

Patterns and Processes of Microbial Community Assembly

Diana R. Nemergut,^{a,b} Steven K. Schmidt,^c Tadashi Fukami,^d Sean P. O'Neill,^{a,c} Teresa M. Bilinski,^{a,c} Lee F. Stanish,^{a,b} Joseph E. Knelman,^{a,c} John L. Darcy,^c Ryan C. Lynch,^c Phillip Wickey,^{a,b} Scott Ferrenberg^c

Institute of Arctic and Alpine Research (INSTAAR),^a Environmental Studies Program,^b and Ecology and Evolutionary Biology,^c University of Colorado, Boulder, Colorado, USA; Department of Biology, Stanford University, Stanford, California, USA^d

SUMMARY	342
INTRODUCTION	342
HOW ARE MICROBES UNIQUE?	343
DEFINITIONS	343
Communities	343
Biodiversity	344
BIOGEOGRAPHICAL PATTERNS	345
Abundance	345
Taxon Turnover	345
Phylogenetic Structure	346
VELLEND'S CONCEPTUAL SYNTHESIS OF COMMUNITY ECOLOGY	346
SELECTION	347
DISPERSAL	347
DIVERSIFICATION	348
DRIFT	348
COMBINING FORCES: COMMUNITY ASSEMBLY	348
TEMPORAL AND SPATIAL SCALES	349
IMPLICATIONS FOR FUNCTION	350
IMPLICATIONS FOR BIODIVERSITY	350
ACKNOWLEDGMENTS	351
REFERENCES	351
AUTHOR BIOS	355

SUMMARY

Recent research has expanded our understanding of microbial community assembly. However, the field of community ecology is inaccessible to many microbial ecologists because of inconsistent and often confusing terminology as well as unnecessarily polarizing debates. Thus, we review recent literature on microbial community assembly, using the framework of Vellend (*Q. Rev. Biol.* **85**:183–206, 2010) in an effort to synthesize and unify these contributions. We begin by discussing patterns in microbial biogeography and then describe four basic processes (diversification, dispersal, selection, and drift) that contribute to community assembly. We also discuss different combinations of these processes and where and when they may be most important for shaping microbial communities. The spatial and temporal scales of microbial community assembly are also discussed in relation to assembly processes. Throughout this review paper, we highlight differences between microbes and macroorganisms and generate hypotheses describing how these differences may be important for community assembly. We end by discussing the implications of microbial assembly processes for ecosystem function and biodiversity.

INTRODUCTION

Molecular phylogenetic approaches continue to revolutionize the field of microbiology: we now possess the tools to understand high-resolution details about the degree of variation in microbial community structure in both space and time (1–5). Sequencing costs have plummeted, while the amount of publicly available data has increased exponentially in recent years. Com-

putational advances (6, 7), as well as new standards for contextualizing environmental microbial community composition data sets (8), will allow us to make the most of these data, facilitating cross-investigator and cross-system meta-analyses. Indeed, after years of citing the many limitations of studying such complex systems, microbiologists now enjoy many advantages that our colleagues who study macrobial communities actually lack. Admittedly, we are still a long way from a “complete” understanding of any but the most simple of microbial communities, which will require continual improvements in both technology and computation. Thus, despite these recent advances, we are faced with questions about how to best sample microbial communities to maximize what we can learn about how they are structured, how they function, and how they change through time (9).

A unified conceptual framework of microbial community assembly—one that incorporates our understanding of community assembly from a macrobial ecology perspective while recognizing the attributes that make microorganisms unique—is needed to help direct the field of microbial ecology through this new era. This is not an easy task, and we argue that it is made more difficult by unnecessarily polarizing debates (e.g., the false dichotomy of the niche-versus-neutral debate [10] as well as the debates over

Address correspondence to Diana R. Nemergut, nemergut@colorado.edu.

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null models [11]) as well as the use of inconsistent and sometimes redundant terminology (e.g., niche based, deterministic, environmental filters, and stabilizing mechanisms, which all refer to similar phenomena). However, we believe that Vellend's (5) conceptual synthesis of community ecology, which distills the myriad of processes affecting community assembly into four basic categories (diversification, dispersal, selection, and drift) and can be applied on different temporal and spatial scales, is a step in the right direction (see also reference 12). The purpose of this review is to integrate microorganisms into this simple framework with the hope of providing microbiologists with a coherent picture of the potential mechanisms governing microbial community assembly.

Here, we begin with a general discussion of the features that make microorganisms unique and definitions of the relevant terms used to describe community structure. Next, we describe the patterns observed in terms of microbial community composition across systems, highlighting the many parallels between microbial and macrobial biogeography. We then describe Vellend's conceptual synthesis of community ecology, which we use to frame our discussion of how diversification, dispersal, selection, and drift affect microbial community assembly. We also describe some examples of how these processes combine to affect community assembly. Next, we highlight the importance of spatial and temporal dynamics in assembly processes. We end by discussing the relationships between community assembly and microbial function and biodiversity. In this review, we deal almost exclusively with molecular-based analyses of microbial community composition. As noted above, these approaches have tremendously expanded our appreciation of microbial diversity and community complexity over past culture-based studies, but they are not without their own limitations (13–15).

HOW ARE MICROBES UNIQUE?

There is copious literature on the mechanisms governing macrobial community assembly, and given the similarities in the observed biogeographical patterns (see below), we use this literature as a starting point to consider the processes guiding microbial community assembly. However, there are some differences between micro- and macroorganisms that could lead to disparities in the importance of different processes to the community ecology of microbes. It should be emphasized that several of these traits are also shared to some degree with at least some members of the macrobial world and that not all microbial taxa exhibit these phenotypes. However, we highlight these traits here because some microbial taxa exhibit all of these traits, and the extent to which these phenotypes are expressed has the potential to affect assembly dynamics in any community.

