Trends in Microbiology

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Opinion

Making the Most of Trait-Based Approaches for Microbial Ecology

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There is an increasing interest in applying trait-based approaches to microbial ecology, but the question of how and why to do it is still lagging behind. By anchoring our discussion of these questions in a framework derived from epistemology, we broaden the scope of trait-based approaches to microbial ecology from one oriented mostly around explanation towards one inclusive of the predictive and integrative potential of these approaches. We use case studies from macro-organismal ecology to concretely show how these goals for knowledge development can be fulfilled and propose clear directions, adapted to the biological reality of microbes, to make the most of recent advancements in the measurement of microbial phenotypes and traits.

Highlights

There is increasing interest in the use of trait-based approaches to microbial ecology, and the study of microbes is becoming more and more multidisciplinary.

The development of new technologies and methodologies for studying microbial biodiversity have increased the availability of large-scale datasets on microbial functional traits from diverse habitats.

Trait-based approaches to macro-organismal ecology have improved our capacity to formulate testable hypotheses on ecological dynamics and to foster the exchange of data, methods, and explanations across research teams.

Trait-based approaches to microbial ecology have improved our understanding of mechanisms driving microbial adaptation and coexistence across different environments and offer the possibility to link microbial traits with evolutionary fitness and ecological dynamics.

Shifting Paradigms: Moving to Trait-Based Ecology

Counts of individual organisms and species across space and time have provided valuable insights into the processes governing species distributions since ecology's early days [1,2], but in recent decades these approaches have been criticized for providing only a partial understanding of the adaptive mechanisms driving ecology and evolution. By focusing on the study of phenotypic characteristics that influence organismal fitness across environmental gradients regardless of species identity, trait-based ecology aims to provide mechanistic **explanations** (see Glossary) to ecological patterns and more robust predictions of ecological dynamics and ecosystem function. Grounded in the long-lasting tradition of studying relationships between traits and fitness in evolutionary and population ecology it has in the past few decades been fueled by conceptual developments in the fields of plant and animal ecology [3–5].

Thanks to the increasing availability of data on the diversity of microbial populations and communities, trait-based approaches to microbial ecology are gaining in popularity [6–10] (Box 1). Direct observations of microbial traits and indirect inferences based on genetic data are increasingly used for investigating fundamental ecological questions and have already contributed to the development of knowledge in microbial ecology [113]. We examine these contributions below.

Trait-Based Approaches Have Expanded Our Understanding of Microbial Ecological Processes

One of the most recognized roles of trait-oriented approaches to microbial ecology has been to provide mechanistic explanations of ecological patterns. Bacterial traits have served in identifying adaptive mechanisms important for survival across different types of environment (e.g., plant roots [11,12]; human organs [13]; sponge tissues [14]; soil [15,16]). By analyzing the genomes of single cells of Poribacteria, Kamke and colleagues [14] discovered metabolic pathways indicative of the ability to degrade chains of proteoglycans – important components of their sponge host tissues – thereby providing a mechanism by which these bacteria could survive in their host. A study of the functional genes of soil bacterial communities across a soil pH gradient revealed that adaptation to high-pH soils was characterized by a greater abundance of multiple

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Box 1. Measuring Microbial Traits

While the use of microbial functional traits in the framework of functional ecology – generally conceptualized as characteristics of microbes that might have an importance for their survival in an environment – is relatively recent, there is a long history in microbiology of measuring phenotypic traits of microorganisms. For example, while recent work in microbiology has moved to the use of sequencing-based approaches to identify microbial taxa, a compendium of phenotypic attributes or traits of bacterial taxa [85] was widely used for bacterial species identification and diagnostic purposes for most of the 20th century. We here describe the most common approaches in use today, by classifying them into direct and indirect approaches.

