mechanistic modeling of ecosystem response to disturbance. As we worked on specific cases we also reflected on the process of interdisciplinary interaction, developing a model for communication in interdisciplinary teams. Here we present four of our case studies and the communication model we used.

Case studies in global change ecology

Each of the four case studies presented here represents an area of active inquiry at the macro-scale where there is high potential for improvement in our understanding and ability to predict system response if we include a micro-scale perspective. Rather than being comprehensive treatments these case studies were chosen to highlight some of the groundbreaking work currently being conducted. For an additional example in greater detail, see the review by Mentzer et al. (this volume).

Case one (soil respiration response to temperature) is given in the most detail, and is also an area where the most work to integrate macro- and micro-scale perspectives has occurred. Cases 2–4 are areas where some work has been carried out, but there is evidence that more would be valuable. In each case, there are several possible roles that microbial community dynamics might play in mediating ecosystem processes (Fig. 2). First, environmental change (in the form of climate change, or anthropogenic disturbance) can directly impact microbial function or activity. For example, enzyme activity rates are directly responsive to rising temperature (Davidson and Janssens 2006). Second, a shift in microbial community structure that results in loss of a functional group (e.g. organisms that are poorly represented, or a group with low functional redundancy) can directly impact occurrence of key biogeochemical processes. For example, lowered soil pH can substantially decrease ammonium oxidizer populations, resulting in the loss of nitrification (Myrold 1998). Third, a shift in microbial community structure can result in a change in process *rate*. For example, if a new dominant group of organisms (e.g. saprophytic fungi) have altered sensitivity to soil temperature

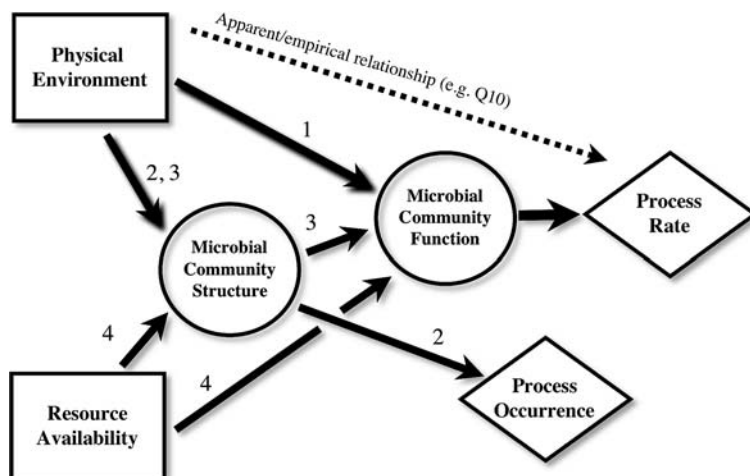


Fig. 2 Hypothetical relationships among environment, microbial community, and ecosystem processes. A change in environment impacts process rates via one of four mechanisms. (1) Direct enzymatic response to altered environment affects microbial function, which alters process rate. (2) Environmental change that causes a shift in microbial community structure can affect the presence/absence (occurrence) of a process. (3) A shift in community structure can result in altered sensitivity to climate or

(or pH, or oxygen, or water potential), then process rates may change, even if the environment remains stable. Community structure can “cap” or limit potential process rates (Fig. 3). Finally, a change in resource availability (e.g. supply of labile carbon) can alter community structure or function and thus affect either process occurrence or rate (Fig. 2). While the importance of each mechanism likely varies across scales and ecosystems, it seems clear microbial community response to changes in environment can have significant consequences for processes measured at the ecosystem scale (Schimel et al. in press). There is a need for more research designed to assess the relative importance of structural or functional shifts in microbial communities across a range of managed and unmanaged ecosystems.

Case 1: acclimation response of soil respiration to ecosystem warming

Biosphere surface temperatures have increased 0.6°C over the past 50 years, and the predictions is

environment (i.e. a change in community function), which impacts process rate. All three are likely to happen simultaneously. (4) A change in resource availability may result in altered community structure. We can improve our mechanistic understanding of ecosystem response to disturbance if we focus studies on the relative importance of these mechanisms at differing spatial and temporal scales

that they will continue to increase exponentially over the next century. According to the Intergovernmental Panel on Climate Change (IPCC) temperatures in northern latitudes will show the most increase, between 4 and 10°C over the next fifty to one hundred years. It is conceivable that with an increase in temperature many other variables will change, creating a complex web of ecological ambiguity. Temperature will direct a host of other variables, such as vapor pressure difference, soil moisture, snowmelt, decomposition and much more. The associated feedback from these changes has the potential to quickly increase or stabilize the increase in temperature (Luo et al. 2001; Fang et al. 2005; Knorr et al. 2005).