First, the passive dispersal (e.g., via wind and air) of microbes is likely to be easier than that of macrobes simply because of their small size (16–19). For example, Finlay (17) used morphological characterizations of free-living protozoa to hypothesize that microbes with lengths of <2 mm are likely to be globally distributed. More recently, Wilkinson and colleagues (19) used computer models of atmospheric circulation to simulate the airborne dispersal of different-sized microorganisms. They found that particles >20 μm in diameter were unlikely to be dispersed between continents within 1 year, while particles >50 μm in diameter were never passively transferred between continents. While active dispersal is rare in microbes (20), microorganisms hitch rides on all macrobes that disperse. Thus, the dispersal potential of most mi-

croorganisms is likely to be much larger than that of macroorganisms.

Likewise, many microorganisms can experience dormancy, in which they enter a reversible state of reduced activity in response to environmental stressors (21, 22). Indeed, several examples of cells being revived after decades to millennia exist in the literature (22). Although this is true of some macrobes as well, the phenomenon is more phylogenetically widespread (i.e., not limited to a specific clade or clades) for microorganisms (22). It has been estimated that less than 10% of a typical microbial community may be active at any one time (23); thus, the dormant component potentially represents a vast reservoir of genetic diversity.

Also, some microbes exhibit significant phenotypic plasticity with regard to the use of electron donors and acceptors (24, 25), and the genetic diversity present within a population of a given "species" can be large (26–28). Consider a typical macrobial community, which is composed of organisms that can either photosynthesize or undergo heterotrophic respiration. Microorganisms perform these functions as well but can use a remarkable suite of additional electron donors and acceptors, including H_2 , Fe , S , and N -based compounds. This diversity, coupled with short generation times, can allow ecological responses to shifting environmental gradients on time scales (hours to days) not attainable by macrobes (29). Finally, microbes can undergo rapid evolution (30), and some can exchange genetic material readily, even with distantly related organisms (31). All of these attributes are likely to affect the ecology and evolution of microbes in ways that may distinguish them from macrobial communities.

In addition to the biological differences highlighted above, there are some artifacts introduced by the ways in which we study microbes that will make an understanding of their community ecology more difficult. In most cases, we know little about the spatial and temporal structure of ecological communities on scales that are relevant to microbes—which organisms are interacting with others, for example. Additionally, given our general sampling approaches, we are almost always answering questions about communities on the macro scale. Consider, for example, the extreme chemical gradients that exist within a single soil particle (32). When we sample a gram of soil, we are averaging across all of this variation and attempting to uncover patterns between community structure and biogeochemistry at a large scale relative to the size of an organism. Moreover, because our approaches typically focus on the sequencing of pools of 16S rRNA genes, it is much more difficult to link traits and taxonomy than it is for macroorganisms. Methodological developments that allow for the characterization of microbial community structure at finer spatial scales, including catalyzed reporter deposition-fluorescence *in situ* hybridization (CARD-FISH) (33) and nano-secondary-ion mass spectrometry (nanoSIMS) (34), are steps in the right direction to overcome these challenges.

DEFINITIONS

Communities

We define a community as a group of potentially interacting species that cooccur in space and time (35) (Table 1). Investigators who study macrobial communities recognize that communities are not discrete and that their boundaries may vary both spatially and temporally (36). As highlighted above, some of these complications may be heightened for microbes, given their potential for

TABLE 1 Definitions of community-related terms used in this paper

Term	Definition	Reference(s)
Community	A group of potentially interacting species that cooccur in space and time	35
Assemblage	A phylogenetically defined group of organisms that cooccur in space and time	39
Guild	Groups of organisms that cooccur in space and time and that share common resources	39
Richness	No. of taxonomic units (e.g., species) in a community, standardized to the no. of individuals sampled	41
Structure	No. of taxonomic units (e.g., species) in a community as well as their relative abundances	This paper
Inventory diversity	Diversity within an environment	43
Differentiation diversity	Turnover in diversity between environments	43
Alpha diversity	An inventory metric that expresses the amount of local diversity or diversity at the smallest spatial scale of analysis; gamma diversity is a similar metric used to refer to diversity at the regional scale	35, 43
Beta diversity	A differentiation diversity metric that refers to turnover at the landscape scale, i.e., turnover between local populations	35, 43

rapid turnover. With regard to geography, community definitions are often arbitrary and reflect our inability to sample at a level that is both small enough to be relevant for microorganisms and large enough to be relevant to ecosystem processes (e.g., 1 g of soil). While communities are not restricted to taxonomic groups (e.g., plants, animals, or microbes), they are often studied in this manner because of logistical constraints (37). For example, although an understanding of macrobial-microbial interactions is desired for a more integrated understanding of community ecology, the vast differences in scales of the factors affecting these organisms also introduce statistical complications into data analysis (38).

Indeed, Fauth et al. (39) suggested a classification scheme in which they define an array of community-related terms based on all possible combinations of shared geography, phylogeny, and/or resources (Table 1). In their scheme, “communities” are defined by geography and not by phylogeny or resource use. In terms of phylogeny, what we refer to as “microbial communities” are often just bacterial communities, as our understanding of membership is typically restricted to the use of certain molecular probes (“universal” bacterial primers, for example). Moreover, different DNA extraction techniques are more effective for different organisms (40), which can complicate our appreciation of community structure. Thus, in the suggested terms of Fauth et al., most studies examine “microbial (bacterial) assemblages,” or a phylogenetically defined group of organisms that cooccur in space and time. Depending on the tools used—denitrifying gene probes, for example—microbiologists also occasionally focus on guilds, or groups of organisms that share common resources.