Direct approaches refer to any trait measurement method that characterizes traits of microbes through direct observation of phenotypes. They comprise traditional techniques of microscopy and cultivation for studying morphological characteristics of microbes (e.g., shape, cell wall structure) [85,86]. They also include phenotypic arrays, quantifying the physiological response of microbes (e.g., respiration) to a large range of substrates or stressors [87]. Resource-use traits of microbes can then, for example, be described as the ability to metabolize different carbon compounds such as fructose, or to survive at different salt concentrations. Direct approaches may also involve the monitoring of metabolites (e.g., glucose, fumarate) produced by microbes of interest in culture or in the field, providing a snapshot of their physiological state [88]. This approach, commonly performed through nuclear magnetic resonance or mass-spectrometry analysis, is referred to as metabolomics [89]. Lastly, metaproteomics refers to the analysis of proteins produced by a given sample of microbes, with each of the proteins with known roles for the organism being considered a trait [90]. It is usually performed through mass spectrometry of isolated proteins.

Indirect approaches quantify microbial traits using the sequencing and analysis of genes via genomics, metagenomics (including targeted sequencing of marker genes, as well as shotgun sequencing of environmental DNA) [91], or sequencing of mRNA (via transcriptomics or metatranscriptomics) [92]. These approaches rely on the comparison of gene sequences to databases of described genes or proteins to infer their function and potential use to the microbes. The emergence of high-throughput sequencing has improved the quality of ecological inferences possible through such approaches by increasing the breadth and depth at which diverse microbial communities can be described. Since interpreting the ecological function of single genes is not straightforward, microbial ecologists have commonly used gene hierarchy schemes to describe microbial traits, classifying genes by their contribution to higher-level traits such as metabolic pathways, or environmental sensing pathways [93,94].

transporters (e.g., ABC transporters), allowing a direct uptake of substrates and cofactors [15]. Attention to microbial traits has also led to important advancements in understanding the consequences of organismal adaptations and interactions for ecosystem functioning and productivity [17–20]. Variation in the diversity of microbial traits based on functional genes found in metagenomic samples of ocean water explained shifts in the primary productivity of these communities across the globe, providing insight into the role of ocean microbes in sustaining global productivity [18].

Developing functional explanations for observed ecological patterns also has the benefit of providing mechanistic bases for the development of **corroboratory predictions** (*sensu* Maris *et al*. [21]), aimed at testing the validity of ecological hypotheses, models, or theories. Traits have been used to develop predictions on the importance of different ecological and evolutionary drivers of community assembly through time and space [22,23]. To distinguish the relative importance of selection and neutral processes in driving the assembly of microbial communities, researchers have compared the trait similarity of microbes living in the same community to communities composed of microbes whose traits were drawn randomly from across all samples. A trait similarity higher than expected by chance in observed communities suggests selection on the traits of microbes in several systems [9,23,24].

Functional ecology also holds the further promise of integrating ecological data, methodologies, and explanatory schemes across research groups and disciplines (see [25]) – the operationalization of which also constitutes its greatest challenge. **Data integration** involves the creation and use of tools and standards for assembling and comparing data collected within and among taxa [26], the analysis and interpretation of which helps to improve understanding. Nowadays, it typically requires online infrastructure for standardizing and storing data to facilitate their use and interpretation by

Glossary

Corroboratory prediction: expectation that can be compared with scientific observations to test hypotheses, models, or theories and provide support (or not) to the understanding of a phenomenon [21].
Data integration: design and implementation of tools and standards for assembling and comparing data [26].
Explanation: identification and description of the mechanisms underlying invariant causal relationships [82].
Explanatory integration: use or combination in a new field of research, of hypotheses, models, or theories developed in other disciplines [26].
Functional trait: morphological, physiological, or behavioral trait that impacts fitness by its effects on growth, reproduction, or survival [5].
Fundamental niche: the range of environmental conditions individuals of a species may thrive under.
Generalization: postulation of the occurrence of a pattern or process on a whole system from observation on a part. Generalization through abstraction can help to reduce the complexity of a system to facilitate its interpretation [83].
Integration: formation of an account of a phenomenon that is built from a variety of ideas possibly coming from different levels of organization or disciplines [84].
Methodological integration: creation and use of various methods for developing a more multifaceted understanding of an ecological phenomenon or process than what could be obtained by using these methods individually [26].
Realized niche: the portion of the range of conditions individuals of a species are actually found to inhabit, due to constraints on the occupancy of their fundamental niche.