Studies designed to assess the response of systems to warming have been focused at the macro-scale level. Soil respiration has been used as an integrative variable to predict soil carbon sensitivity to increasing temperature. Soil respiration (R_s), which is comprised of both autotrophic (R_A) and heterotrophic (R_H) components, is the second largest flux in the global carbon cycle (Raich

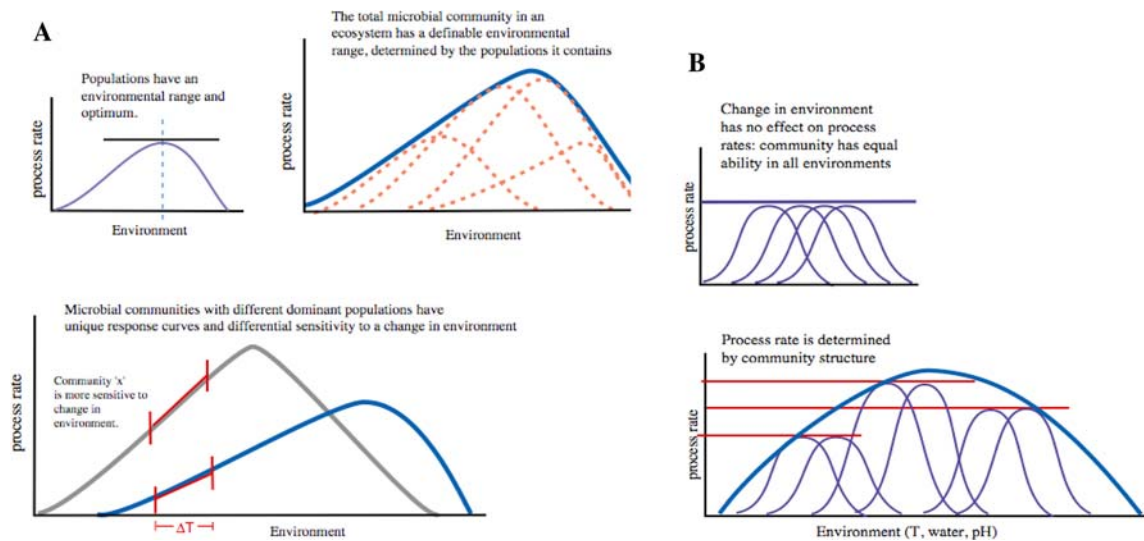


Fig. 3 Mechanisms for microbial community impact on process. **(A)** Process rate is determined by the environmental sensitivities of populations in the community. A shift in community structure can result in a change in

environmental sensitivity, and thus altered process rates in a given environment. **(B)** If community shift creates no change in environmental sensitivity of new dominant populations, there is no apparent impact on process

and Schlesinger 1992). Autotrophic respiration can comprise up to 60% of the total respiration, while the more dominant heterotrophic component can comprise between 50 and 100% of total soil respiration (Bond-Lamberty et al. 2004a, b). The Q10 model (which states that as temperature increases, soil respiration increases) has been used to characterize the relationship between soil respiration and temperature (Kirschbaum 1995).

Currently, the subject of soil carbon and respiration sensitivity to temperature increase is hotly debated (Cox et al. 2000; Rustad et al. 2000; Knorr et al. 2005). Results from in situ field temperature manipulations indicate that the accepted view of soil respiration increasing with temperature may be mistaken. Growing evidence suggests that a solely macro-scale focus may result in poor predictive capacity and generalization (Giardina and Ryan 2000). Zhang et al. (2005) have conducted temperature manipulation studies that show no long-term increases in soil respiration. These findings contradict the held belief that soil respiration and temperature are directly linked and highlight many new questions as to why. Many of the proposed explanations require an understanding of a micro-scale, ecological perspective.

The first hypothesis is that a change in soil temperature alters microbial community structure, with a concurrent change in temperature sensitivity (e.g. pathway 3, Fig. 2). A laboratory study by Zogg et al. (1997) showed that with 5, 15, and 25°C temperatures Gram-positive and Gram-negative bacterial abundance significantly increased, perhaps due to a shift in available substrate. Respiration rates were much higher for the treatments that received an increase in temperature, leading to a possible conclusion that an increase in temperature can also increase overall R_H . However, changes in microbial community structure have also been observed in an in situ tallgrass warming study (Zhang et al. 2005). Treatments experimentally warmed 2°C above ambient temperature showed a significant increase in fungal abundance but no significant changes in bacterial abundance. This resulted in an increased fungal:bacterial ratio. In this case, there was no obvious change in temperature sensitivity. A shift in microbial community structure to populations having different temperature optima for growth could result in an acclimation of respiration, or net zero effect (Balser 2000; Balser et al. 2002; Ellert and Bettany 1992).

