REVIEW SUMMARY

MICROBIOME

Microbiomes in light of traits: A phylogenetic perspective

Jennifer B. H. Martiny,* Stuart E. Jones, Jay T. Lennon, Adam C. Martiny

BACKGROUND: Microbial communities—microbiomes—are intricately linked to human health and critical ecosystem services. New technologies allow the rapid characterization of hundreds of samples at a time and provide a sweeping perspective on microbiome patterns. However, a systematic understanding of what determines microbiome diversity and composition and its implications for system functioning is still lacking. A focus on the phenotypic characteristics of microorganisms—their traits—offers a path for interpreting the growing amount of microbiome data. Indeed, a variety of trait-based approaches have been proposed for plants and animal communities, and this approach has helped to clarify the mechanisms underlying community assembly, diversity-process relationships, and ecosystem responses to environmental change.

Although there is a growing emphasis on microbial traits, the concept has not been fully appreciated in microbiology. However, a trait focus for microorganisms may present an even larger research opportunity than for macroorganisms. Not only do microorganisms play a central role in nutrient and energy cycling in most systems, but the techniques used to characterize microbiomes usually provide extensive molecular and phylogenetic information.

ADVANCES: One major difference between macro- and microorganisms is the potential for horizontal gene transfer (HGT) in microbes. Higher rates of HGT mean that many microbial traits might be unrelated to the history of the vertically descended parts of the genome. If true, then the taxonomic composition of a microbiome might reveal little about the health or functioning of a system. We first review key aspects of microbial traits and then recent studies that document the distribution of microbial traits onto the tree of life. A synthesis of these studies reveals that, despite the promiscuity of HGT, microbial traits appear to be phylogenetically conserved, or not distributed randomly across the tree of life. Further, microbial traits appear to be conserved in a hierarchical fashion, possibly linked to their biochemical and genetic complexity. For instance, traits such as pH and salinity preference are relatively deeply conserved, such that taxa within deep clades tend to share the trait. In contrast, other traits like the ability to use simple carbon substrates or to take up organic phosphorus are shallowly conserved, and taxa share these traits only within small, shallow clades.

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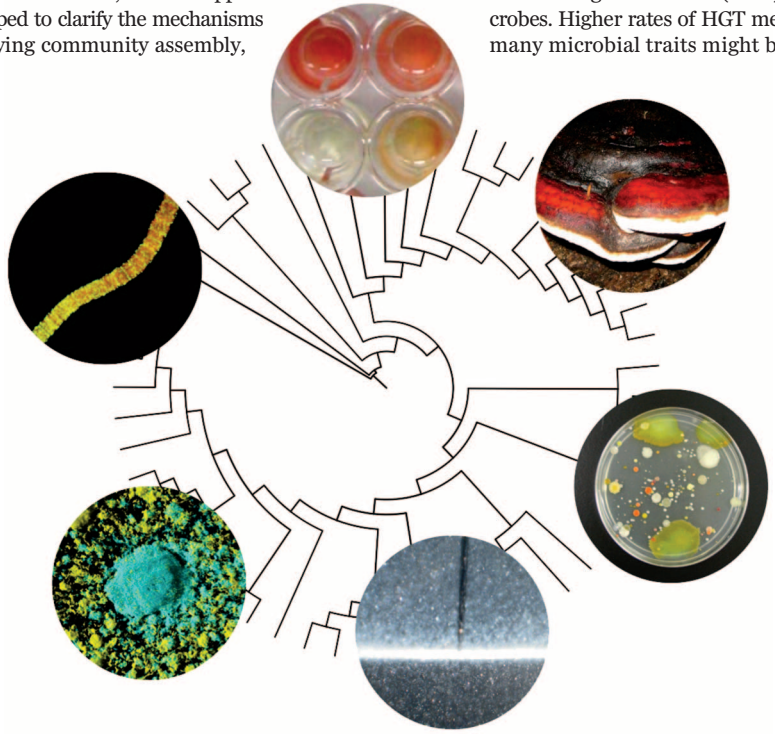

Measuring and mapping the phylogenetic distribution of microbial traits. Microbial traits encompass a range of phenotypic characteristics that vary in complexity, including (clockwise from top) virus resistance, cellulose degradation, salinity preference, nitrogen fixation, biofilm formation, and the production of alkaline phosphatase. Each trait can be measured in innumerable ways. For instance, it can be described by discrete or continuous metrics (e.g., the presence of a gene versus the number of gene copies) of potential or realized phenotypes (e.g., those assayed by functional metagenomics versus in situ activity). [Credits: C. Wiehe; M. Maltz; J. Martiny; L. Riemann; J. Haagensen; K. Frischkorn]

OUTLOOK: The phylogenetic, trait-based framework that emerges offers a path to interpret microbiome variation and its connection to the health and functioning of environmental, engineered, and human systems. In particular, the taxonomic resolution of biogeographic patterns provides information about the traits under selection, even across entirely different systems. Parallels observed among human and free-living communities support this idea. For instance, microbial traits related to growth on different substrates (e.g., proteins, fats, and carbohydrates) in the human gut appear to be conserved at approximately the genus level, a resolution associated with the level of conservation of glycoside hydrolase genes in bacteria generally. A focus on two particular types of traits—response and effect traits—may also aid in microbiome management, whether that means maintaining human health or mitigating climate change impacts. Future work on microbial traits must consider three challenges: the influence of different trait measurements on cross-study comparisons; correlations between traits within and among microorganisms; and interactions among microbial traits, the environment, and other organisms. Our conclusions also have implications for the growing field of community phylogenetics beyond applications to microorganisms. ■

The list of author affiliations is available in the full article online.
*Corresponding author. E-mail: jmartiny@uci.edu
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REVIEW

MICROBIOME

Microbiomes in light of traits: A phylogenetic perspective

Jennifer B. H. Martiny,[1]* Stuart E. Jones,[2] Jay T. Lennon,[3] Adam C. Martiny[1,4]

A focus on the phenotypic characteristics of microorganisms—their traits—offers a path for interpreting the growing amount of microbiome data. We review key aspects of microbial traits, as well as approaches used to assay their phylogenetic distribution. Recent studies reveal that microbial traits are differentially conserved across the tree of life and appear to be conserved in a hierarchical fashion, possibly linked to their biochemical complexity. These results suggest a predictive framework whereby the genetic (or taxonomic) resolution of microbiome variation among samples provides information about the traits under selection. The organizational parallels seen among human and free-living microbiomes seem to support this idea. Developments in this framework may offer predictions not only for how microbial composition responds to changing environmental conditions, but also for how these changes may alter the health or functioning in human, engineered, and environmental systems.

