

## Introduction



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Conceptual challenges in microbial  
community ecology

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Microorganisms play fundamental roles in all environments. Through their vast genetic, metabolic and physiological diversity, they drive global nutrient cycles, degrade waste material and pollutants and produce and consume greenhouse gases. These different aspects of diversity provide interesting and exciting scientific challenges and ensure that an understanding of the ecology of microbial communities, or microbiomes, is essential for predicting an ecosystem's 'health' and its resilience, whether in the human gut, agricultural soil or the open ocean.

In the past, our understanding of microbial communities was severely limited by our ability to grow microorganisms in the laboratory. The development and application of cultivation-independent techniques based on molecular analysis of genes and, more recently, (meta)genomes and proteins, have revealed a previously unimaginable amount of microbial diversity, including newly discovered phyla whose existence was not suspected. These techniques have been supplemented with a range of methods designed to determine functional characteristics, again without the need for cultivation.

As the technical challenges for microbial community ecology are increasingly met, however, a new challenge has been exposed. It is now straightforward and relatively inexpensive to quickly catalogue the microbial diversity of a sample, but conceptual frameworks for studying microbial communities lag far behind the production of these data. This thematic issue thus aims to highlight developing concepts of potential importance to microbial community ecology. We see at least three reasons for this need. First, the application of conceptual frameworks and associated analytical and theoretical approaches will increase the rate of scientific progress in this field. Future studies can be better designed to identify or test general principles and move beyond location-, technique- and laboratory-specific findings. Second, general ecological theory is not 'general' unless it applies to communities of microbes, which are the most abundant, diverse and globally impactful. Finally, microbial communities are much easier to control, manipulate and monitor than those of plants and animals; they therefore provide the potential for more critical testing and development of ecological theory.

As is commonly the case with the introduction of new techniques, microbial community ecology has recently been heavily dominated by descriptive studies, providing surveys and inventories of gene sequences or descriptions of the effects of environmental factors or environmental change on microbial communities. This has led to a diminution in conceptual and theoretical approaches to microbial ecology and it is fitting, therefore, that Prosser opens this theme issue [1] with a plea for a renewed focus on question- and hypothesis-driven approaches in microbial ecology.

In the remainder of the issue, four major themes then emerge, suggesting priority areas that may be ripe for advancement in the field. The first of these themes is touched on by nearly every paper—that microbial community ecology cannot ignore evolution and, further, must simultaneously consider ecological and evolutionary processes. Such 'eco-evolutionary' processes drive microbial community composition and diversity in nature and, conversely, microbial communities provide amenable systems to study such processes in any community. The contributing authors consider this challenge across both micro- and macro-evolutionary scales. For instance, VanInsberghe *et al.* [2] consider the relationship

between population genomics and microbial communities. They discuss how estimates of contemporary gene flow can be used to define populations on the basis of biological mechanisms that are ecologically meaningful. Rainey & Quistad [3] argue for studying eco-evolutionary processes in the context of microbial community diversity, given the prevalence of horizontal gene transfer and its implications for community functioning. Kohl [4] then reviews evidence of how both ecological and evolutionary forces, including macroevolutionary relationships among hosts and microevolution of symbionts, combine to shape the assembly of microbial communities within a host.

A second theme is a need for more attention to the interactions between microbes. Many of these papers focus on the evolution of those interactions, and microbial systems are uniquely amenable to contributing to this area of research. This is exemplified by Bernhardt *et al.*'s [5] study of experimental evolution of model phytoplankton, showing the potential for rapid evolution (less than 300 generations) in resource limitation and salt tolerance. The authors then use resource competition theory to demonstrate that such changes could alter the predicted outcomes of competition. Gorter *et al.* [6] discuss evidence that evolutionary processes are important in driving microbial community composition at ecological timescales and propose a conceptual model for the evolution of interspecies interactions in multispecies communities. Castledine *et al.* [7] offer an alternative perspective on microbial interactions by discussing community coalescence, or the mixing of whole communities. Even from this angle, however, they highlight the need to consider the interplay of ecological and evolutionary processes.

Other contributions on microbial interactions focused on metabolic cross-feeding between microbes. Considering the pervasiveness of such interactions in microbial communities versus those of larger organisms, it is fitting that this area is attracting the development of new conceptual theory. Douglas [8] reviews the role of extracellular metabolites (the exometabolome) in generating diversity in natural communities. She highlights the various types of cross-feeding interactions and considers how such interactions might be shaped by interactions with host organisms, including a human host. Pascual-García *et al.* [9] introduce the concept of metabolically cohesive consortia. They propose that close metabolic interactions allow the formation of stable groups of microbes and discuss how eco-evolutionary processes influence community-level metabolism.