A second hypothesis as to why an acclimation of soil respiration to increases in temperature exists is that plant litter quality and quantity decreases over time, leading to an overall reduction in respiration rate (pathway 4, Fig. 2). Rustad et al. (2001) observed an NPP_A increase in response to warming at high latitudes, but the increase was short-term. The increase in NPP_A quickly leveled off and returned to normal productivity levels despite more warming. The decline in NPP is commonly attributed to nutrient and water limitations following warming (Gholz 1982; DeLucia et al. 1999; Kuijper et al. 2005). In order to test the relative importance of this second hypothesis, accurate measurements of the response of NPP to increases in temperature and an understanding of the effect of NPP on microbial biomass composition and function are needed. These testing needs highlight the urgency for more collaboration between micro- and macro-ecologists.

A third hypothesis is that a change in the relative abundance of labile versus recalcitrant soil organic matter (SOM) explains the lack of increase in soil respiration to temperature. Depletion of labile carbon results in R_H acclimation to increased temperature. Microbial activity increases as temperatures increase, resulting in depletion of the labile pool (Fierer et al. 2005). This produces a short-term increase in soil respiration followed by a steady decline as the labile carbon decreases. Microbial utilization of recalcitrant carbon (and thus the temperature sensitivity of recalcitrant carbon) is a subject of debate (Giardina and Ryan 2000). Because passive carbon composes approximately 60–90% of the SOM, its response is vital. Some studies show passive carbon in mineral soils decreases in sensitivity due to low Redfield ratios, while others demonstrate that passive carbon can be just as sensitive to decomposition as the labile carbon (Eliasson et al. 2005; Fang et al. 2005). Giardina and Ryan (2000) state temperature alone will not affect turnover rate of the soil carbon. Davidson et al. (2000) argues temperature cannot be the only factor viewed, as temperature affects many other environmental parameters as well and that, in turn, will change turnover rates. Because carbon utilization is ultimately a question of micro-

bial physiology, a greater understanding of carbon sensitivity or response to temperature will require an integration of microbiological study with process study. To date, such integrative studies are few.

Case 2: regulation of nitrogen transformation

Nitrogen fixation by humans has now surpassed total fixation by all other non-human sources (Vitousek et al. 1997). Excess nitrogen from agricultural and urban sources, where they are used to fertilize and enrich terrestrial systems, moves through watersheds into streams and rivers (USGS 1999). Nitrogen leaches into groundwater, streams and reservoirs where it contaminates drinking water supplies and increases eutrophication of freshwater systems. This in turn stimulates algal, macrophyte and bacterial growth (Carpenter et al. 1998). A dramatic example of the deleterious effects of nutrient eutrophication occurs when nitrate–nitrogen from the agriculturally influenced Mississippi River drainage basin enriches surface waters in the main channel and the Gulf of Mexico. This nitrate enrichment increases biotic activity and oxygen demand, which in turn increases the growth of the hypoxic zone, a region of extremely low oxygen that can cause stress or death to the benthos (benthic fauna) and other organisms that cannot actively escape the low oxygen zone (Rabalais et al. 1996).

As with soil respiration, nitrogen cycling in aquatic systems has largely been subject to macro-scale research focus, yet is controlled by micro-scale community dynamics. Ecosystem ecologists and biogeochemists have developed numerous models to explain rates of nitrogen transfer in aquatic systems, and the majority of approaches relate nitrification and denitrification rates to environmental conditions such as temperature, dissolved oxygen concentrations, hydrologic export (Forshay and Stanley 2005), nitrogen species concentrations (Peterson et al. 2001) and dissolved organic matter levels (Bernhardt and Likens 2002). However, here too there is a role for specific microbial control over process occurring at the large-scale. Whereas carbon

availability and temperature (pathways 4 and 3, Fig. 2) appear to determine soil respiration response, controls over the soil nitrogen cycle are more likely related to community structure and enzyme activity (pathways 1 and 2). Unlike carbon metabolism, the genes for nitrogen species oxidation occur in a taxonomically restricted group of bacteria, providing greater possibilities for differences in ecophysiology and nitrogen oxidation rates (Balsler et al. 2002).