Microbial communities—microbiomes—are intricately linked to human health (*1*) and critical ecosystem services (*2*). New genetic technologies allow for the rapid characterization of hundreds of microbiome samples at a time (*3*, *4*). Although these data provide a sweeping perspective on microbiome patterns, we still lack a systematic understanding of what determines microbiome diversity and composition and its implications for system functioning.

A focus on microbial traits could help address this challenge. All of biology deals with traits, the phenotypic characteristics of organisms. Natural selection operates on traits within a species, altering or maintaining trait frequencies and the genes underlying them. An organism's traits govern its physiology and its interactions with other species and the environment. Ultimately, the collective traits of a community interact with the environment to regulate ecosystem functioning—the biological, chemical, and physical processes that transform nutrients and energy within an ecosystem.

Driven by an effort to be more quantitative and predictive, community ecology has renewed its focus on organismal traits. This approach has helped to reveal mechanisms underlying community assembly (*5*), the relationship between biodiversity and ecosystem functioning (*6*), and an ecosystem's response to environmental change (*7*). Much of current microbiome research—whether in human, natural, or engineered systems—aims to understand similar phenomena. Therefore, a trait-based approach could be useful for microorganisms as well.

Although there is a growing emphasis on microbial traits (*8*–*13*), the concept has not been fully appreciated in microbiology. On the one hand, characterizing microbial traits presents unique challenges. While plant traits, such as leaf thickness and biomass, can easily be measured on individuals from many species in a community context, similar in situ trait quantification of microbial individuals is technically difficult. Grappling with the breadth of evolutionary history of microorganisms also adds enormous complexity.

On the other hand, there are several reasons why a trait focus for microorganisms presents an even larger opportunity than for macroorganisms. First, a primary motivation for a trait-based approach is that particular traits should be closely linked to ecosystem functioning (*14*, *15*). Generally, traits that affect ecosystem functioning are termed "effect traits" (*7*). Most metabolic traits of microorganisms might be considered effect traits as they directly influence processes such as nutrient cycling (e.g., carbohydrate degradation and phosphate acquisition) and trace gas emissions (e.g., methanogenesis and methanotrophy). Thus, the number of gut microbes with the trait to degrade cellulose likely influences the digestion efficiency of plant material, just as the prevalence of microbes that can metabolize or produce methane likely influence the rate of methane emissions from soil.

Second, new approaches allow microbiologists to target the molecular underpinnings of traits from many individuals in a community (*16*), whereas plant traits are either measured on a handful of individuals in a community or inferred from trait databases (*17*). For microbiomes, metagenomics may offer a way to scale from the traits of individual organisms to community processes based on a random sample of individuals from a community (*16*), although not without some limitations (*18*).

Third, genomic techniques available to microbiologists provide phylogenetic information of the traits being characterized and give simultaneous insight into their evolutionary constraints. This phylogenetic context can be applied across different levels of genetic resolution to provide a path to compare results across systems and taxa. The same trait can be studied over short time scales within a population or across the entire tree of life, allowing both strain-level differences and macroevolutionary patterns to be considered. Such a flexible framework is imperative for microorganisms where the time scales of evolutionary and ecological processes overlap (*19*, *20*), but may also be useful for larger organisms (*21*).

Here, we summarize key aspects of microbial traits and recent approaches used to map their phylogenetic distribution onto the microbial tree of life. We place special emphasis on how traits vary in their degree of phylogenetic conservation and discuss the implications of this variation for interpreting microbiome variation. Finally, we present a phylogenetic framework for understanding how traits determine microbial composition and biogeographic patterns across diverse environments, including the human body, oceans, and soils.

Classifying and measuring microbial traits

We define traits broadly to encompass the physiological, morphological, or behavioral characteristics of a microorganism, without regard to whether they can be deconstructed into simpler traits (*22*, *23*). The flexible nature of the trait concept means that it is crucial to consider how traits are classified and measured when making cross-study comparisons (*15*).

One way to classify microbial traits is by their complexity (Fig. 1). The simplest traits are encoded by just one genetic locus, such that an organism's genotype matches a particular phenotype. But most traits are much more complex. Complex traits involve the interactions of many parts of the genome (i.e., epistasis), and their phenotypic manifestations are altered by interactions with the environment (*24*). An example of a simple trait is the ability to produce alkaline phosphatase (encoded by the presence of one gene) and therefore hydrolyze phosphorus from organic compounds (*25*) (Fig. 1A). A bacteriophage's host range might also be considered a relatively simple trait (Fig. 1B), as the ability to infect a particular host can be determined by a point mutation at a single locus (*26*). Like any classification system, however, this one is imperfect. When viewed at a broader scale, different constraints operate on host range. Coliphages are restricted to infecting coliform bacteria, whereas cyanophages are restricted to infecting cyanobacteria. Thus, host range probably involves most of a phage's genome and, in this way, is quite complex.