For all of these organizationally and operationally defined units (e.g., community and assemblage) (Table 1), we use the term richness to refer to the number of taxonomic units (e.g., species) in a community, standardized for the number of individuals sampled (41). By contrast, we use the term structure to describe the composition of taxonomic units present as well as their relative abundances. It is worth noting an inherent assumption of the molecular methods typically used to describe microbial communities, specifically that one 16S rRNA gene equals one organism, a relationship which can vary by an order of magnitude between different bacterial taxa (42). However, these methods also enable phylogenetic-based examinations of richness and structure.

Biodiversity

Quantifying and comparing biodiversity allow us to tease apart the effects of different ecological processes on community structure. There are many different ways to assess biodiversity (35), but

all break down into two general classes: either inventory diversity or differentiation diversity. Inventory diversity metrics describe diversity within an environment (alpha diversity sensu Whittaker [43]), while differentiation diversity describes the turnover in diversity between environments (beta diversity [see reference 44 for a recent review]). Thus, a community displaying high inventory diversity harbors high biodiversity within a habitat at a defined spatial scale, while two distinct communities exhibiting high differentiation diversity have relatively few species in common.

There are a variety of inventory diversity metrics that describe biodiversity using a suite of parameters. All consider the number of different types of taxa present in a given sample, and others also include information on the evenness in terms of relative abundance (e.g., Shannon index and heterogeneity measures). Still others take into account the amount of phylogenetic diversity (PD) within samples, which may be particularly important for diverse microbial communities (45, 46). It is beyond the scope of this paper to describe these metrics in detail, but others have commented extensively on the strengths and weaknesses of various diversity metrics in general (35) and more specifically as they relate to microbial communities (47–49).

Importantly, inventory diversity metrics can be applied to examine biodiversity at any scale. Typically, alpha diversity, sometimes called “local diversity,” refers to diversity at the smallest spatial scale of analysis, and gamma diversity is a metric for regional (landscape) diversity. These scales (and their definitions) are subjective and defined by the researcher. However, because of the near-universal relationship between species richness and area (see below), it is essential that samples of the same size be analyzed to facilitate meaningful comparisons between systems. Also, undersampling can lead to issues for diversity comparisons, and mathematical methods to overcome these problems have been proposed (50).

Likewise, there are a variety of methods to assess differentiation diversity. The Z value, which is the slope of the relationship between the log of area versus the log of species richness, is a geographically explicit method with which to examine species turnover for hierarchically sampled communities. It is important to note that, as is the case with inventory diversity, differentiation diversity is also sensitive to sampling intensity (159). Some metrics feature pairwise comparisons between samples relative to total diversity, and the degree of overlap in community structure is represented on a scale of 0 to 1 as either a dissimilarity (sometimes distance) or similarity value. Like inventory diversity metrics, dif-

ferentiation diversity metrics can take into account relative abundance as well as the degree of phylogenetic overlap between two communities (51, 52). Again, differentiation diversity can be calculated at a variety of spatial scales at the discretion of the researcher. Beta diversity is typically used to refer to either species turnover or the difference in species composition between sampling sites at the regional scale (i.e., alpha diversity relative to gamma diversity [44, 53]).

As described above, both classes of diversity metrics are inter-related. Beta diversity can be affected by changes in both alpha and gamma diversity; for example, an increase in beta diversity can reflect both a decrease in alpha diversity as well as an increase in gamma diversity. An understanding of what is driving changes in diversity can be central to an appreciation of community assembly processes (54–56).

BIOGEOGRAPHICAL PATTERNS

After several decades of using molecular phylogenetic tools to examine microbial community composition, we now know that there are similarities in biogeographical patterns in macrobial and microbial communities (20, 57). Although there are still many questions about how our past and current methodological limitations may affect our observations, we review some of the common patterns that are observed in the microbial world below. It is also worth noting that there are some patterns that have been shown for many macrobial systems that have not been shown for microbes, including relationships between latitude and diversity as well as elevation and diversity (58–60). It is unknown why these differences exist, but, for example, it could be the case that latitude serves as a proxy for another driver of macrobial community composition that does not covary with latitude at the same scale for microbes. However, these disparities could also reflect real differences between assembly mechanisms and biogeography in macrobial and microbial communities.

Abundance

Nearly all communities examined to date feature species abundance distributions (SADs) in which the majority of taxa tend to be found in low relative abundances (we avoid the use of the term “rare” here, as it has been used to refer to both organisms with low abundance and patchy distribution patterns) and only a few are more abundant (35, 61). Much discussion in the literature has focused on the statistical shape of this relationship (e.g., log normal versus geometric) as well as the possible biological mechanisms driving these relationships. Microbial communities are no exception to this rule, although they tend to show a longer “tail” of low-abundance species (62), possibly because of the relative scale over which we examine microbial versus macrobial communities (Fig. 1).

Although there is much debate on the definition of and the potential methodological and computational artifacts associated with our understanding of the presence of these low-abundance organisms (e.g., chimeras generated by PCR and overestimation of diversity with certain OTU [operational taxonomic unit]-clustering algorithms), it is clear that microbial communities tend to harbor a great number of low-abundance taxa, many of which may be inactive. For example, Hubert and colleagues (63) found hyperthermophilic microorganisms in cold deep-sea sediment samples that became active in laboratory experiments after temperatures were raised to 50°C. Statistical approaches reveal that