To better understand the causes and consequences of nitrogen movement on the landscape that leads to pollution or eutrophication, and to fully characterize the nitrogen cycle we must identify the effects of environmental change on the microbial community drivers of the nitrogen cycle. While there has been recent focus on soil respiration and microbial communities, there have been few directed efforts to understand how microbial communities may control nitrogen pollution in aquatic systems. Some notable efforts do stand out.

The second pathway in our proposed conceptual frame (altered community sensitivity to environmental parameters; Fig. 2) has been demonstrated in aquatic nitrogen cycle research. In a study using laboratory isolates from estuarine sediment and characterized for their ecophysiology, Ogilvie et al. (1997) evaluated the temperature–growth profiles for two isolates and their competitive abilities for nitrate. The isolates were found to have different optimal temperatures and different affinities for nitrate at their optimal growth rates. In this case temperature, either through seasonal change or global warming, impacted the system wide rates of nitrate reduction. The conclusion is if a different species dominates the nitrate reducing community due to a higher growth rate at a given temperature, but has a lower affinity and rate of nitrate reduction, then the total nitrate reduction by the community can also decrease.

Pathway three in Fig. 2 has also been investigated. In terrestrial systems, it has been demonstrated that differences in terrestrial microbial community structure may result in significant differences in nitrogen cycling rates (Cavigelli and Robertson 2000, 2001; Balsler and Firestone 2005). However, in aquatic systems research

concerning the role of microbial communities in nitrogen cycling has made little progress in directly linking community composition change with a change in nitrification or denitrification rates. Braker et al. (2001) found differences in denitrifying communities at three locations in Puget Sound. Community similarities were analyzed by cluster analysis using both the 16S gene encoding on a portion of a small ribosome subunit and the nirS gene of the denitrification pathway. These communities most likely arose from differences in depth, temperature and carbon substrate levels at the sampling sites. However, no denitrification rates were recorded for the sites. Therefore, the effects of prokaryotic community structure on the rate cannot be evaluated for this study. Creating a mechanistic linkage between process and microbial community structure will require studies that measure both.

Case 3: rapid spread of invasive plant species

Our third case centers on rapid spread of invasive plant species. Human activities, whether deliberate or inadvertent, are often responsible for the initial introduction of non-native species into an area (Mack et al. 2000; Sakai et al. 2001; Gray 2005). In the Midwestern US plant invasions in wetlands are a monumental problem. Reed canary grass (*Phalaris arundinacea* (L.)) invasion is particularly problematic, with over 40,000 of wetlands invaded (Kercher and Zedler 2004). *Phalaris* has invaded over 100,000 acres of fens and sedge meadows in the Great-Lakes-St. Lawrence system, altering ecosystem functions and threatening rare plant species. While growing evidence suggests the role of anthropogenic nutrient additions in facilitating widespread invasion, recent studies have shown that the invasion persists after nutrient amelioration has ceased, and that combined herbicide treatments and low nutrient conditions fail to reverse invasions in highly affected systems. The reasons for the persistence and spread of *Phalaris* after nutrient additions have ended remain poorly understood. We suggest that the answer to this macro-scale “mystery”, as with the others presented here,

lies in increasing our understanding of the role microbial communities play in mediating plant species invasion. One possible reason for *Phalaris* persistence may be that the plant alters microbial communities in a manner that increases mineralization of nitrogen and phosphorus, thereby improving short-term plant growth (positive feedback to enhance its own growth; Bever 2003). Effects on microbial communities may also lead to increase the success and competitive ability of seedlings emerging from the seedbanks after adults have been removed (Perry and Galatowitsch 2003).

However, there is a lack of research that includes soil or microbial ecology. Proposed feedbacks among *Phalaris* growth, soil microbial communities, and nutrient availability include several unanswered questions. Does *Phalaris* change soil microbial communities, or does *Phalaris* impact nutrient or soil carbon (resource) availability? Answers to these questions could help us understand why the invasive persists after anthropogenic disturbances have ceased, and could ultimately lead to the development of promising, long-term control methods.

Case 4: land use and land cover changes

Our final case focuses on land use and land cover change. The recovery of degraded land is a topic of critical importance that is almost exclusively the domain of macro-scale research. As in the previous cases, increased focus on microbiological responses may prove important to achieving macro-scale goals (such as restoration, increased carbon storage, conservation of biodiversity). Land use impacts microbial community structure directly. Tillage, forest clear-cutting, or urban development all physically disrupt the soil, and have been shown to alter the relative abundance of major microbial functional types (Beare 1997; Pennanen et al. 1999; Wardle et al. 1999; Fraterrigo et al. 2006). In addition, environmental conditions altered by changing land use may impact microbial communities or alter soil trophic interactions,

thus indirectly effecting changes in microbial communities (Schimel and Gullledge 1998; Wardle et al. 1998; Wolters et al. 2000).