[1]Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA. [2]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA. [3]Department of Biology, Indiana University, Bloomington, IN, USA. [4]Department of Earth System Science, University of California, Irvine, CA, USA.
*Corresponding author. E-mail: jmartiny@uci.edu

Examples of traits		Trait	Type of measurement: Discrete – Potential	Discrete – Realized	Continuous – Potential	Continuous – Realized
Simple	A	Organic phosphate utilization	Alkaline phosphatase activity in culture	Presence of strain in high/low P regions	Enzyme kinetics	Correlation of abundance with organic P gradient
	B	Bacteriophage host range	Infection of a particular host culture	Co-occurrence patterns with bacterial hosts	Rate of adsorption to susceptible hosts	Fraction of bacteria that a phage can infect in a community
	C	Cellulose degradation	Presence of cellulases or cellulosome complex in genome	In situ cellulose degradation	Number of cellulases in a genome	In situ rate of cellulose degradation
	D	Biofilm formation	Ability to form a biofilm in culture	In situ biofilm formation	Biofilm thickness in culture	Relative abundance in biofilm versus nonbiofilm samples
	E	Nitrogen fixation	Ability to fix nitrogen in culture	In situ expression of *nif* genes	Kinetics of nitrogen fixation	Correlation of *nif* genes with N fixation rates
	F	Methanogenesis	Presence of genetic pathway in genome	Ability to produce methane in situ	Methane production kinetics	In situ rate of methane production
Complex	G	Salinity preference	Preference for marine or freshwater media	Found in marine versus terrestrial habitats	Salinity optimum in lab assay	Salinity corresponding with peak abundance

Fig. 1. Examples of microbial traits and their measurement. The traits are ordered vertically from simple to complex and consider not only how many genes are directly involved in encoding the trait, but also how integrated the trait is with the rest of the organism's cellular machinery. While each trait can be measured in a variety of ways, the matrix contrasts discrete versus continuous and potential versus realized measurements (see text). Photos: (**A**) *Trichodesmium* trichome from the Sargasso Sea incubated with the ELF 97 phosphatase substrate. Green labeling indicates sites of alkaline phosphatase activity; orange is autofluorescence of the phycoerythrin pigment. (**B**) Infection of a bacteriophage on the marine cyanobacterium *Synechococcus*. The pink wells are *Synechococcus* without phage; the bottom wells include phage, which lyses the cells and clears the culture's pigments. (**C**) Brown rot fungi like *Antrodia juniperina* degrade cellulose. (**D**) Biofilm of two green fluorescent protein–labeled *Vibrio cholerae* strains imaged by confocal microscopy. (**E**) Growth of a heterotrophic diazotroph in N-free medium with a vertical oxygen gradient. An oxygen microelectrode points to the band of growth. (**F**) Methanogens produce large amounts of methane in the rumens of cattle. (**G**) Diversity of salt marsh heterotrophs growing on high-saline agar. [Photo credits: K. Frischkorn, Dyhrman Lab, Columbia University; C. Wiehe; M. Maltz; J. Haagensen; L. Riemann, University of Copenhagen; K. Dill-McFarland, University of Wisconsin-Madison; J. Martiny]

To further complicate matters, the same trait can be measured in innumerable ways. For instance, all traits can be described discretely or continuously (Fig. 1). The ability of a fungus to degrade cellulose is a discrete metric (Fig. 1C), but the kinetic parameters of a particular cellulase enzyme are continuous, as they describe activity as a function of substrate concentration. The salinity preference of bacteria can be classified into freshwater or marine-occurring species (Fig. 1G), much as plants are traditionally classified into shade-tolerant and sun-loving species. Alternatively, its preference could be defined quantitatively by the salinity of optimal growth.

Another key axis of trait measurement is whether the metric assesses potential or realized phenotypes. Analogous to the fundamental versus realized niche concept used in classical ecology (*27*), the range of an organism's potential phenotypes is likely broader than the range of realized phenotypes that occur in its natural habitat. Thus, the presence or absence of particular genes or pathways in a microbial genome is a discrete assessment of its potential phenotype (*28*, *29*). For instance, codon usage bias and ribosomal RNA (rRNA) operon copy number provide continuous estimates of potential growth strategies (*30*, *31*).

Laboratory assays also measure potential traits, although more directly than genomic information. In particular, physiological performance curves provide detailed predictions about the potential range (niche width) and optimal conditions for a microbe's growth across an environmental gradient [e.g., temperature (*32*) or soil moisture (*23*)]. Laboratory cultures can also be used to test predicted phenotypes on the basis of genome sequences—for instance, whether the number of extracellular enzyme genes reflects an organism's potential to degrade carbohydrates (Fig. 1C). A laboratory study supports this idea for some genes; the number of polyphenol oxidase

genes in fungal genomes was correlated with the enzyme's activity in cultures (*33*).

Nonetheless, an organism's realized phenotype in situ may differ from measures of its potential phenotype. Traits can be modified by interactions with the environment (i.e., trait plasticity) and interactions with other organisms. As a result, a microbe's optimal temperature for growth in the laboratory might differ from the temperature of its maximum abundance in the field (*34*), or the sequence-based inference of gene function may be incorrect (*35*). For plants, realized phenotypes are often quantified in the field (e.g., leaf area or photosynthetic rate). In microbial systems, direct quantification of trait phenotypes "in the wild" is challenging, although technologies such as microautoradiography and fluorescence in situ hybridization (MAR-FISH), nanoscale secondary ion mass spectrometry (NanoSIMS), and cell sorting show great promise (*36*–*38*). Mostly, however, realized phenotypes are inferred from the biogeographic patterns of microorganisms (*39*), which we will return to below.

Phylogenetic conservatism of traits

The collection of traits that defines an organism depends on its evolutionary history. However, the potential for horizontal gene transfer (HGT) among microorganisms means that many traits might be unrelated to the history of the vertically descended parts of the genome (*40*). Gene loss and rapid evolution can further obscure a trait's phylogenetic signal. Yet, recent work indicates that most traits are at least somewhat conserved across Bacteria and Archaea (*11*, *41*), as well as microbial eukaryotes like Fungi (*42*). Specifically, despite the promiscuity of HGT, closely related microbial taxa share more similar traits than expected if the traits were distributed randomly across a phylogenetic tree. [This test of trait conservatism differs from that of phylogenetic niche conservatism, which only considers changes by vertical descent (*43*).]