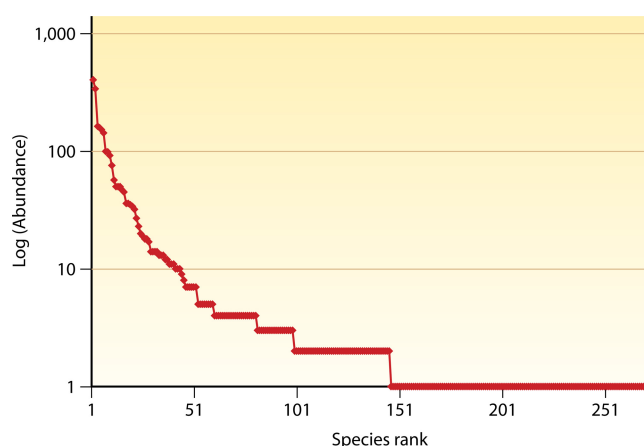


FIG 1 Typical rank-abundance plot, where each point represents the abundance of one organism within the community (data from reference 120). A common feature of many biological communities is that few organisms are present in high abundances, while the majority of taxa are found in low abundances.

removing data on low-abundance taxa can result in better correlations between community composition and environmental parameters (64). Although this may suggest that these taxa are not actively interacting with their environment, it could also suggest that abundant organisms act as “ecosystem engineers,” directly altering the environment, while the activity of low-abundance taxa has much less impact. Recent work also suggests that low-abundance organisms may be important for the response to disturbances in terrestrial (65) and aquatic (66) environments. Are these low-abundance taxa nothing more than seed banks that bloom when conditions are right? There is some evidence for this; however, other studies suggest that low-abundance organisms may be disproportionately active in comparison to more abundant taxa (21).

Taxon Turnover

The species-area relationship reflects the fact that larger areas tend to harbor greater species richness. This pattern has been widely established for macrobes and has also been demonstrated for free-living fungi, bacteria, and archaea (67–70). As described above, the Z value measures the rate of species addition per unit area. The Z values for microbes range and appear to be affected by spatial scale (71), sampling intensity (50), and species definitions (72). Related to the species-area relationship is the distance-decay relationship (Fig. 2), in which turnover in microbial community composition is observed over space and communities become less and less similar, in terms of community composition, the further apart they are geographically (68, 73).

Similar relationships in terms of species richness and taxon turnover have also been observed over time. Preston (74) originally hypothesized a positive relationship between the duration of observation and the number of taxa, a pattern referred to as the species-time relationship. This pattern has received much less attention than the species-area relationship in the macrobial literature, perhaps because of difficulties inherent in observing slower-changing and larger ecosystems over time. However, recent studies have shown that such a relationship exists for many taxa (75). Likewise, this relationship has been shown for microbial

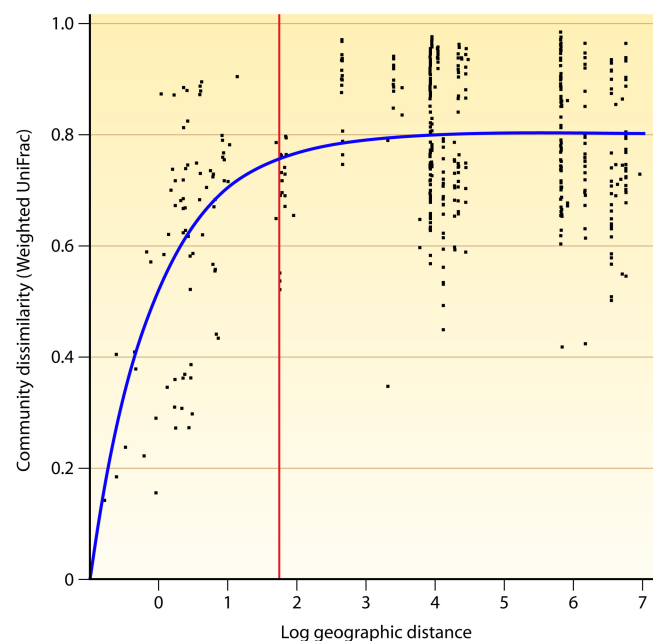


FIG 2 Variogram showing how phylogenetic distance between soil rotifer communities (community dissimilarity) varies with the log of geographic distance between communities. Weighted UniFrac values (a measure of phylogenetic distance between communities [51, 52]) close to 1 indicate very different communities, and values close to 0 indicate almost identical communities. The red vertical line is an estimate of the autocorrelation range (~ 60 m), beyond which communities show very little autocorrelation. Replotted from data reported by Robeson et al. (143).

communities, including bacteria on the surfaces of leaves and communities present in activated sludge (76–78).

Both the species-area and the distance-decay relationships as well as their temporal analogues are so much a part of our experience as observers of the natural environment that they seem to be common sense, yet the mechanisms underlying these relationships for both macrobes and microbes are still poorly understood (see discussion below). Given the current sampling challenges for microbial communities, it may be premature to compare the turnover rates of macrobial and microbial communities, but some work does suggest that Z values may be somewhat lower for microorganisms (60, 70), perhaps because of the high degree of dormancy in microbial communities (21).

Phylogenetic Structure

Microbial communities tend to be more phylogenetically clustered than expected by chance (68, 79), harboring groups of closely related taxa that exhibit microscale differences in genomic diversity. However, a few communities show the opposite patterns, in which taxa are less clustered and are less related than expected by chance (i.e., overdispersed) (28, 80). Both types of patterns have also been observed in macrobial communities (81).

VELLEND'S CONCEPTUAL SYNTHESIS OF COMMUNITY ECOLOGY

What processes are driving the biogeographical patterns described above? The field of community ecology seeks to understand the mechanisms of assembly and how they produce patterns in both space and time. Given the overlap in the fields of biogeography

and community ecology, it is unfortunate that inconsistent terminology is sometimes used to describe the same patterns and processes across fields. As the training of many microbiologists reflects a reductionist approach emphasizing the genetics and physiology of individual taxa rather than their ecology, these fields can be even more difficult to navigate and unify. Here, we make an effort to clarify synonyms that have been used in the literature and present a consistent framework with which to discuss patterns and processes in community ecology. A more complete integration of microorganisms into these fields will allow researchers to test broader theories on organisms, some of which can be easier to manipulate and most of which are faster to respond than macrobes.