researchers of different backgrounds. Data integration has been one of the strengths of microbial ecology, having relied on the development of databases for storing, organizing, and sharing large amounts of genetic data [27,28]. Benefitting from those infrastructures, phenotypic data and functional annotations of full genomes and metagenomes are now being added to existing or new databases such that trait information is more readily retrievable and comparable (e.g., [29–33]). The growth of protein description databases has also helped to develop more precise and accurate functional predictions [34]. Data integration in microbial functional ecology is lastly being fostered by the development of elaborate methodologies (e.g., [35]), refined ontologies (e.g., [36,37]) and standardized pipelines (e.g., [38]) for collecting and processing massive standardized trait data sets (see also Box 1). Such methodologies are further making the collection of data more uniform and comparable among research groups, facilitating **generalization**.

Methodological integration concerns the development and use of a range of methods for the study of a given ecological pattern or process. It is aimed at developing a multifaceted understanding of the results that improves on using each method individually [26]. The concurrent use of phenotypic microarrays and next-generation sequencing have, for example, been used to characterize the real-time functional capabilities of specific microbial taxa to understand adaptive mechanisms underlying their endophytic lifestyle [39]. The parallel sequencing of a microbial community's genomes and transcriptomes has similarly helped to characterize differences between the **fundamental niches** and **realized niches** of these communities [7,40].

Finally, **explanatory integration** involves the use of a combination of hypotheses or theories developed in other disciplines in a new area of research, which may or may not lead to theoretical unification [26]. While a call for explanatory integration in microbial ecology to foster ecological understanding was made more than a decade ago [41], such types of integration are now just emerging. For example, Werner and colleagues [42] proposed a reapplication of market theory adapted from economics to provide explanations of cooperative behaviors in microbes by characterizing resource investment strategies (a key concept in functional ecology) across varying conditions. In order to partition the relative contributions of different processes carried on by microbial communities to dinitrogen production in a marine habitat (here anammox and denitrification), Reed and colleagues [43] adapted models of chemical dynamics developed in biogeochemistry to functional gene abundance data from environmental genomic studies. Comparing their model with experimental data, they were able to confirm a larger role for denitrification in N_2 production. This type of integration, however, remains rare.

When achieved via **functional traits**, explanation, prediction, and integration may finally serve a further goal for the development of knowledge in ecology. They provide a foundation for the generalization of research results irrespective of taxonomic identity across the globe, facilitating the search for general laws, theory development, and the elaboration of large-scale predictive models. A world-wide comparison of the relative abundance of nitrogen-cycling pathways in soil microbial communities has, for example, revealed that, while the abundance of nitrogen pathways tended to vary biogeographically as a function of C and N concentrations, their relative proportions tended to correlate across soil samples [44]. This observation supported the hypothesis that habitats in which microbes can successfully exploit one pathway will also support higher number of cells that can exploit other N pathways, possibly leading to faster nutrient cycling rates.

Opportunities and Challenges in the Study of Functional Microbial Ecology

The various types of studies mentioned above provide examples of the opportunities for using traits in microbial ecology with the objective of improving ecological understanding. Specific opportunities provided by microbial study systems include their large variety of physiologies and resource-use strategies, providing a playground for the study of adaptive mechanisms and the ecoevolutionary generation of biological diversity. For example, the incorporation of organismal optimum temperatures and light intensities for growth, as well as their capacity for assimilating nitrate and metabolizing silica, all contribute to improving models of community structure and predictions of ecosystem function and biogeography in marine phytoplankton [45]. From integrative and pragmatic standpoints, microbial ecologists can also benefit from existing infrastructure developed for the sharing of trait data, as well as several free online platforms for standardizing the treatment and analysis of functional trait data [46,47]. This potential has, however, not yet been fully realized (Figure 1, Key Figure). We next examine current challenges in the implementation of microbial functional ecology and their consequences for the different aspects of knowledge development.