Work to date has suggested that shifts in microbial community structure may have implications not only for rates of biogeochemical processes but also for the range of processes available in an ecosystem (Bradford et al. 2002; Schimel and Gullledge 1998). Thus, the extent of the impact of land use changes on microbial-mediated functions may depend on whether a specific function is broadly distributed among microbes or restricted to a narrow group of organisms (CO₂ vs. CH₄ cycling, for example). However, many studies examining the impact of land use change on microbial communities focus on aggregate measures of microbial populations, including biomass or process measurements (respiration, denitrification, etc.). While there are several study examples that examine the microbial community composition as it relates to changing land use (Balsler et al. 2002; Steenworth et al. 2003; Waldrop et al. 2000; Yao et al. 2000), many studies instead infer the importance of microbial community composition from models of microbial-mediated processes (Bergsma et al. 2002; Hunter et al. 2001; Schimel and Gullledge, 1998; Steenworth et al. 2003; Stuedler et al. 1996; Valentine et al. 1994).

In order to assess, and eventually predict, the linkage between land use change, microbial communities, and ecosystem processes we need more information about the functional groups of microbes that are likely to be affected. First, an appreciation of the natural range of temporal and spatial variation in the abundance or composition of microbial populations in a given ecosystem is needed. We also need to be better informed about the specific populations that contribute to biogeochemical processes of interest. Not only their identity, but also the conditions that control the abundance and activity of these populations, as well as the influence that variation in these populations may have on process rates at the level of the ecosystem (Schimel and Gullledge 1998; Whitham et al. 2003).

A model for effective interdisciplinary collaboration

Each of the cases described has a focus in macro- or process ecology, but can benefit from the synthetic perspective gained from linking the macro- and micro-scales. However, truly integrative, collaborative efforts are rare. Often this is simply a result of communication barriers resulting from our separate scientific “cultures”. Thus an increase in collaboration may be assisted by intentionally cultivated skills in interdisciplinary communication. We propose a communication model that may prove valuable as a framework for interdisciplinary teams in macro- and micro-ecological studies (Fig. 4).

One of the key elements of this model was the recognition that we each have our own perspective and scientific “cultural past”. Effective collaboration, therefore, needs mutual respect and a conscious effort to understand each others’ epistemology (beliefs about the nature of knowledge and learning; Lattuca et al. 2004). This includes clarifying discipline-specific use of terms and jargon, as well as assumptions about “proper” scientific procedure. We noticed disciplinary differences in our (a) ways of asking questions (what is the purpose in asking); (b) our ways of approaching science (e.g., what counts as evidence in a macro- or micro-scale experiment); and (c) our respective level of comfort with uncertainty (e.g. a discipline born from medical science has quite a different level of acceptable risk compared to a discipline coming from a natural history heritage).

The elements of the model are as follows:

1. *Brainstorm ideas and expectations.* Create a disciplinarily-transparent framework. This includes initial surveys of disciplinary expertise and discussions. It is also an initial brainstorming session, where all expectations and preconceived notions about the problem or the process are laid out on the table. Allow all possible answers to be “correct” and not judged. Winnowing and prioritizing can come later. It may be necessary to return to this step periodically.
2. *Agree on the issue at hand.* Come to consensus on the goal and on whatever scale is of importance (e.g., do we have interdisciplinary or disciplinary questions? Or a mix of both? What information do we each think we need from the other?). What is the ultimate goal of this project/activity/problem to be solved?
3. *Generate priorities.* Begin with individual or disciplinary priorities. If I were to study this on my own, how would I approach it? How do I think it should be approached in a team?
4. *Cross-correlate priorities.* Discuss and reach consensus on priorities. Return to steps 1–3 if necessary. Discuss and decide on key concept(s) underlying the project/problem.
5. *Create consensus statement of project goal(s) and priorities and outline of approach.* Achieve consensus on logistics, what is feasible, budget, methods, etc. Assign tasks. If disagreement occurs or communication breaks-down, return to steps 2–4.