We begin with what has been called one of the only “laws” in ecology, the species-area relationship, and use it to illustrate how the processes involved in community assembly are actually quite simple (5, 82). We note that many of these examples could also apply to the species-time relationship. We use Vellend’s (5) approach (Table 2) to classify the possible drivers of this relationship. First, larger areas are more likely to encompass greater diversities of habitat types, allowing for a greater diversity of organisms to coexist through selection, defined as “deterministic fitness differences between individuals” (in other work, this has been referred to as niche processes, environmental filters, and deterministic processes). Larger areas may also provide a larger “target” for the dispersal of organisms from outside the ecosystem. Thus, the species-area relationship could reflect greater dispersal, or the “movement of organisms across space.” Likewise, as larger areas allow for larger population sizes, the role of extinction through drift, or the “random changes in organism abundances,” will be less likely. Finally, larger areas may provide more chances for diversification through both larger population sizes and more diverse niches. This represents a slight modification of the Vellend model, which identified “speciation” as the process of interest. However, evolutionary change can alter community dynamics, even if new species are not created (83). Likewise, as the Vellend model operates at the individual level, it seems more appropriate to consider diversification rather than speciation.

All of these processes operate in combination, but some processes may vary in relative importance across different groups of organisms and for different systems. Like Roughgarden (12), Vellend (5) acknowledges the two forces that act to bring new organisms into communities (speciation and dispersal) and the processes that affect changes in the presence and absence as well as the relative abundance of organisms over time (drift and selection). This framework is analogous to the theory of population genetics, in which allele frequencies are explained through a combination of mutation, gene flow, genetic drift, and natural selection.

TABLE 2 Vellend’s four processes for community assembly

Process	Description
Diversification	Generation of new genetic variation
Dispersal	Movement of organisms across space
Selection	Changes in community structure caused by deterministic fitness differences between taxa
Drift	Stochastic changes in the relative abundances of different taxa within a community through time

Although this conceptual model was not borne out of a specific consideration of microbial communities, the same basic forces should also guide their assembly (84). We find this framework to have a number of strengths, particularly with regard to microorganisms. Importantly, rather than including evolutionary forces as an afterthought, this conceptual model recognizes the central role that diversification plays in driving community ecology (83). Vellend's approach also avoids unnecessary and polarizing debates while still allowing for the possibility, if not the probability, that unique combinations of these processes will likely drive assembly in different systems. For example, this model encompasses both niche-based processes (driven by fitness differences between organisms) and neutral processes (driven by stochastic processes) in shaping communities. This is important because these debates can often be misleading when not presented within a simplified framework. Consider, for example, Baas-Becking's "everything is everywhere" hypothesis, which emphasizes selection as a driving force in microbial community assembly (85). While this is traditionally thought of as a niche-based hypothesis, neutral processes are also central to this model, as dispersal is considered to be a constant across all organisms in space in time. Likewise, the neutral theory of biodiversity posits that organisms at the same trophic level are equivalent with respect to fitness within a specific environment (86, 87). This model explicitly includes three of Vellend's processes: dispersal, drift, and evolutionary diversification. In the sections that follow, we highlight how the life history traits of microbes may affect the relative importance of the four processes for microbial community assembly.

SELECTION

Selection is a large force shaping microbial community assembly (20, 59, 88). Different habitat types (e.g., seawater versus soils) harbor different suites of microorganisms (89), and a copious amount of data supports the role of a variety of environmental factors in determining bacterial assemblage structure and diversity, including pH, salinity, and the abundance and quality of carbon (59, 88, 90, 91). Together, these relationships support the importance of selection via abiotic factors in determining microbial community structure.

However, we know much less about how biotic interactions (e.g., commensalism, mutualism, and parasitism) shape microbial communities. While there is a rich history of studying these processes in macrobial communities, such interactions are much more difficult to observe and document in microbial communities. Many examples of microbial interactions have been described from the organismal perspective, (e.g., H_2 syntrophy and endosymbiosis of plastids), yet we know little about how these scale to shape entire communities. Weiher and Keddy (11) have proposed a continuum of how abiotic and biotic factors may drive community composition and how this may relate to phylogenetic structure. They hypothesized that phylogenetically overdispersed communities are characterized by strong species-species interactions and that competition for similar resources or facilitation may result in these patterns (92), excluding more similar taxa that are more likely to feature niche overlap. By contrast, it has been hypothesized that communities that are phylogenetically clustered, like many microbial communities (79), are driven by strong selection acting over broad phylogenetic scales. Indeed, Philippot and coworkers (93) have shown the deep phylogenetic coherence of ecological traits, suggesting that lineages of microbes may display

ecological similarities over large phylogenetic distances, potentially accounting for the clustering of such communities.

By contrast, others have hypothesized that such clusters may develop over time through evolutionary processes and may actually be a reflection of weak selection (27). Another factor that may weaken the effects of selection in microbial communities is dormancy, because dormant cells are essentially invisible to selection processes. Consider persister cells, which are bacteria that are genetically sensitive to antibiotics but, because they are in an inactive state, can persist in populations following exposure (94). Although there is a physiological cost to dormancy mechanisms (22), given the large selective advantage of being able to persist under harsh conditions, dormancy may be a common phenotype in microorganisms.

Although selection should be similar in macrobial and microbial systems, the specifics of these processes will no doubt be quite different due to the vast metabolic diversity harbored within microbial communities and even within individual organisms. Thus, the complexities of the potential environmental and biological drivers of fitness are greatly magnified for these communities. Indeed, the metabolic breadth of microorganisms has been hypothesized to be a key factor in the generation and maintenance of microbial diversity. Support for this hypothesis has emerged from the discovery that sediment environments, which feature strong spatial gradients in electron donors and acceptors, harbor the most diverse of microbial communities (88).