Lack of a Working Definition of a Microbial Functional Trait

As much as scientific progress has been made by the use of traits in microbial ecology, individual studies have rarely defined the functional trait concept for microbes or explicitly linked traits to components of fitness as has been done for macro-organisms (but see [48,49]). This has limited the capacity of traits to identify adaptive mechanisms and the potential for explanatory power. The lack of a standardized definition of microbial traits has further limited our possibility to compare results across trait-based studies, impacting the potential for integration. This issue

Key Figure

Key Steps for Trait-Based Approaches in Improving Understanding of Microbial Ecology

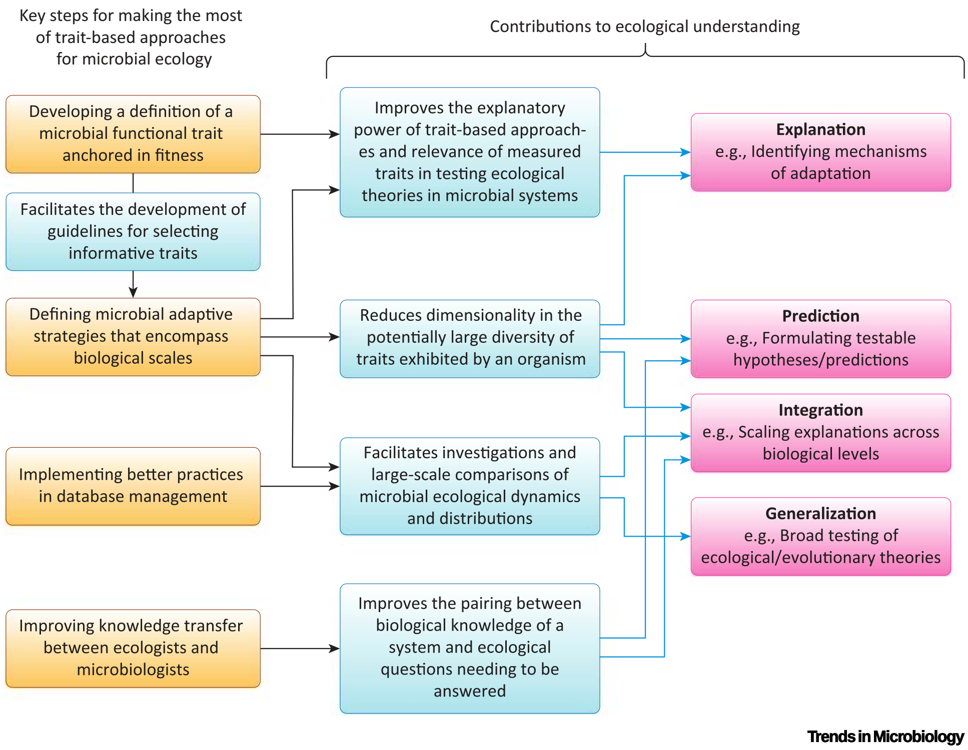

Figure 1. Each step can contribute to ecological understanding via different mechanisms, described in the blue boxes.

may stem in part from the difficulty of applying existing concepts of functional traits developed in plant and animal ecology to the reality of microbial life (Box 2).

Large Diversity of Microbial Lifestyles

The diversity of microbial lifestyles is another facet of the challenge to the standardized use of functional trait approaches. It encompasses three distinct issues. First, a large diversity of traits may be of potential adaptive significance. Second, many potentially important microbial traits may not have been documented yet [50]. This problem is especially evident when trying to attribute functions to gene sequences for which associated proteins are rarely experimentally characterized, and in many cases do not sufficiently match any characterized protein to allow their function to be predicted by homology [51,52]. Third, this diversity of traits has led to a diversity of ways by which researchers select traits to study [53], leading to the study of potentially distinct gene families depending on the specific interests and expertise of a research group; examples include methane oxidation [54], glucose utilization [55], and nitrogen cycling [44]. In turn, we are witnessing a diversity of ways in which microbial traits are studied (Box 1).

These situations have led to consistent context-dependence in interpreting ecological patterns and dynamics of microbial traits among systems, making integration and generalization more challenging among research groups and study systems. In part to address such concerns, and also to account for the fact that the functions of many individual genes are still poorly understood, microbial traits are frequently classified and analyzed at broad levels, for example ‘metabolism’ or ‘cellular processes’ (Box 1). This approach seems necessary given the inability to characterize the precise function of many genes, but it limits inference of adaptive mechanisms driving differences in relative abundances of microbes across habitats. Finding the right level at which to aggregate microbial trait data to maximize explanatory power will require more investigation and improvement in our ability to annotate and classify gene functions [53,56].