Not only are microbial traits phylogenetically conserved, but the depth of their conservation differs among traits. This result holds true when using at least three different approaches. The first approach links phenotypic traits of isolates to their evolutionary relatedness. In such studies, microbial traits are quantified by using laboratory isolates and a genetic estimation of phylogenetic relatedness among the isolates. For example, a variety of continuous trait metrics, ranging from maximum respiration rate to optimal soil moisture, were quantified for a collection of heterotrophic bacteria and fungi isolated from soil communities (*23*). Subsequently, the variation of each trait among taxonomic levels was partitioned. For traits associated with soil moisture preference, much of the variation among strains was deeply conserved; more than half of the variation in moisture niche breadth (the tolerance of a strain to variation in soil moisture) could be assigned at the phylum level. In contrast, only one-third of the variability in motility could be accounted for at the class level (Fig. 2A).

Another example comes from a study that probed hundreds of bacterial isolates to determine their ability to grow on a diverse array of carbon substrates (*41*). Here, the depth of phylogenetic conservatism of a trait was estimated from the average sequence distance to the root node of clades, where at least 90% of taxa share the trait. In general, the ability to use each substrate was nonrandomly distributed across the phylogeny; however, the level of conservation of these traits was shallow. Thus, closely related strains of >98% similarity in 16*S* rRNA sequence may still have distinct substrate use profiles.

A second approach quantifies trait conservation by extracting information from the wealth of microbial genome sequences that are available (presently ~30,000). For simple traits, one can quantify the presence or absence of individual genes in a genome. For instance, the potential ability to degrade various carbohydrates can be assayed by the presence of various families of glycoside hydrolase genes (*44*). For more complex traits, one can target particular genomic subsystems or whole-cell metabolic networks (*45*). For example, in an analysis of 19 subsystems across 26 prokaryotic phyla, oxygenic photosynthesis, a trait found only in the phylum Cyanobacteria, was the most deeply conserved subsystem (*41*). In contrast, metabolic capabilities like sulfur oxidation and nitrogen fixation were less conserved, albeit more so than carbon substrate usage (Fig. 2B).

A third way to estimate phylogenetic conservation of traits relies on compositional variation among sampled communities. These patterns can provide correlative evidence about the taxonomic and genetic level at which microbial groups share response traits, or traits that influence how a species' abundance or biomass is altered by an environmental change (*7*, *46*). Thus, the ability to enter dormancy is a trait that may influence a microorganism's response to environmental stresses, such as fire and drought (*47*). Often, however, it is useful to consider a taxon's response to the environment as a trait itself (*22*, *48*), rather than the conglomerate of traits underlying the response (*49*). For instance, the abundance of some bacterial phyla (e.g., Verrucomicrobia, Bacteriodetes, and Acidobacteria) showed significant correlations with soil properties like pH and inorganic nutrient concentrations within a pasture, suggesting that taxa within these phyla share similar traits (*39*). In a larger-scale study of soils collected throughout the United States, bacteria within the class β-Proteobacteria and phylum Bacteroidetes tended to be more abundant in soils with higher organic carbon availability (as measured by carbon mineralization rate), whereas those within the phylum Acidobacteria were more abundant in soils with lower carbon availability (*50*). This pattern indicates that the traits underlying an oligotrophic (low nutrient) or copiotrophic (high nutrient) strategy may be deeply conserved among soil bacteria.

Experiments can also provide evidence about the conservation of response traits. For example, the responses of soil microbes to added water were quantified by rRNA abundances in dry California grasslands (*51*) (Fig. 2C). The response strategies to sudden water availability were highly conserved. Taxa within a phyla responded in a consistent manner; representatives from Verrucomicrobia and Actinobacteria responded quickly, whereas Proteobacteria tended to show more delayed responses. In a longer-term experiment, the responses of grassland leaf litter microbes to 3 years of drought (reduced by temporary rain shelters) and added nitrogen were also significantly conserved (*52*). Here, the depth of response was quantified by correlating the genetic distance between all taxon pairs and the similarity of their response. The responses of fungal taxa to drought and nitrogen were both positively correlated at the finer taxonomic levels (<5% shared 28*S* rDNA sequence similarity; Fig. 2D). However, drought responses were also signficantly correlated at broader levels of taxonomic resolution (up to 7.6% sequence similarity) than were nitrogen responses, indicating that drought responses are more deeply conserved than nitrogen responses.

A hierarchy of trait conservation

To quantify patterns of microbial trait conservatism, we searched for published studies that estimated (or allowed us to estimate) the depth of clades where prokaryotic taxa consistently shared trait values. For instance, clades of the marine cyanobacterium *Synechococcus* show distinct temperature profiles (a continuous, realized metric) on the basis of their biogeographic patterns (*53*). We then estimated the median depth of these different clades using a 16*S* rRNA phylogeny in another study (*54*). In another example, the estimate of the depth of methanogenesis was based on a discrete, potential metric—the presence of this subsystem across all sequenced bacterial genomes (*41*). Such cross-study differences in trait classes and measurement could bias the estimates of phylogenetic depth in some unknown way. At the same time, phylogenetic depth was assayed with the same phylogenetic marker (the 16*S* rRNA gene) in all but one study (table S1), and in this way, the estimates are comparable.

Despite these complications, the synthesis reveals a hierarchy of phylogenetic conservatism among traits. The response traits of pH and salinity preference appear to be relatively deeply conserved (Fig. 3), in agreement with past studies showing that pH and salinity affect the biogeographic distribution of deep phylogenetic clades (*55*, *56*). In contrast, long-term drought response and temperature optimum are more finely conserved, or only shared consistently by taxa within smaller clades of bacteria. A similar hierarchy appears to apply to effect traits involving the use of alternative electron acceptors; methanogenesis is the most deeply conserved trait noted in Fig. 3, whereas dissimilative sulfate reduction and denitrification are notably less so. The effect traits of simple carbon use and organic P uptake seem to be much shallower than those modifying the electron transport chain. Finally, resistance to specific bacteriophage varies depending on particular point mutations and thus, one might argue that this trait is not conserved at all.