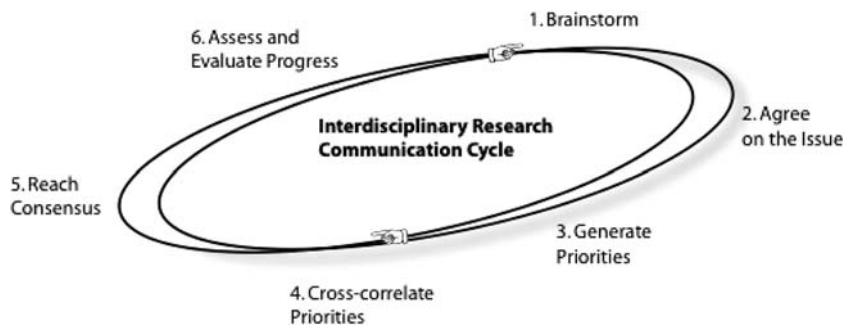


Fig. 4 Proposed iterative-framework for problem solving in an interdisciplinary group. Six steps (actions) are contained within the continuous willingness to learn from

one another and respect disciplinary differences. If at any point communication becomes stalled, return to any of the previous steps and begin again

6. *Over time, reassess (formative evaluation).* Establish checkpoints for progress evaluation. Be open to the need for a change in direction as information input changes.

Conclusions

Interdisciplinary research has the potential to answer many challenging ecological questions but to get to that stage, scientists must be willing to learn from their peers as well as teach them. The purpose of the case studies presented here is to understand control over—and prediction of—processes important in global change ecology. We discovered that while no one factor controls process rates, when multiple manipulations are made we can lose sight of what is controlling the effect. Better solutions come not from creating overly complex experiments but from answering the same question from different levels of resolution. In that way we gain new observations from the integration of macro- and micro-scale perspectives. Differences in our approach to micro- and macro-scale ecology influence our interpretation of a given system under study. Successful interdisciplinary collaborations are created by awareness of academic cultural differences, mutual respect and active communication. We propose that explicit communication and open-mindedness are the best ways to foster productive and beneficial interdisciplinary collaboration. Cultivating an attitude of respect and mutual peer-mediated learning can best serve all involved.

Acknowledgements We thank the Andrew W. Mellon Foundation, and the US National Science Foundation and Departments of Energy and Agriculture for support of the Ecosystem Microbiology group at UW-Madison and the Balsler laboratory. Two anonymous reviewers provided excellent feedback leading to substantial improvements in the manuscript.

References

- Balsler TC (2000) Linking soil microbial communities and ecosystem functioning. Doctoral Dissertation, University of California, Berkeley
- Balsler TC, Firestone MK (2005) Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. *Biogeochemistry* 73:395–415
- Balsler TC, Kinzig AP, Firestone MK (2002) Linking soil microbial communities and ecosystem functioning. In: Kinzig A, Pacala S, Tilman D (eds) *The functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton University Press, Princeton, pp 265–293
- Bardgett RD, Bouman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and belowground ecology. *Trends Ecol Evol* 20: 634–641
- Beare MH (1997) Fungal and bacterial pathways of organic matter decomposition and nitrogen mineralization in arable soils. In: Brussard L, Ferrera-Cerrato R (eds) *Soil ecology in sustainable agricultural systems*. CRC Lewis Publishers, Boca Raton, pp 37–70
- Bernhardt ES, Likens GE (2002) Dissolved organic carbon enrichment alters nitrogen dynamics in a forest stream. *Ecology* 83:1689–1700
- Bever JD (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol* 157:465–473
- Bond-Lamberty B, Wang C, Gower ST (2004a) A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob Change Biol* 10:1756–1766
- Bond-Lamberty B, Wang C, Gower ST (2004b) Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence. *Tree Physiol* 24:1387–1395
- Bradford MA, Jones TH, Bardgett RD, Black HJJ, Boag B, Bonkowski M, Cook R, Eggers T, Gange AC, Grayston SJ, Kandeler E, McCaig AE, Newington JE, Prosser JI, Setälä H, Staddon PL, Tordoff GM, Tscherko D, Lawton JH (2002) Impacts of soil faunal community composition on model grassland ecosystems. *Science* 298:615–618
- Braker G, Ayala-del-Rio HL, Devol AH, Fesefeldt A, Tiedje JM (2001) Community structure of denitrifiers, bacteria, and archaea along redox gradients in Pacific Northwest marine sediments by terminal Restriction Fragment Length Polymorphism analysis of amplified nitrate reductase (*nirS*) and 16S rRNA genes. *Appl Environ Microbiol* 67(4):1893–1901
- Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol Appl* 8:559–568
- Cavigelli MA, Robertson GP (2000) The functional significance of denitrifier community composition in a terrestrial ecosystem. *Ecology* 81:1404–1414
- Cavigelli M, Robertson G (2001) Role of denitrifier diversity in rates of nitrous oxide coconsumption in a terrestrial ecosystem. *Soil Biol Biochem* 33:297–310
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to feedbacks in a coupled climate model. *Nature* 408:184–187

- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173
- Davidson EA, Trumbore SE, Amundson R (2000) Soil warming and organic carbon content. *Nature* 408:789–790
- DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH (1999) Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* 284:1177–1179
- Eliasson PE, McMurtrie RE, Pepper DA, Stromgren M, Linder S, Agren GI (2005) The response of heterotrophic CO₂ flux to soil warming. *Glob. Change Biol* 11:167–181
- Ellert B, Bettany J (1992) Temperature dependence of net nitrogen and sulfur mineralization. *Soil Sci Soc Am J* 56:1133–1141
- Ettema CH, Wardle DA (2002) Spatial soil ecology. *Trends Ecol Evol* 17:177–183
- Fang C, Smith P, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature* 433:57–59
- Fierer N, Craine J, McLauchlan K, Schimel J (2005) Litter quality and the temperature sensitivity of decomposition. *Ecology* 86:320–326
- Forney LJ, Zhou X, Brown CJ (2004) Molecular microbial ecology: land of the one-eyed king. *Curr Opin Microbiol* 7:210–220
- Forshay KJ, Stanley EH (2005) Rapid nitrate loss and denitrification in a temperate river floodplain. *Biogeochemistry* 75:43–64
- Fraterrigo JM, Balsler TC, Turner MG (2006) Microbial community variation and its relationship with nitrogen mineralization in historically altered forests. *Ecology* 87:570–579
- Gholz HL (1982) Environmental limits on aboveground net primary productivity, leaf area index, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469–481
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404:858–861
- Golley FB (1993) A history of the ecosystem concept in ecology – more than the sum of the parts. Yale University Press, New Haven
- Gonzalez C (2001) Undergraduate research, graduate mentoring, and the University's mission. *Science* 293:1624–1626
- Gray AN (2005) Eight nonnative plants in western Oregon forests: associations with environment and management. *Environ Monit Assess* 100:109–127
- Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Horner-Devine MC, Carney KM, Bohannan BJM (2004a) An ecological perspective on bacterial biodiversity. *Proc R Soc London Ser B-Biol Sci* 271:113–122
- Horner-Devine MC, Lage M, Hughes JB, Bohannan BJM (2004b) A taxa–area relationship for bacteria. *Nature* 432:750–753
- Horz HP, Barbrook A, Field CB, Bohannan BJM (2004) Ammonia-oxidizing bacteria respond to multifactorial global change. *Proc Nat Acad Sci USA* 101:15136–15141
- Intergovernmental Panel on Climate Change (2001) [Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p 881
- IPCC (2001) Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report
- Jessup CM, Kassen R, Forde SE, Kerr B, Buckling A, Rainey PB, Bohannan BJM (2004) Big questions, small worlds: microbial model systems in ecology. *Trends Ecol Evol* 19:189–197
- Jiang L, Morin PJ (2004) Productivity gradients cause positive diversity-invasibility relationships in microbial communities. *Ecol Lett* 7:1047–1057
- Kercher S, Zedler J (2004) Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. *Aquat Bot* 80:89–102
- Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic C storage. *Soil Biol Biochem* 27(6):753–760
- Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature* 433:298–301
- Kuijper LDJ, Berg MP, Morrien E, Kooi BW, Verhoef HA (2005) Global change effects on a mechanistic decomposer food web model. *Glob Change Biol* 11:249–265
- Lattuca LR, Voigt LJ, Fath KQ (2004) Does interdisciplinarity promote learning? Theoretical support and researchable questions. *Rev High Educ* 28:23–48
- Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413:622–625
- Mack R, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Myrold DD (1998) Transformations of Nitrogen. In: DM Sylvia et al. (eds) Principles and Applications of Soil Microbiology. Prentice Hall, pp 259–294
- NRC, N.R.C. (2003) BIO 2010: transforming undergraduate education for future research biologists. National Academy of Sciences, Washington DC, p 191
- Ogilvie BG, Rutter M, Nedwell DB (1997) Selection by temperature of nitrate-reducing bacteria from estuarine sediments: species composition and competition for nitrate. *FEMS Microbiol Ecol* 23(1):11–22
- Pellmar TC, Eisenberg L (eds) (2000) Bridging disciplines in the brain, behavioral, and clinical sciences. National Academy Press, pp 1–130
- Pennanen T, Liski J, Bååth E, Kitunen V, Uotila J, Westman CJ, Fritze H (1999) Structure of the