The complexity of microbial trait measurement methods likewise constitutes a barrier to integration and generalization, promoting compartmentalization of research groups around technical specialties (e.g., metabolomics, metagenomics, proteomics – see Box 1). This compartmentalization is further encouraged by the prohibitive costs of some technologies, with costs for analysis running to hundreds or thousands of dollars per sample (e.g., SWATH-MS for assessing protein identity [57]), leading to technical limitations and cost-determining methodology for many research groups. Finally, the

Box 2. Challenges in Translating the Concept of Functional Trait from Macro-organismal to Microbial Ecology

The concept of a functional trait used in macro-organismal ecology is essentially a selective one: ecologists aim to use traits that explain differences in fitness among individuals [5]. For plants and animals, the notion of fitness and heritability of traits is relatively straightforward, as they are generally multicellular organisms that reproduce and transmit their traits vertically to their descendants. As a result, both the trait and the measure of fitness (e.g., the number of descendants) can be traced back to a single individual. Microbial ecologists trying to adapt this concept of the trait to the reality of microbial biology have been confronted with several challenges. First, it has been difficult to apply an individual-based definition of trait to microbes due to their potential for horizontal gene transfer with other cells irrespective of phylogenetic identity [95]. Other phenomena, such as the aggregation of microbes into biofilms that can be selected upon as a group [96], or oppositely the presence of genetically diverse nuclei observed in single fungal mycelia [97], make it even harder to target individual microbes as units of selection. The difficulty in measuring trait and fitness at the level of individual cells is another facet of the problem. Commonly used environmental sequencing approaches do not allow the attribution of sequences to individuals, but are rather grouped by sequence variants or taxonomic units [98]. The lowest level at which they are defined is thus generally the population, requiring the use of fitness measures such as the population growth rate, or population size. Technical solutions such as flow cytometry and single-cell genomics [99] offer the possibility of characterization of functional traits of individual cells, but these approaches are still in their early stages of development. Whether these approaches will provide a standard and easily applicable way to perform trait-based ecology remains unknown. Whether a definition of functional traits focusing on individual cells or organisms can or should be adopted in microbial ecology is yet another open question (see main text and [100]).

analysis of high-dimensional microbial trait space data poses a technical challenge to traditional statistical analyses, both in terms of bioinformatics infrastructure and expertise requirements, and due to the expense associated with replication of samples [58].

Incomplete and Biased Databases

Annotation of microbial functional traits requires the use of reference databases, but current databases of microbial traits are phylogenetically incomplete and biased. These databases have far better representation of microbial taxa associated with certain ecosystems, in particular those microbes of importance for human health and those that can be grown in culture [59]. While these data are valuable for certain microbial systems, such as the human microbiome, the extent to which the ecology of human-associated microbes matches that of their relatives in other environments limits the quality of the inference that can be drawn from using their genomes for predicting traits of microbes from environmental samples [60]. Biases in the phylogenetic origin of microbes in trait databases further limit the investigation of general (i.e., context-independent) drivers of ecological and evolutionary dynamics in microbial communities.

Certain data management practices have also been limiting progress in integration. The general lack of metadata associated with sequence data complicates meta-analyses on fundamental ecological questions among studies and ecosystems. For example, different studies may define or measure different environmental variables when quantifying microbial functions. Data curation practices prior to integration in a database, such as sample preservation conditions, are often undescribed, despite the fact that these conditions can have significant impacts on the measured diversity and relative abundance of key taxa in the samples [61].