Our findings are consistent with the view that traits encoded by more complex subsystems

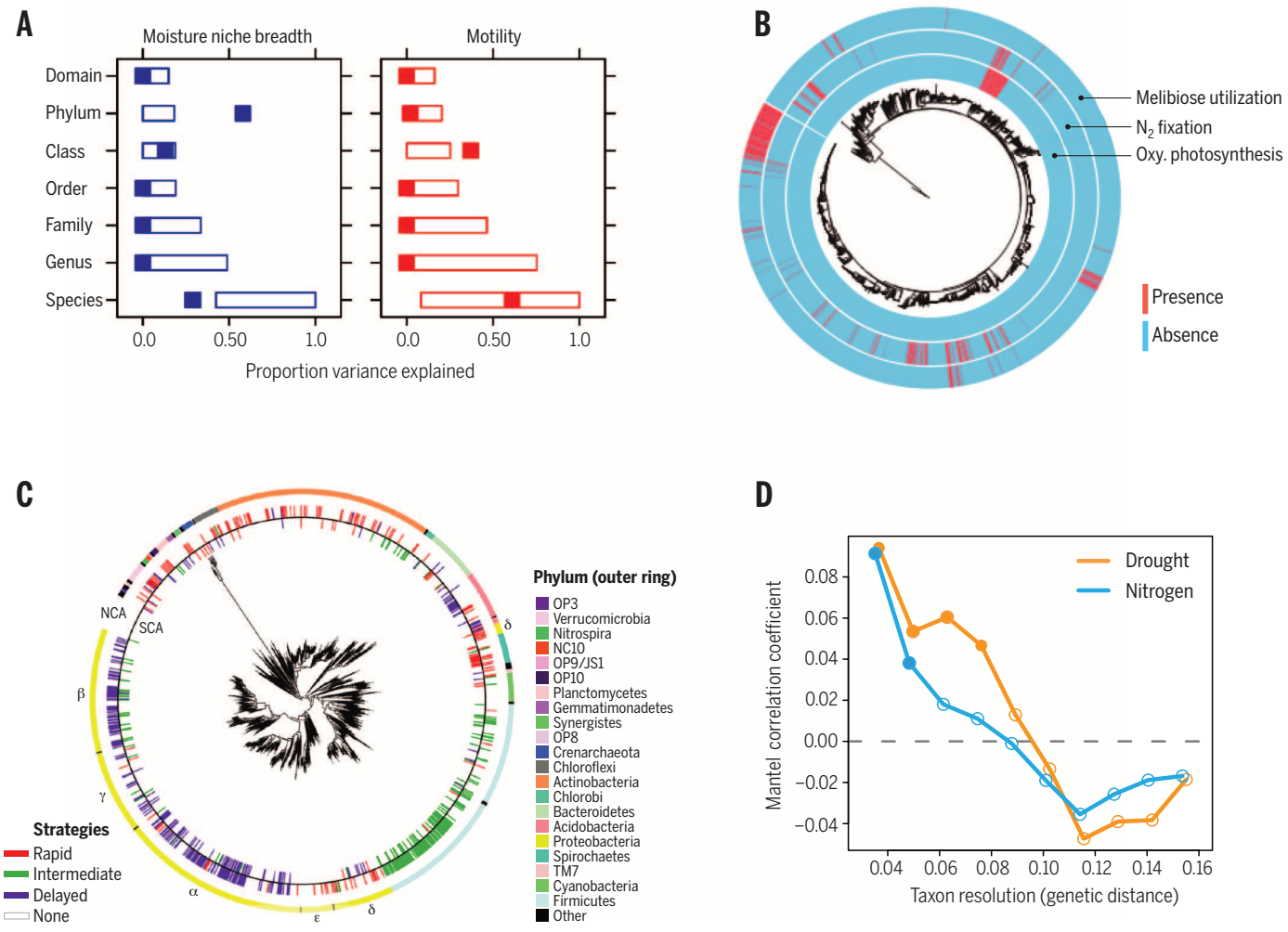

Fig. 2. Evidence for the phylogenetic conservatism of microbial traits. (**A**) By measuring phenotypic traits among a collection of bacterial and fungal soil isolates, variation in moisture niche breadth and motility can be attributed to different taxonomic levels (*23*). (**B**) With the use of data from fully sequenced prokaryotes, the presence (red lines) or absence (blue lines) of genes encoding three traits (the three concentric rings) can be determined. The phylogenetic depth of each lineage sharing this trait can then be quantified and compared against a random model. [Reprinted with permission from (*41*)]. (**C**) An experiment provides information on the phylogenetic distribution of a prokaryote's response to increased water availability. The response strategy (rapid, intermediate, or delayed) of each soil taxon to added water is shown by the red, green, and purple lines in the inner two circles (one for each of two field locations labeled NCA and SCA) around the phylogenetic tree. The outermost ring indicates the phylum designation of the taxa. [Reprinted with permission from (*51*)]. (**D**) A global change experiment suggests that the response of leaf litter fungi to drought (orange) is more deeply conserved than that to nitrogen addition (blue). The significance of the correlation relating the genetic distance between two fungal taxa and the similarity of their response to the treatment (drought or nitrogen addition) depends on the genetic resolution of the taxon definition (filled circles denote a significant correlation and open circles, a nonsignificant correlation). The drought response shows significant correlations at broader resolutions (the genetic distance of the taxon definition) than the nitrogen response. [Redrawn with permission from (*52*)]

involving many interacting proteins are less likely to be subject to horizontal transfer (*41*, *57*). Methanogenesis, the most deeply conserved trait examined, involves a large subsystem of genes for conversion of CO_2 (or acetate) to methane, as well as for synthesizing unique cofactors. In comparison to methanogenesis, dissimilative sulfate reduction requires fewer additional proteins, but does use a unique membrane-bound cytochrome complex and an atypical mechanism for translocation of protons (*58*). Although denitrification uses several unique membrane proteins, it is widely distributed among prokaryotes (*59*) and biochemically quite similar to aerobic metabolism. Thus, it is perhaps relatively easy for denitrification proteins to transfer into an aerobic ancestor (or evolve convergently). At the same time, it seems somewhat surprising that conservation of temperature preference is so shallow, when this phenotype could potentially involve a variety of underlying traits throughout a cell's machinery. However, while this reasoning may apply to extreme temperature adaptation (*60*), a shallow level of conservation suggests that adaptation to minor temperature differences involves simpler traits that evolve on shorter time scales (*61*).

