MEETING REVIEWS

Microbial Ecology Meets Macroecology: Developing a Process-Based Understanding of the Microbial Role in Global Ecosystems

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Microorganisms inhabit all biomes on Earth. The terrestrial microbiome spans from leaf to soil, including all surrounding organisms, and microbial effects extend across ecological, spatial, and temporal scales. The terrestrial microbiome mediates plant invasions, plant succession, nutrient cycling, and even ecosystem carbon feedback to the atmosphere. Yet, for far too long, a lack of data constrained the elucidation of macroecological phenomena of terrestrial microbial communities over space and time. However, during the 2000s, breakthroughs in DNA sequencing technology were co-opted by environmental microbiologists to look deeper into the terrestrial microbiome than ever before possible. Rapid declines in the cost of DNA sequencing technology spurred more than a decade of work to understand spatial patterns of microbial communities (Fierer and Jackson 2006, Amend et al. 2012, Tedersoo et al. 2014, Davison et al. 2015). This accumulation of knowledge has enabled new global analyses of microbial communities (Ramirez et al. 2018) and their associated functions (Bahram et al. 2018) in both space (Tedersoo et al. 2014) and time (Averill et al. 2019). While discovery science remains an essential and important part of microbial ecology, these data are pushing the field of microbial macroecology toward process- and hypothesis-driven science. For example, species distribution models of microbial species (Kivlin et al. 2017) and dominant functional groups (Delgado-Baquerizo et al. 2018) allow us to explicitly include microbial guilds into process-based ecosystem models of carbon and nutrient cycling

(Sulman et al. 2019). Furthermore, combining microbial distribution data with that of plants, animals, and humans reveals that microbial associations can influence ecosystem-level processes such as plant nutrient cycling (Mushinski et al. 2019, Averill et al. 2019) and litter decomposition (Steidinger et al. 2019), as well as plant community response to global change (Averill et al. 2018, Jo et al. 2019). These studies, among others, demonstrate the critical influence of microorganisms over entire ecosystems and highlight the need to incorporate microbial interactions with other components of ecosystems if we intend to fully appreciate the fate of global ecological populations, communities, and ecosystems.

At the Ecological Society of America 2019 Annual Meeting, we convened a symposium to synthesize strides made toward a process-driven understanding of microbial communities at large scales and subsequent impacts on ecosystem functions. Here, we provide an overview of the findings in this symposium and highlight key areas for future microbial macroecology discovery and integration.

Presentation Highlights

Following the trend over the past decade, the exponential decline in sequencing costs and increase in computational capacity allowed for more extensive microbiome collection and analysis. This was highlighted best by the presentation by Dr. Anthony Amend and colleagues who sequenced the entire microbial landscape of a Hawaiian watershed (abiotic landscape, plants, and animals). Their sampling efforts from mountaintop to the ocean discovered that microbiomes are structured by trophic cascades (covered by Pennisi 2019). Microbiomes of animals at top trophic levels are subsets of lower trophic levels which are subsets of plants which are themselves subsets of the surrounding abiotic environment. This streamlining of microbiomes among higher trophic levels mirrors that of other processes, such as energy and isotope flows, and highlights the need to examine entire ecosystems to understand how microbial communities are organized. Dr. Mark Anthony presented on a similar theme, detailing how interactions among plants and their fungal symbionts structure these fungal communities across the globe. His work demonstrated that interactions (both positive and negative) among arbuscular mycorrhizal fungi control network and community assembly of the mycorrhizal fungi. Notably, communities assembled more via random processes in higher-latitude ecosystems where environmental variation was low and primarily via species niches in lower-latitude temperate and tropical systems where there were wider gradients in environmental conditions.

The remaining speakers used plant-based data on mycorrhizal associations to demonstrate that the plant microbiome is fundamental for understanding plant biogeography. Dr. Kabir Peay used global forest inventory data to map the global distribution of arbuscular mycorrhizal, ectomycorrhizal, and nitrogen-fixing tree symbiont types. Dr. Songlin Fei used forest inventory data to show how nitrogen pollution and fire are fundamentally re-arranging these forest symbiont types across North America. Dr. Rich Phillips linked the presence of contrasting forest mycorrhizal types to differences in key soil carbon and nitrogen cycling rates. Dr. Colin Averill showed positive feedbacks within these dominant plant mycorrhizal types are likely generating contrasting forest species syndromes and alternative stable states of the forest mycobiome. All of these scientists' work demonstrates how features of the ecosystem microbiome are fundamentally shaping the biogeography of entire ecosystem types and their functions, at massive spatial scales.