Lack of Clear Ecological Hypotheses in Many Trait-Based Studies

Initial studies on microbial traits have mostly focused on describing phenotypes and physiological mechanisms for understanding the biology of microorganisms and for identification of different microbial taxa in culture [62]. While some have argued that microbial ecology is still in a ‘discovery’ phase where collection of data without specific tests of ecological hypothesis is normal or desirable [63], there have been ongoing calls by microbial ecologists to develop a more explicitly hypothesis-based science of microbial ecology in order to move forward [41,64]. Some go further in arguing that microbial systems could actually represent ideal systems to test and expand on existing theory [65,66]. While researchers have been using trait-based approaches to identify linkages between microbial community structure and ecosystem processes, direct empirical tests of these predictions are still largely lacking ([67], but see [68]).

Next Steps for Trait-Based Approaches in Microbial Ecology

Developing a Definition of a Microbial Functional Trait

A first major step to be taken in improving the contribution of microbial functional trait approaches would be to develop a definition of a functional trait in the microbial realm. In particular, this definition would include identification of the units of selection that are being discussed and worked on. A clear definition of a microbial functional trait would facilitate the development of guidelines for selecting informative traits, which should consequently improve the explanatory power of trait-based approaches. We suggest adopting the definition of a functional trait in current use for plants and other macro-organisms – that a functional trait is any attribute of an organism that can be linked to its fitness [5]. This adoption will require a shift from purely sequence-based approaches to quantifying microbial functions, towards incorporation of data from direct measurement of microbial population and cellular growth, performance, and survival (e.g., monitoring of cell densities, biomass incorporation, or respiration rates) [69,70].

Defining Microbial Adaptive Strategies That Encompass Biological Scales

A next step forward in microbial ecology research would be the search for major axes of adaptive variation within and among taxa, as has been performed in fields such as plant ecology [71–73] (Box 3). In other words, questions such as 'Are there universal adaptive strategies across microbes?' or 'What types of functional traits have driven the generation of their evolutionary diversity?' should be addressed. The investigation of overarching adaptive strategies among organisms also serves the pragmatic purpose of reducing dimensionality in the potentially large diversity of traits exhibited by an organism. While some researchers have attempted to apply some of the categorizations developed in macro-organismal ecology to the microbial realm [74,75], their use has so far been limited as these categories have not been easily applicable and measurable across taxa. Reducing thousands of potential traits to a smaller number of measurable functions that are consistently correlated with each other and with the ecological strategies of microbes will help researchers focus investigations and, in turn, address common issues such as time and budget limitations. For the foreseeable future, collecting microbial trait data will remain fairly expensive and time-consuming, making the use of a limited set of functional traits to study even more important.

Implementing Better Practices in Database Management

Much of the research in microbial ecology makes use of online databases of information on microbial phenotypes, functional genes, and proteins. An ongoing challenge to make the most of these data is the improvement of metadata collection and reporting to facilitate investigations and large-scale comparisons of microbial ecological dynamics and distributions (see also [63,76]). Such metadata include the methods used in preliminary analysis of the data and environmental conditions in which the data were collected, including relevant features of the host or habitat from which microbes were collected. While minimal information standards have been developed [77,78], their adoption and appropriation by practicing scientists remain difficult without proper large-scale consultations of all experts