Finally, the prominent role of horizontal gene transfer (HGT) (and recombination in general) in microbial diversification may affect microbial community assembly through selection. For example, recent work demonstrates that selection acts on traits that are subject to horizontal gene transfer (27, 95). Burke and coworkers (95) found that patterns in microbial assembly processes were related to functional genes (i.e., traits) rather than taxonomy. This finding highlights the need for trait-based approaches to understand community assembly processes, as recombination can scramble the relationship between phylogenetics and function (96).

DISPERSAL

Because of the small size, high abundance, and short generation time of microorganisms, dispersal processes have not been rigorously studied, much less quantified. Thus, the distributions of microbes are often used as proxies for dispersal. Given that it is difficult to conclude that an organism is absent from a specific environment, and that the current distribution of organisms could also reflect selection processes that have excluded less "fit" organisms and/or speciation, there are severe limitations to our understanding of the role of dispersal processes in community assembly. Thus, here, we emphasize that "dispersal" is different from migration, in which a new organism is incorporated into a community from outside. Migration events are the result of dispersal as well as selection and possibly drift. We also highlight that it is often the case that dispersal is discussed only in terms of how limited it is ("dispersal limitation"). However, dispersal can have other dimensions with consequences for community assembly, including rates and the order in which taxa are added to communities.

Microbial dispersal is typically a passive process. While some microbes can propel themselves to some degree, these processes are unlikely to result in long-distance dispersal events (20). Trans-

port via wind, water, and hitchhiking onto mobile macrobes are all common mechanisms for microbial dispersal. As noted above, many have asserted that free-living microorganisms do not experience passive dispersal limitations (17, 58). This is supported to some degree by the distribution of “unlikely inhabitants,” including the presence of spore-forming hyperthermophiles in inhospitable locations such as arctic fjord sediments (63) or temperate soils (97). However, microbial communities in air and water show differences in both space and time (98, 99), thereby affecting dispersal patterns. Curtis and coworkers (61) estimate that the lowest-abundance soil organisms may be present at densities approaching 1 cell in every 27 km². Given the estimates put forth by Papke and Ward (100), it would take 2 to 220 times the age of the earth for all microbes to disperse through the atmosphere.

Likewise, while passive dispersal is often considered stochastic, it is not entirely so: taxa vary in dispersal ability, making dispersal probability not entirely random among species. For example, dormancy mechanisms may make organisms more resistant to the environmental stressors (e.g., extremes of temperature, water availability, and UV exposure) encountered during dispersal (22, 23). Indeed, examinations of microbial biogeographical patterns provide support for the potential role of microbial life history traits in affecting dispersal. Darcy and coworkers (16) found *Betaproteobacteria* from the genus *Polaromonas* to be globally distributed among high-altitude alpine environments and identified a potential dormancy mechanism that could permit these bacteria to travel through the upper atmosphere. Likewise, Bissett and colleagues (71) found that the distribution of spore-forming organisms was decoupled from environmental parameters. By contrast, the relative abundances of organisms within the *Rhizobiaceae*, *Bradyrhizobiaceae*, and *Xanthomonadaceae*, which they classified as poor dispersers because of their tendency to form associations with macroorganisms, were correlated with edaphic factors. While there are caveats to interpretations of these data, including the fact that abundant organisms are easier to detect, they present an interesting case for the differences in dispersal potential between organisms.

DIVERSIFICATION

The process of evolutionary diversification is fundamental to biogeography and community ecology, but historically, evolution has been given only lip service as a potential factor in ecological processes. However, scientists are increasingly recognizing that both processes can act on the same spatial and temporal scales (101). Unfortunately, as is the case with dispersal, we understand little about the spatial and temporal dynamics of how microbes evolve, as these processes are difficult to study empirically. Again, we typically make inferences regarding evolution based on the distribution of microbial genetic diversity in space and time. While the influence of evolutionary history in explaining community structure over long temporal scales is well known, recent work demonstrates that active processes of diversification can play a more immediate role in microbial community assembly (27).

The process of dormancy is likely to affect microbial evolutionary processes with potential implications for community assembly. As mentioned above, dormancy can protect cells from the possibility of death, at least temporarily. Dormant cells can sit, frozen in time, until favorable conditions or stochastic factors (102) lead to their growth. This could result in dramatic variation in evolutionary rates over time. More importantly, it could also

result in raw material for evolutionary processes that are somewhat decoupled from the recent history of the environment, which may produce more rapid and dramatic differences in the phylogenetic and functional diversity of community members.

The process of horizontal gene transfer (HGT) may also change community assembly dynamics for microorganisms compared to macrobes. In addition to changing the rate and tempo of evolution, as HGT can act as both a diversifying and a homogenizing force (103), this mechanism may alter the role of historical processes in community assembly. For example, consider one microbial species that has evolved to cope with an environmental toxin through selection for a particular gene sequence, providing it with a competitive advantage over other organisms. If another organism acquires this resistance determinant through horizontal gene transfer, it is no longer subject to the same genomic environment in which the allele evolved, potentially allowing this organism to explore new fitness landscapes.

Also, microorganisms can evolve through mutation rapidly, which may have implications for community assembly. For example, single-species biofilms can quickly generate diversity that promotes ecological stability (104, 105). Some bacteria can also initiate increased rates of mutation and horizontal gene transfer, particularly as a strategy in facing inhospitable environments, again increasing diversity at variable evolutionary rates over time with implications for adaptation in such communities (106). Although it is important to emphasize that, to some degree, rapid evolution may be an artifact of nutrient-rich, laboratory conditions (107), the evolution of microorganisms in response to the introduction and proliferation of antibiotic use demonstrates that these processes can happen rapidly under more “real-world” conditions.