Future Research Priorities

While spatially explicit models of microbial distributions and the processes behind them are becoming increasingly well understood, the temporal dynamics of microbial communities in ecosystems are largely undescribed (Shade et al. 2007). If interannual turnover in microbial communities follows that of other organisms (e.g., deciduous trees), then modeling microorganisms over time may be relatively easy (Averill et al. 2019). However, as temporal microbial datasets accumulate (Kivlin et al. *unpublished manuscript*, Carini et al. 2018), idiosyncratic and ecosystem-specific patterns of microbial turnover over time have been revealed, indicating that temporal scaling of microorganisms may be more complex than originally estimated. Understanding the spatial and temporal consistency and turnover in microbial communities and function are the next necessary steps to integrating microbiomes into Earth system models and ecological forecasts. Furthermore, for the most part, microbial communities are currently modeled as functional guilds, with no regard to variation within those guilds or across environmental gradients. If intra-guild variation in microbial function is large and/or plastic over space and time, then a species-based approach is necessary to provide accurate microbially informed estimates on ecosystem function.

Conclusion

For decades, the role of microbes in soils and ecosystems was considered a "black box." The arrival of DNA sequencing technology gave scientists new ways to observe and describe these soil microbes, and how they may vary within local environments. However, recently collected data allow a truly global understanding of the distribution of the Earth microbiome, and how it is changing in time. We do not expect this trend to slow down any time soon. As observational data on the Earth microbiome continue to accumulate at an accelerating pace, we expect the links between microbial communities and ecosystem processes to only become clearer. We expect to discover new connections between the microbiome and Earth function. We suspect new data will reveal connections between the microbiome, ecology, and Earth science which are deeper, more complex, and more pervasive than we can even imagine today.

Literature Cited

Amend, A. S., et al. 2012. Macroecological patterns of marine bacteria on a global scale. Journal of Biogeography 40:800–811.

Averill, C., M. C. Dietze, and J. M. Bhatnagar. 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. Global Change Biology 24:4544–4553.

Averill, C., L. A. L. Cates, M. C. Dietze, and J. M. Bhatnagar. 2019. Spatial vs. temporal controls over soil fungal community similarity at continental and global scales. ISME Journal 13:2082–2093.

Averill, C., J. M. Bhatnagar, M. C. Dietze, W. D. Pearse, and S. N. Kivlin. 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. Proceedings of the National Academy of Sciences USA 116:23163–23168.

Bahram, M., et al. 2018. Structure and function of the global topsoil microbiome. Nature 560:233.

Carini, P., M. Delgado-Baquerizo, E.-L. Hinckley, T. E. Breweder, G. Rue, C. Vanderburgh, D. McKnight, and N. Fierer. 2018. Unraveling the effects of spatial variability and relic DNA on the temporal dynamics of soil microbial communities. BioRxiv 402438. https://doi.org/10.1101/402438

Davison, J., et al. 2015. Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism. Science 349:970–973.

Delgado-Baquerizo, M., A. M. Olivero, T. E. Brewer, A. Benavent-Gonzalez, D. J. Eldridge, R. D. Bardgett, F. T. Maestre, B. K. Singh, and N. Fierer. 2018. A global atlas of the dominant bacteria found in soil. Science 359:320–325.

Fierer, N., and R. B. Jackson. 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences 103:626–631.

Jo, I., S. Fei, C. M. Oswalt, G. M. Domke, and R. P. Phillips. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. Science Advances 5:eaav6358.

Kivlin, S. N., R. Muscarella, C. V. Hawkes, and K. K. Treseder. 2017. The predictive power of ecological niche models for global arbuscular mycorrhizal fungal biogeography. Pages 143–158 *in* L. Tedersoo, editor. Biogeography of mycorrhizal symbiosis. Springer-Verlag, Berlin, Germany.

Mushinski, R. M., R. P. Phillips, Z. C. Payne, R. B. Abney, I. Jo, S. Fei, S. E. Pusede, J. R. White, D. B. Rusch, and J. D. Raff. 2019. Microbial mechanisms and ecosystem flux estimation for NOy emissions from deciduous forest soils. Proceedings of the National Academy of Sciences USA 116:2138–2145.

Pennisi, E. 2019. No microbiome is an island, survey reveals. Science 365:851.

Ramirez, K. S., et al. 2018. Detecting macroecological patterns in bacterial communities across independent studies of global soils. Nature Microbiology 3:189.

Shade, A., A. D. Kent, S. E. Jones, R. J. Newton, E. W. Triplett, and K. D. McMahon. 2007. Interannual dynamics and phenology of bacteria communities in a eutrophic lake. Limnology and Oceanography 52:487–494.

Steidinger, B. S., et al. 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbiosis. Nature 569:404.

Sulman, B., E. Shevliakova, E. R. Brzostek, S. N. Kivlin, S. Malyshev, D. N. L. Menge, and X. Zhang. 2019. Diverse mycorrhizal associations enhance terrestrial C storage in a global model. Global Biogeochemical Cycles 33:501–523.

Tedersoo, L., et al. 2014. Global diversity and geography of soil fungi. Science 346:1256688.