Trait conservatism and biogeography

The idea that traits are hierarchically conserved is directly applicable to the interpretation of microbial biogeography, broadly defined as the spatial and temporal variability in microbial composition among free-living and host environments. To illustrate this point, we first consider the case study of the Cyanobacterium *Prochlorococcus*, for which we know a great deal about both the phylogenetic distribution of its traits and its biogeographic patterns. This phototroph is found throughout the world's oceans, spanning multiple environmental gradients. At the deepest phylogenetic level, *Prochlorococcus* is broadly divided into two groups: high- and low-light adapted clades (Fig. 4A), first defined by physiological measurements of cultured isolates (*62*). At the next-deepest level, metagenomic sequencing suggests that the

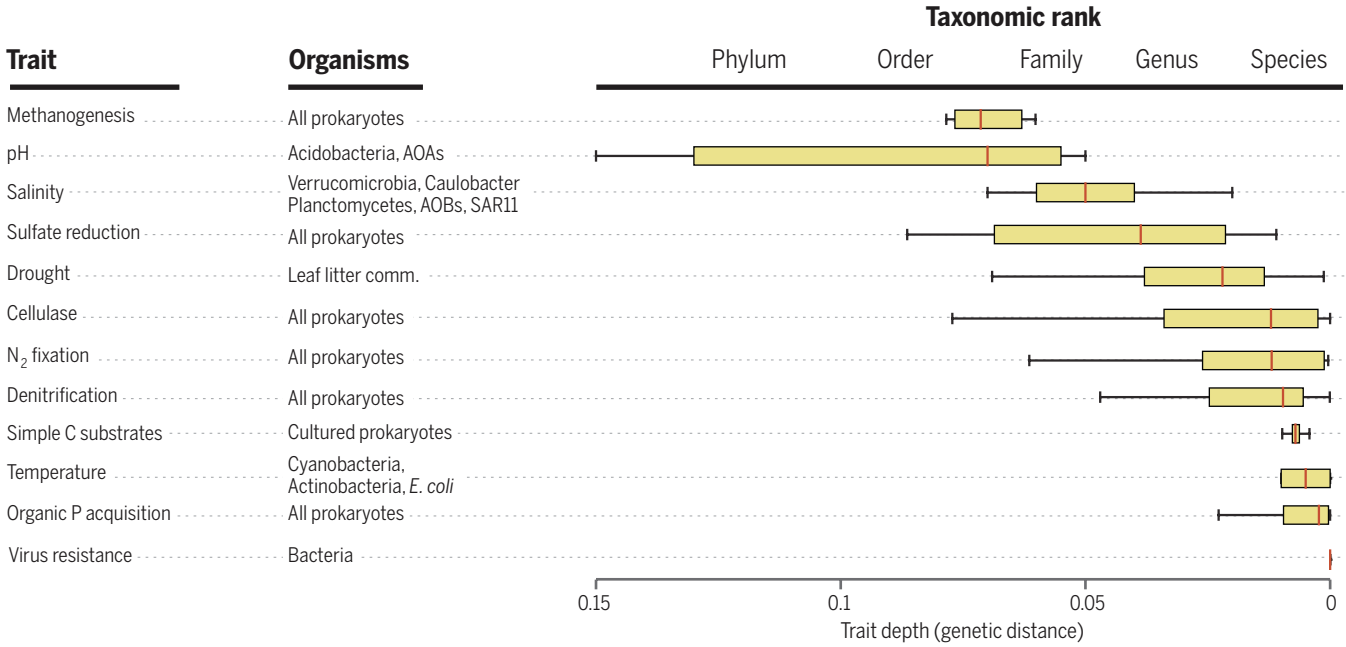

Fig. 3. Prokaryotic traits are conserved at different phylogenetic depths. A box plot of the depth of clades within which taxa consistently share a trait measured as the genetic distance to the root node of a clade (bottom axis; usually of the 16*S* rRNA gene). For some traits, the distribution is based on several studies, each with one estimate. For other traits, we report the distribution calculated by a single study. For comparison, we show rough taxonomic levels on the top axis. Details of studies are reported in table S1.

high-light clade can be divided into high- and low-iron adapted clades (*63*). The high-iron clade can be further divided into subclades that differ in their temperature preferences (Fig. 4A) (*64*), and at the finest phylogenetic scale, genomic and physiological analyses demonstrate variability in nitrogen and phosphorus acquisition traits (*65*–*67*).

The macroevolutionary picture of *Prochlorococcus* traits that emerges is consistent with how its biogeographic patterns depend on phylogenetic resolution. Depending on the sequence similarity used to define a taxon, the ability of specific environmental variables to explain *Prochlorococcus* composition varies in agreement with the relevant traits (Fig. 4B) (*68*). Hence, light level explains a significant amount of compositional variation across samples from the Pacific and Atlantic oceans when *Prochlorococcus* is grouped into broad taxa, whereas nutrient concentrations only explain variation at the finest taxonomic levels.

Although our detailed understanding of the *Prochlorococcus* lineage is exceptional, the idea of differentially conserved traits may generally help to predict compositional variation in any microbial system. Specifically, changes in the environment that select on deep traits should alter microbiome composition at broad taxonomic levels (orange versus blue symbols in Fig. 5). In contrast, selection on shallow traits should result in compositional shifts at finer taxonomic levels (solid versus hatched symbols in Fig. 5). Thus, the resolution at which microbiome composition varies among samples may give information about the phylogenetic conservation of the traits under selection.