DRIFT

Ecological drift, or stochastic changes in the relative abundance of organisms, may play an important role in microbial community assembly. Empirical and theoretical studies of macrobial systems have demonstrated that drift is most important when selection is weak, alpha diversity is low, and the total number of community members is small (reviewed in reference 54). These conditions can be met in certain types of microbial communities, including nutrient-rich systems such as wastewater treatment facilities (108, 109) as well as host-associated environments (110). The vast majority of taxa in microbial communities are found in low relative abundances. Low-abundance microorganisms are more vulnerable to the effects of drift, since slight negative changes in their abundance could result in their extinction on a local scale (111). However, low-abundance individuals may exist in dormant states, protecting them from extinction. A better understanding of the dynamics between dormancy and local extinctions is vital to an appreciation of the role of drift in community assembly, particularly for microbial assemblages.

COMBINING FORCES: COMMUNITY ASSEMBLY

How do combinations of these processes (Table 2) influence microbial community assembly? Specifically, which features of a community may make certain processes more or less important? What aspects of these processes need to be quantified and integrated with existing models to better understand microbial community assembly? In the following sections, we attempt to address some of these questions.

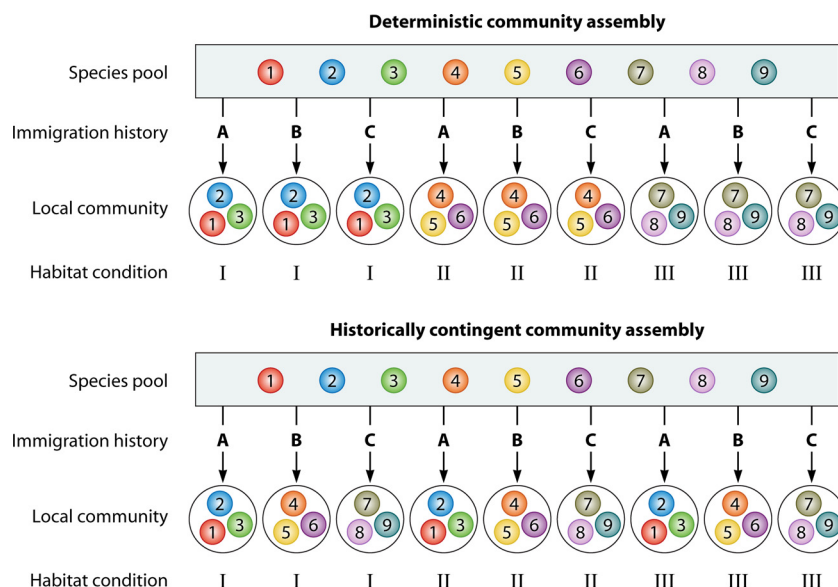


FIG 3 Contrasting hypotheses of community assembly. Numbers represent hypothetical species, arrows represent species immigration, letters represent different immigration histories, and roman numerals represent variations in habitat conditions. (Top) Local communities converge in species composition under the same environmental conditions regardless of immigration history. (Bottom) Local communities diverge in species composition when immigration history is variable, even under the same environmental conditions (i.e., priority effects). (Adapted from references 123 [p. 45] and 158 with permission.)

First, several factors should affect the relative importance of selection in microbial community assembly. Recent reviews have highlighted the fact that many microbial communities are sensitive to disturbances to abiotic and biotic features of their environment and that community resilience is related to the severity and duration of the disturbance, community diversity, disturbance history, and abiotic factors (112–114). Drift should be most important in assembly when the degree of ecological equivalence within community members is high (115). As many microbial communities are phylogenetically underdispersed (68, 79, 116), it is possible that many ecologically equivalent organisms coexist in microbial communities. Importantly, even if the genetic potential for functional differences between these taxa exists, if the ecosystem does not feature variation to make these differences relevant for fitness, the taxa are effectively ecologically equivalent. The potential for the community to undergo significant turnover through either drift or selection is related to growth rates and will thus be sensitive to the nutrient status of the environment. By contrast, the effects of evolutionary diversification and dispersal on assembly processes may be most important in new or changing environments when newly arriving organisms face less competition from resident organisms (115).

As noted above, however, all of these processes operate in combination, and changes in the interactions of dispersal, drift, selection, and diversification will have large impacts of community assembly. While little is known about the dynamics of microbial invasions, some work suggests that communities may experience more dramatic shifts in response to the introduction of new individuals (via diversification and dispersal) following a disturbance event, likely due to changes in selection (114, 117). Indeed, disturbance has also been shown to increase the relative importance of selection in structuring communities (118, 119). However, other studies suggest that neutral processes increase following disturbance events. We recently examined the response of soil microbial

communities to a wildfire and found evidence for an increase in the effects of neutral processes 1 month following the disturbance but an increase in the effects of selection after 4 months (120). Such transitions over very short time scales may reconcile the fact that different studies have yielded disparate patterns in community assembly in response to disturbance.

TEMPORAL AND SPATIAL SCALES

Two aspects of assembly that have not been explored extensively for microbial communities are the role of temporal and spatial scales. For example, temporal scales can be important for understanding the roles of “priority effects” (121–124). Here, selection causes changes in community structure when dispersal, drift, and/or diversification introduces variation in the initial relative abundance (i.e., frequencies) of species (Fig. 3). Gleason (125) was the first to imply that the order of species colonization can result in divergence between communities, even when environmental conditions and regional species pools are identical. In these communities, early-colonizing organisms can have inhibitory or facilitative effects on late-arriving organisms (123), either through direct interactions (e.g., competition and symbiosis) or through environmental modification (126).