A third theme is the importance of space for microbial communities. While studying the role of space in community ecology is not new, investigations on the microscale are especially challenging and our ignorance has hindered conceptual advances. Ciccacese *et al.* [10] use a synthetic bacterial community to investigate the role of the physical surface on spatial patterns and visualize its impacts on local diversity. Intersecting with the second theme, they also consider how metabolic interactions influence these results. Nunan *et al.* [11] review how soil heterogeneity, particularly at the microscale, influences microbial resource use. They then present a spatially explicit model to showcase the potential for soil heterogeneity to influence organic matter decomposition by a bacterial community. Locey *et al.* [12] round out the discussion by reporting macroscale (over tens of kilometres) biogeographic patterns of active and inactive bacterial cells. They then develop a mechanistic model to investigate the role of dormancy and dispersal in shaping these patterns.

The final emergent theme considers the response of microbial community composition to environmental changes and how such compositional variation is related to functioning. This theme touches on one of the most important challenges of our time, predicting how anthropogenic global changes will alter microbial communities and, in turn, feedback to affect our climate. The contributions in this section showcase an array of approaches to tackle this topic. Focusing first on the response of microbial communities, Sorensen & Shade [13] take an experimental approach to demonstrate greater resilience to increased temperature for communities open to dispersal and the importance of resuscitation of dormant, thermotolerant members of the community. Van der Waal & Litchman [14] take a trait-centric approach to understand the combined effects of multiple stressors on phytoplankton nutrient acquisition through phenotypic plasticity, evolutionary change and shifts in community composition. Their conceptual framework predicts that climate change will allow a reallocation of energy that favours larger-celled phytoplankton, necessitating consideration of size-dependent responses to climate-related stressors. Isobe *et al.* [15] synthesize microbial community data from global change field experiments and find that the responses of soil bacterial communities are phylogenetically conserved and consistent across locations. The results indicate that a macro-evolutionary approach is useful for predicting bacterial responses to various environmental changes.

Ultimately, the relevance of microbial community ecology lies in its ability to increase understanding and prediction of ecosystem functioning. While the relationship between biodiversity and ecosystem functioning has received considerable attention in animal and plant communities, these links are arguably more direct in microbial communities but more difficult to investigate. Morris *et al.* [16] present a new approach, integrating biodiversity–ecosystem function research and genotype–phenotype mapping. They illustrate this idea using data on methane oxidation in tropical soils. Garcia *et al.* [17] introduce the idea of using (meta)genomic changes as indicators or biosensors of the biogeochemical environment. Combined with a trait-based model, the genomic data improved predictions of changes in elemental composition of marine planktonic communities. Finally, Quistad *et al.* [18] describe an experimental study that links horizontal gene transfer, facilitated by increasing dispersal of selfish genetic elements, to changes in functional gene abundance and nitrogen cycling processes in soil microcosms. These studies offer innovative directions to translate the extensive genetic diversity of microbial communities into its consequences for ecosystem functioning, whether in the environment or associated with a host organism.

Together, these articles identify fundamental challenges for the field and demonstrate the importance and advantages of moving beyond descriptive surveys and inventories of microbial diversity. Sophisticated technologies enable discoveries and open new avenues for research, but applied by themselves are unlikely to increase our understanding. Instead, the complexity of microbial communities and their environments requires a careful wielding of methods to critically test concepts, hypotheses and theory to advance microbial community ecology.

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## Editor biographies



Jim Prosser is Professor in Environmental Microbiology in the School of Biological Sciences at the University of Aberdeen. He was awarded a PhD by the University of Liverpool in 1975 for research on experimental and theoretical modelling of soil nitrification. His research focuses on the ecophysiology, diversity and ecosystem function of soil microorganisms, with particular emphasis on ammonia oxidizers. His research group have demonstrated the impact of pH and ammonia supply on ammonia oxidizer communities, the influence of community composition on ecosystem function, including nitrous oxide emissions, and the implications for nitrogen fertilizer strategies.



Jennifer Martiny is a Professor of Ecology and Evolutionary Biology at the University of California, Irvine. She received her BS in Ecology, Behavior, and Evolution at UC San Diego and her PhD at Stanford University. Her research aims to uncover fundamental principles of the generation and maintenance of diversity in microbial communities. Her work has contributed to the establishment of the field of microbial biogeography and to the understanding of how microbial communities respond to environmental change.

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