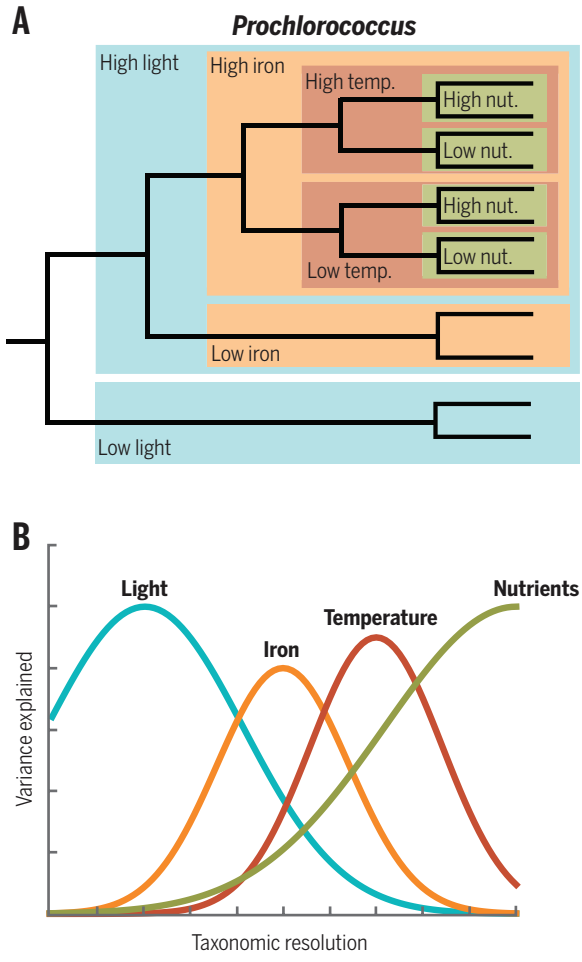

Fig. 4. Trait conservation in *Prochlorococcus* is related to its biogeographic patterns. (**A**) Traits involving adaptations to light, iron concentration, temperature, and nutrient acquisition levels map onto the *Prochlorococcus* phylogeny in a hierarchical manner. (**B**) A schematic of the relationship between taxonomic resolution (usually defined by sequence similarity of a marker gene) and the ability of various environmental variables to explain variation in *Prochlorococcus*. The resolution at which the environmental variables best explain composition (the peak of the curves) corresponds to the phylogenetic depth of distinct trait divisions shown in (A). [Adapted from (*68*)]

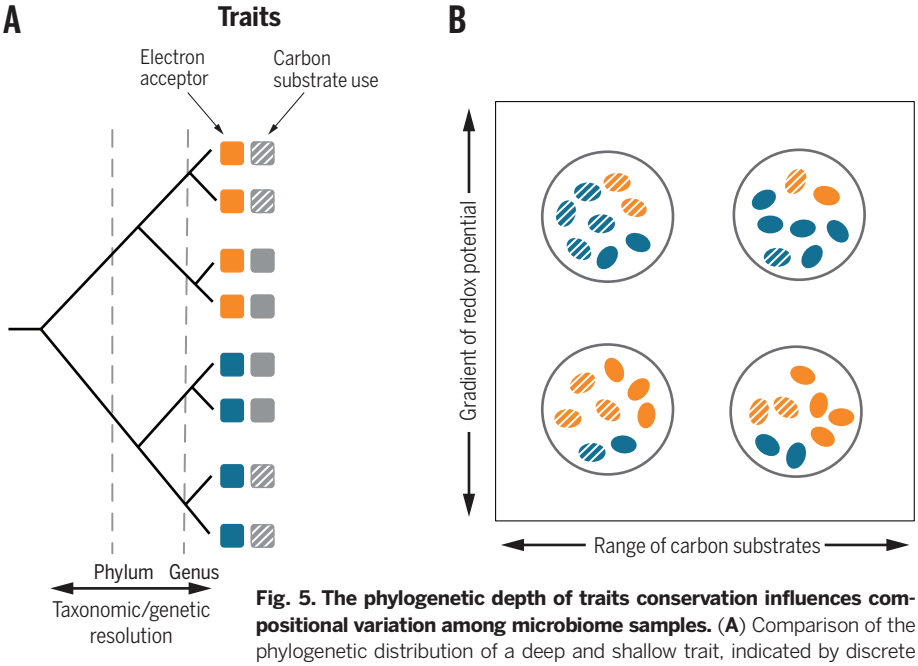

Fig. 5. The phylogenetic depth of traits conservation influences compositional variation among microbiome samples. (**A**) Comparison of the phylogenetic distribution of a deep and shallow trait, indicated by discrete categories for each taxon at the tips of the tree. A deeply conserved trait, such as the ability to use some alternative electron acceptors, is denoted by the orange and blue symbols. A shallower trait, like the ability to use a particular carbon substrate, is denoted by the solid and striped gray symbols. (**B**) How microbial composition shifts among samples will depend on the depth of conservation of the traits under selection. In this cartoon landscape, the large circles represent a sample; the cells within that sample carry traits designated by the colors and patterns in (A). In this example, a change in redox potential across a landscape (*y* axis) alters microbial composition at the phylum level, such that the relative abundance of blue and orange cells is altered. A change in carbon substrate availability (*x* axis) alters composition at the genus level, so that the relative abundance of striped and solid cells shifts, but not that of orange and blue cells.

Both host-associated and free-living systems provide examples of this connection between trait conservation and microbiome variation. The human skin microbiome differs in composition among three habitat types: dry, moist, and sebaceous skin (*69*). Further analysis reveals that these habitat preferences are only consistent [or "coherent" sensu (*39*)] among taxa within the genus or sharing at least 97% 16*S* rRNA sequence similarity (*70*). Exactly which traits are driving this distribution remain to be determined. A common species in moist skin sites, *Staphylococcus epidermidis*, grows aerobically and uses urea as a nitrogen source, whereas the most common species in sebaceous sites, *Propionibacterium acnes*, is a facultative anaerobe and hydrolyzes the triglycerides in skin lipids (*71*).

In contrast, virulence traits of skin microorganisms appear to be even more finely conserved than habitat preference. For example, the genetic differences among strains of *P. acnes* associated with acne versus healthy skin are relatively minor (*72*). Similarly, virulent strains of *S. epidermidis* differ from nonvirulent strains by a four-gene operon involved in biofilm formation and an insertion sequence element, genetic changes that may be associated with horizontal gene transfer (HGT) events (*73*). In general, virulence potential may be a shallow trait, as it often appears to evolve independently via HGT—for instance, among microbes such as *Escherichia coli* (*74*) and *Pseudomonas aeruginosa* (*75*).