- microbial communities in coniferous forest soils in relation to site fertility and stand development age. *Microbial Ecol* 38:168–179
- Perry L, Galatowitsch S (2003) A test of two annual cover crops for controlling *Phalaris arundinacea* invasion in restored sedge-meadow wetlands. *Restor Ecol* 11:297–307
- Peterson BJ, Wolheim W, Mulholland PJ, Webster JR, Meyer JL, Tank JL, Marti E, Bowden WB, Valett HM, Hershey AE, McDowell WH, Dodds WK, Hamilton SK, Gregory S, Morrall DD (2001) Control of nitrogen export from watersheds by headwater streams. *Science* 292:86–90
- Rabalais NN, Turner RE, Justic D, Dortch Q, Wiseman WJ Jr, Gupta BKS (1996) Nutrient changes in the Mississippi river and system response on the adjacent continental shelf. *Estuaries* 19:386–407
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in a soil respiration and its relationship to vegetation and climate. *Tellus B* 44B:81–99
- Real LA, Brown JH (eds) (1991) Foundations of ecology – classic papers with commentaries. University of Chicago Press, Chicago, pp 1–905
- Rustad LE, Huntington TG, Boone RD (2000) Controls on soil respiration: implications for climate change. *Biogeochemistry* 48:1–6
- Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126:543–562
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O’Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332
- Schimel J (2004) Playing scales in the methane cycle: from microbial ecology to the globe. *Proc Nat Acad Sci USA* 101:12400–12401
- Schimel JP, Gullledge J (1998) Microbial community structure and global trace gases. *Glob Change Biol* 4:745–758
- Schimel J, Balser TC, Wallenstein M Microbial stress-response physiology and its implications for ecosystem functioning. *Ecology* (in press)
- Sinsabaugh RL, Saiya-Corka K, Long T, Osgood MP, Neher DA, Zak DR, Norby RJ (2003) Soil microbial activity in a Liquidambar plantation unresponsive to CO₂-driven increases in primary production. *Appl Soil Ecol* 24:263–271
- Steenwerth KL, Jackson LE, Calderon FJ, Stromberg MR, Scow KM (2002) Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. *Soil Biol Biochem* 34:1599–1611
- Stuedler PA, Jones RD, Castro MS, Melillo JM, Lewis DL (1996) Microbial controls of methane oxidation in temperate forest and agricultural soils. In: Murrell JC, Kelly DP (eds) *Microbiology of atmospheric trace gases*. Springer, Berlin, pp 69–81
- Sung NS, Gordon JL, Rose GD, Getzoff ED, Kron SJ, Mumford D, Onuchic JN, Scherer NF, Sumners DL, Kopell NJ (2003) Educating future scientists. *Science* 301:1485
- USGS (1999) The quality of our nation’s waters – nutrients and pesticides. U.S. Geological Survey Circular 1225, Reston, Virginia
- Valentine DW, Holland EA, Schimel DS (1994) Ecosystem and physiological controls over methane production in northern wetlands. *J Geophys Res Atmos* 99:1563–1571
- Vitousek PM, Mooney HA, Lubchenco J, Milillo JM (1997) Human domination of Earth’s ecosystems. *Science* 277:494–499
- Wardle DA, Verhoef HA, Clarholm M (1998) Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Glob Change Biol* 4:713–727
- Wardle DA, Yeates GW, Nicholson KS, Bonner KI, Watson RN (1999) Response of soil microbial biomass dynamics, activity and plant litter decomposition to agricultural intensification over a seven-year period. *Soil Biol Biochem* 31:1707–1720
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633
- Whitaker RJ, Grogan DW, Taylor JW (2003) Geographic barriers isolate endemic populations of hyperthermophilic archaea. *Science* 301:976–978
- Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, Shuster SM, Wimp GM, Fischer DG, Bailey JK, Lindroth RL, Woolbright S, Kuske CR (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84:559–573
- Wolters V, Silver WL, Bignell DE, Coleman DC, Lavelle P, Van der Putten WH, De Ruiter P, Rusek J, Wall DH, Wardle DA, Brussaard L, Dangerfield JM, Brown VK, Giller KE, Hooper DU, Sala O, Tiedje J, Van Veen JA (2000) Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: implications for ecosystem functioning. *Bioscience* 50:1089–1098
- Zhang W, Parker KM, Luo Y, Wan S, Wallace LL, Hu S (2005) Soil microbial responses to experimental warming and clipping in a tallgrass prairie. *Glob Change Biol* 11:266–277
- Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, White DC (1997) Compositional and functional shifts in microbial communities due to soil warming. *Soil Sci Soc Am J* 61:475–481