Macroecology for microbiology

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What is macroecology? — To microbiologists, the term macroecology may conjure iconic images of wildebeests grazing in African savannahs or hummingbirds pollinating flowers in a tropical rain forest. Contrary to what the name implies, macroecology is not the ecological study of macroscopic organisms. Rather, macroecology is the study of ecological relationships through patterns in abundance, distribution, and diversity. Macroecology is an interdisciplinary effort that draws heavily from the fields of biogeography, community ecology, physiology, as well as quantitative and computational disciplines. Macroecologists often combine large ecological datasets and biodiversity theory with models and data from climatology, geology, and paleoecology to predict and explain shifts in geographic ranges, variation in body-size, community structure and assembly, as well as classic biogeographic patterns like diversity gradients. Instead of being the focus of an entire study, individual species and geographic sites often represent one of thousands of data points that span orders of magnitude. With data compilations and quantitative tools in-hand, macroecologists focus on broad sweeping relationships with the goal of providing general explanations for robust and predictively powerful patterns that, together, can lead to unified ecological theories.

A retrospective gaze — Microbiology has been headed for macroecology since the advent of environmental sequencing, which created the first real opportunity for characterizing the diversity of microbial communities. At the turn of the century, microbial ecologists fixated on biogeography and challenged a long-held notion that microbes have unlimited dispersal capacities. This paved the way for determining whether or not microbes exhibit textbook biogeographic patterns such as the species-area and distance-decay relationships. High-throughput sequencing improved the ability to evaluate the processes that potentially produce diversity patterns and led microbiologists to unveil a seemingly universal pattern known as the microbial "rare biosphere", whereby most microbial taxa account for relatively little abundance.

The future of microbial macroecology — Here, we prognosticate the coming years of a more macroecologically inspired form of microbial ecology. We see scientists continuing to catalog the diversity of microbial communities from environmental, engineered, and host-associated ecosystems. Microbiologists will intensify their curiosity for the mechanisms underlying commonness and rarity and will generate massive datasets to advance the understanding of microbial biodiversity using central themes of macroecology. In the process, microbial ecologists will uncover scaling laws that reveal how microbial biodiversity is structured from the smallest to largest ecosystems. The resulting breakthroughs will couple microbial processes and patterns, transform the understanding of global biodiversity, infuse microbial ecology with theoretical underpinnings, and firmly place microorganisms at the forefront of macroecology and its related fields. Owing to unique features of microbial life, the tools used to study it, and the fact that microbes account for most of Earth's metabolic, functional, and taxonomic diversity, microbiology will drive the forefront of macroecology. In the following sections, we highlight some of the pressing questions, challenges, and opportunities for microbial macroecology.

<u>Data science and ecoinformatics:</u> Macroecology relies on large data sets produced by hard-working naturalists, citizen scientists, government agencies, and academic researchers. The greatest advances in macroecology have emerged when these data are curated, annotated, and made publicly available, which is fast becoming a requirement of journals and funding agencies. We foresee the development of databases that not only document the occurrence and abundance

of microbial taxa but also provide metadata (i.e., geographic location, temperature, pH, nutrients, etc.) in a standard format (e.g., ecological metadata language). These databases will be user-friendly for mainstream ecologists and microbe-minded macroecologists alike. The integration of metadata, "-omics" data, and other trait-based information will facilitate the synthetic investigations of local-to-global scale microbial biodiversity. Increased computational power and sequencing technology along with faster and more efficient algorithms will lead to databases containing billions of species. Such advances will require the cutting edge of computer science and may usher in a new era of bioinformatics.

Deep insights into biogeography: Understanding the mechanisms that shape species geographic distributions is a major goal of macroecology that has often attracted the attention of microbial ecologists. While past efforts have focused on whether microbes have biogeography at all, future efforts will combine sequencing depth and species distribution modeling to quantify microbial geographic ranges and reveal the rates, pathways, and networks of microbial dispersal. Microbiologists will lead interdisciplinary efforts to track the movement of microbial taxa within and across ecosystems and shed light on the transfer of biomass from shallow ocean currents, through microbial snow, and along the deep ocean conveyor belt. Microbial ecology will move beyond catalog-based efforts akin to 18th century zoology and embark on what 19th century biogeographers began to establish, i.e., the driving force of geographic barriers on the diversification of taxa through deep time. The resulting range maps of microbial taxa will allow microbiologists to identify geographical boundary-lines similar to what Alfred Wallace discovered for bird species more than 150 years ago. These dispersal limits will reflect the influence of geological and biogeochemical forces along with the biogeography of host

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organisms.

Scales of microbial life: Macroecology has long-focused on the scales of space, abundance, and size among macroscopic life. However, microorganisms have more "scales" than all reptiles, fish, and insects combined. For example, Earth is carpeted by ~10^{30} microorganisms and is home to perhaps 10^{12} species that have resulted from ~4 billion years of evolution. There is no grander expanse across which to demonstrate how patterns of abundance, distribution, and diversity emerge from the uncertainties and complexities of individual-level interactions and metabolism. For macroecologists, body size is a variable of particular interest that spans more than 20 orders of magnitude in plants and animals, while explaining important phenomenon such as longevity, geographic range size, and metabolism. Though microbes are small by definition and their body size is bound by the lower and upper limits of independent unicellularity, microbial body size still spans four orders of magnitude, from 0.2 to 750 microns. In the near future, microbial ecologists will determine if body size is as powerful a predictor of microbial ecology and physiology as it has been for, say, mammals ranging from the 30-gram pocket mouse to a 136,000-kilogram blue whale. It remains to be seen whether microbes and macrobes will follow the same rules.

Experimental macroecology: Historically, macroecologists have relied on patterns when making scientific inference. Although this comparative approach has many merits, multiple and opposing processes can give rise to a single pattern. This can be a problem if one is attempting to elucidate the mechanisms that give rise to patterns in abundance, distribution, and diversity. Experiments provide a means of resolving underlying processes, but given the large spatial and temporal scales that are involved with studying the macroecology of plants and animals, manipulative approaches are often infeasible. In contrast, microbial systems provide opportunities for testing mechanisms that underlie macroecological phenomena. Because of their small body sizes and large population sizes, we see scientists beginning to tackle long-standing questions in macroecology using experiments in the laboratory (microcosm or chemostat) or manipulations in the field (mesocosm), while leveraging other cutting-edge molecular, physiological, and imaging-based tools. Macroecologists will tackle problems pertaining to the temporal turnover of microbial communities and diversity. Owing to their capacity for rapid evolution, it may be possible for scientists to consider and test questions related to macroevolutionary processes that give rise to macroecological patterns.

Global change and conservation: In the coming years, it is predicted that natural and managed ecosystems will increasingly be subjected to global-scale forces of environmental change. These forces include, but are not limited to habitat destruction, rising temperatures, eutrophication, and increasing drought and desertification. Global change is expected to drive the distribution, abundance, and diversity of species in ways that are central to conservation efforts, the production of food, the management of diseases, and the functioning of ecosystem. Some macroecologists are beginning to address the risks of global change through the use of species distribution modeling, which has proven to be useful for predicting the abundance or range distributions of taxa arising from changes in environmental conditions and habitat availability. We expect that these types of models will become more commonly used to predict geographic range shifts, invasions, and extinctions of microbial taxa associated with global change. Furthermore, we envision more sophisticated ecosystem models that when combined with

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species distribution models will allow teams of researchers to forecast the impacts and feedbacks of global change and microbially mediated ecosystem functioning.