Microbial traits related to growth on different substrates (e.g., proteins, fats, and carbohydrates) in the human gut appear to be conserved at approximately the genus level, a resolution also associated with gut enterotypes (*76*). In response to both short- and long-term dietary patterns, gut taxa within a genus seem to respond similarly, whereas the responses of genera within phyla are not consistent (*77*, *78*). Specifically, within the phylum Bacteroidetes, *Bacteroides* species are generally enriched in diets high in protein and fat, whereas *Prevotella* species are enriched in diets high in carbohydrates. These compositional shifts may be due to selection for traits, such as the ability to degrade particular carbohydrates (*79*) and bile tolerance (*77*). Echoing the taxonomic level of these diet responses, an analysis of bacterial genome sequences finds that bacterial glycoside hydrolase (GH) genes are generally conserved at the genus or species level (*44*). Supporting this pattern, family level is not predictive of the abundance of carbohydrate-active enzymes (GHs and polysaccharide lyases) encoded by human-associated bacterial genomes (*80*).

Finally, chronic gut syndromes in humans appear to differ from those of healthy microbiomes at even broader taxonomic levels. Thus, the composition of gut microbiomes from inflammatory bowel disease (IBD, including ulcerative colitis and Crohn's disease) patients differs from that of healthy microbiomes at the class and phylum levels (*81*). The relative abundance of taxa within the class Clostridia and phylum Bacteroidetes decreased in IBD patients, whereas taxa within the Proteobacteria and Bacilli increased. Similar community patterns were observed in patients with *Clostridium difficile* infections relative to that of healthy volunteers also receiving antibiotic treatment (*82*). These broad-scale shifts suggest that inflammatory conditions impose selection for deep microbial traits, perhaps related to oxygen and redox potential preference. Likewise, the phylum-level shifts found along redox gradients in ocean oxygen minimum zones or sediment profiles (*83*, *84*) are parallel to the broad changes found in chronic gut syndromes.

Challenges and implications

Microbial traits appear to vary consistently in the degree to which they are conserved. Further, the parallels among host-associated and free-living communities suggest that this hierarchy of trait conservation may underlie similar community shifts across entirely different systems. Specifically, we propose that selection on shallow traits in a microbiome will lead to fine-scale taxonomic shifts, whereas selection on deeper traits will lead to broader-scale shifts. Thus, viewing microbiome patterns in light of traits in one system can provide an initial hypothesis for the distribution of traits in other systems. Such hypotheses may further shed light on unexplained microbiome variation by narrowing down the traits that might be under selective pressure.

It is worth highlighting several obstacles to inferring the level of trait conservation from distributional patterns. First, interpretations about trait conservation will be sensitive to the particular taxa present in a study. If a phylum is only represented by a handful of narrow lineages, then these lineages may not be representative of the phylum in other systems. A similar issue arises when interpreting variation in the abundance of broad taxonomic groups, without regard to whether individual lineages within those groups vary consistently (*70*). In both cases, the trait of interest might be conserved at a finer phylogenetic level than suggested by the samples at hand.

Second, we have primarily discussed traits in isolation to one another, but for a variety of reasons, traits within and among taxa are often correlated (*85*), presenting challenges and opportunities for studying microbial traits. For example, within an organism, the use of methods such as metagenomics and metatranscriptomics to characterize some traits might be misleading, because interactions with other traits might be essential to their realized phenotype (*18*). Across taxa, if many traits are correlated, then one may be able to reduce the multidimensionality of microbial traits. This idea is demonstrated well by the leaf economic spectrum in plants; the combination of leaf traits in a plant species appears constrained by physiological trade-offs (correlations) between these traits (*86*). Correlations between response

and effect traits may also present an opportunity for predicting how changes in environmental conditions lead to changes in microbial functioning (*46*, *48*). For example, a model based on the response and effect traits of phytoplankton performed well in predicting gross primary production in lakes across a variety of environmental conditions (*87*).

Last, the extent to which gene-by-environment interactions (trait plasticity) and biotic interactions (such as microbe with microbe or host with microbe) influence microbial composition is unclear. Such interactions might hinder inferences across systems, but with so little comparative data on these issues [but see (*88*)], it is difficult to speculate about the importance of this complication.

Our conclusions also have implications for the growing field of community phylogenetics (*89*–*91*) beyond applications to microorganisms. For instance, one question of broad interest is whether phylogenetic diversity (the amount of phylogenetic distance between all species in a community) influences ecosystem functioning (*92*, *93*). A hierarchy of trait conservation would imply that the strength of this relationship should depend on the traits involved. Variation in traits that are generally finely conserved (such as simple carbon usage or nutrient uptake for microbes) may not be captured by phylogenetic relatedness metrics that emphasize deep relationships between species. This might explain why some studies find a phylogenetic diversity-functioning relationship (*94*) and others do not (*95*).

Likewise, differences in trait conservation may help to explain the mixed support for the hypothesis that evolutionary relatedness can help predict the outcome of species interactions (*96*). For example, if the outcome of competition depends on a microbe's ability to acquire organic phosphate, a trait that seems to be finely conserved, then the large phylogenetic distance between most species in the community may not be correlated with their competitive outcome. In contrast, if the outcome depends on niche partitioning of a moisture axis, which seems to be more deeply conserved, then phylogenetic distance might better capture this trait variation.

There is growing evidence that microbial composition can directly affect functioning in human and environmental systems (*97*, *98*). This fact has practical implications for human health, engineering, and natural environments (*99*–*101*). However, it remains unclear when and where microbial composition will be functionally relevant. For microorganisms specifically, a phylogenetic trait framework offers a path toward a predictive understanding of this role. Pinpointing the effect and response traits responsible—and their degree of phylogenetic conservation—may aid in microbiome management, whether that means maintaining human health or mitigating climate change impacts.

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SUPPLEMENTARY MATERIALS

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Table S1
References (*102*–*118*)

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