Box 3. History of Research on Functional Strategies in Macro-Organismal Ecology

The classification of living organisms has a long history and has allowed comparisons of taxa to each other via measurable differences in their morphology, physiology, or behaviors [101]. One of the first major contemporary ecological classification systems was the r-K selection spectrum which aimed to explain life-history evolution [102]. This classification recognizes a trade-off between r-selected species, reproducing at fast rates with less investment in each offspring, and K-selected ones, reproducing at slower rates and investing more in the success of each reproductive unit. Popularized by MacArthur and colleagues in the 1960s and 1970s, it was most famously used in building models of population dynamics as part of the theory of island biogeography [2]. Since then, it has more generally been used to conceptualize how density-dependent regulation and resource availability may be shaping the evolution of life-history [103]. Building on the r-K spectrum, the CSR (competitor – stress-tolerant – ruderal) classification system was later developed by plant ecologists [72] to explain species variation to environmental variation, based on two types of gradient: stress and disturbance. Competitive species (C) grow best in low-stress and low-disturbance habitats, while the stress-tolerant (S) thrive under high-stress and low-disturbance, and the ruderal (R) is most adapted to low-stress and high-disturbance environments. Until recently [104,105], the difficulty of classifying animals and plants using these systems without prior study in cultivation or captivity made it difficult to apply them at large scales to facilitate integration and generalization of research results across biological scales and biomes (see main text). The identification of main axes of measurable trait variation across species, and the investigation of their global distribution, was the next step in addressing this issue. Thus, plant ecologists developed the leaf-height-seed (LHS) scheme [71,106], representing three important axes of adaptive strategies that could easily be measured across many species and which explained more precisely the ecological trade-offs and variation among plant species at local and global scales. The LHS scheme proposed three phenotypic traits of plants that could be used as surrogate measures for plant ecological strategies: (i) specific leaf area (the area of the leaf divided by its dry mass) as a proxy of resource conservation strategies, (ii) height as a proxy for energy acquisition and response to disturbance strategies, and (iii) seed weight as a proxy for dispersal and colonization strategies. Subsequent development of plant functional trait strategy schemes have included the incorporation of below-ground resource investment strategies [107], and as world-wide observations of plant functional traits are being collected, this framework has been expanded [73,108]. Plant functional traits are increasingly reported in open-access databases [109], and the availability of these data has helped to explain the distribution of plant species among habitats and coexistence within habitats [110,111]. They have also been used in building predictive models of ecosystem function [112].

concerned. Built-in support for third-party annotations of records by expert users may also represent a way forward in improving the completeness of data in curated databases [28]. Enforcement of these standards by database managers is nevertheless challenging and will require better funding for the operation and curation of these databases.

Improving Knowledge Transfer between Ecologists and Microbiologists

The limited use of microbial traits in testing ecological theories might be due to a divide in the current practice of microbial ecology by microbiologists versus nonmicrobial ecologists, separated by a history of distinct scientific traditions and publishing journals [79]. The pairing between ecological questions needing to be answered and the biological knowledge of a system that could best serve these questions is made difficult for each side in the absence of active knowledge transfer. While there is no panacea in bridging that divide, it will be extremely important to work towards developing common definitions of concepts and providing their explicit definitions and explanations in publications and conferences that cross disciplinary boundaries (e.g., [80]). Fostering pre- and postpublication peer review by researchers with different backgrounds will also help to make the most of each discipline's experience.

Concluding Remarks

Fostered by the development of high-throughput sequencing technologies, trait-based approaches to microbial ecology have accelerated the development of ecological knowledge of a highly diversified branch of the tree of life. These approaches have yet been successful in documenting the mechanisms by which microbes adapt to their environment, providing explanations to the variation in microbial life observed across several systems as well as insight into the generation of biological diversity. A strong bioinformatics capital in the discipline has further simplified online data sharing and thus increased opportunities for integration of results worldwide.

Knowledge development in microbial ecology could, however, be improved by a more consistent use of functional traits in generating predictions for testing ecological theories, and in better data and theory sharing between all practitioners of microbial ecology to facilitate integration and generalization of research results. We have argued here that the first step in reaching these goals should be to reach an agreement on what constitutes a valuable microbial trait to study [81]. Building on definitions of functional traits developed in plant ecology, we suggest that adopting a concept of functional traits anchored in adaptation and fitness would increase both the explanatory power of trait-based approaches and their relevance in testing ecological theories in microbial systems. The identification and use of major microbial adaptive strategies, combining numerous covarying traits, could further facilitate the methodological integration of trait-based results among research teams studying trait variation at different biological levels and with different methodologies and simplify the high-dimensionality of microbial trait data, which remain challenging to analyze and interpret (see Outstanding Questions). All in all, adopting a plan of action that seeks to firmly link microbial functions with fitness offers the promise to greatly accelerate knowledge development in microbial ecology.

Outstanding Questions

How should we define, identify, and measure the functionally important traits of microbes?

Are there universal adaptive strategies across microbes?

What types of functional traits have driven the generation of evolutionary diversity in microbes?

Are the ecological processes driving the distribution of microbes worldwide analogous to those driving the distribution of macro-organisms such as plants and animals?

What should minimum information standards for reporting microbial trait data be, and what incentives would be necessary for their generalized implementation?

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