The importance of assembly history for community ecology has been likened to that of evolutionary processes: “While not denying the importance of current adaptations, we cannot ignore the long and apparently capricious pathways taken by evolutionary lineages” (127). Some work has even demonstrated the existence of “Humpty-Dumpty” communities (128), or communities that cannot be put back together with only the species that they contain (129), further supporting the role of assembly history in community structure. The role of priority effects on model microbial communities has been studied extensively (129–134). Microbial systems have played a central role as a model system to generate, test, and refine general hypotheses on community assembly

because the short generation time and other logistical ease associated with microbes make them convenient experimental tools (135–137). Some studies demonstrate that assembly order can affect not only community structure but also ecosystem-level processes, such as decomposition and carbon flux (138). However, much of this research has been conducted in the laboratory, and experiments are needed that test hypotheses under more realistic conditions.

Also, spatial scales are important in community ecology (123), and metacommunity theory is the study of spatially distinct communities that are linked through dispersal (36). Given the high dispersal potential of many microorganisms, these linkages are likely to happen over multiple spatial scales. The same basic processes are influencing community assembly, but selection, drift, and evolution can be decoupled spatially but linked through dispersal. For example, extinction events in one community can be “rescued” through dispersal from a nearby patch. Thus, tradeoffs can exist in which less-fit organisms persist within metacommunities because of high dispersal rates.

These types of spatially explicit differences in patterns and processes likely exist for microbial communities as well and may explain some of the variation in microbial community composition. Recently, Martiny and coworkers (139) suggested that geographic distance contributed to community differences within salt marshes (local scale) but not between marshes (regional scale). Various environmental factors, however, contributed to community difference at all scales. As has been determined for some macrobial communities (e.g., see reference 55), a hierarchical understanding of the links between microbial populations and communities should be developed, focusing on rates of dispersal and genetic change over space and time. Spatial factors such as the size of local patches (140–142), the distance or isolation between communities (143–145), and how continuous habitats are across the landscape (146) are all features that will affect the metacommunity dynamics of microorganisms.

IMPLICATIONS FOR FUNCTION

Microbes regulate all major biogeochemical cycles and directly influence plant, animal, and human welfare. However, our understanding of how assembly processes might ultimately influence ecosystem function remains limited. Since microbial community structure and function are inextricably linked, some argue that there is intrinsic value in knowing “who does what” to understand broader controls over ecosystem processes (147). Indeed, the belief that community composition determines, or at least influences, ecosystem function is widely held in community ecology and is supported by recent work with microbial systems (138, 148). However, many studies have documented correlations between microbial community structure and an array of environmental factors (59, 88, 90), and a large body of literature demonstrates that many of these same parameters are important in controlling rates of ecosystem processes (149). On the other hand, Burke and colleagues (95) recently showed that microbial community succession on algae in the ocean showed functional convergence but lacked taxonomic coherence. This suggests a high degree of functional redundancy in microbial communities, which may decouple structure and function. Thus, the question remains, does information on microbial community structure provide added value beyond data on key chemical and physical factors in an environment? Put another way, if the environment

dictates microbial community structure, do we need to know “who is there” to predict “what they will do”?

Answering this question will require a more complete understanding of the links between structure and function, which may be affected by the degree of functional redundancy (150) as well as horizontal gene transfer within communities. Moreover, we argue that this will require disentangling the roles of the four processes in community assembly (Table 2) and developing a better understanding of where and when these matter. Some of the arguments against the added value of community composition data are predicated on the assumption that microbial community assembly is entirely selection based. Communities that are assembled primarily through neutral processes should be less affected by differences in environmental parameters. Thus, while environmental factors will still affect processes in these communities to some degree by regulating the physiologies of individual organisms, microbial communities assembled via stochastic processes may exhibit less of a direct link between the environment and processes (Fig. 4). Describing communities based on functional traits in addition to species richness patterns could be a particularly useful addition to community ecology as a whole. Microbial species traits may yield new insights into various measures of ecosystem function (151–153) and remedy the shortcomings of the use of species richness for evaluating ecosystem function and microbial ecology in general (96). However, selecting and measuring microbial traits that are relevant to community assembly and ecosystem function are formidable tasks.

IMPLICATIONS FOR BIODIVERSITY

We conclude by returning to the age old question of, “Why are there so many species of microorganisms?”, also called the “paradox of the plankton” (154). Ecological community theory suggests that a high level of biodiversity within the same trophic level is unlikely due to competition and drift. Coexistence should require the partitioning of resources in time and space or tradeoffs between species-species interactions and dispersal (155, 156). So why are microbial communities so diverse?

As mentioned above, the microbial communities with the highest alpha diversity occur in sediments (88). Our analyses also suggest that sediments feature more beta diversity than other microbial communities (T. M. Legg and D. R. Nemergut, unpublished data). Although the source of this beta diversity is unknown, one hypothesis is that local- and regional-scale heterogeneity in terms of redox gradients and nutrient availability could be an important driver of diversity (88). So-called “storage effects” through dormancy mechanisms may be strong for microorganisms given that a changing environment permits coexistence, as no single species can be competitively superior under all conditions (101, 156).

However, the spatial scale under which we sample microbial communities may confound comparisons of patterns in diversity between macrobes and microbes. Sampling over an entire gram of soil, for example, will homogenize across many communities, thereby reducing beta diversity estimates (89). Thus, the high alpha diversity observed for environmental microbial analyses may represent high gamma diversity driven by high beta diversity. Aspects of our approach to examining microbial communities may also influence observed patterns of diversity. For example, 16S rRNA gene phylogenetic analyses and our working definitions for microbial species do not capture ecological differentiation among

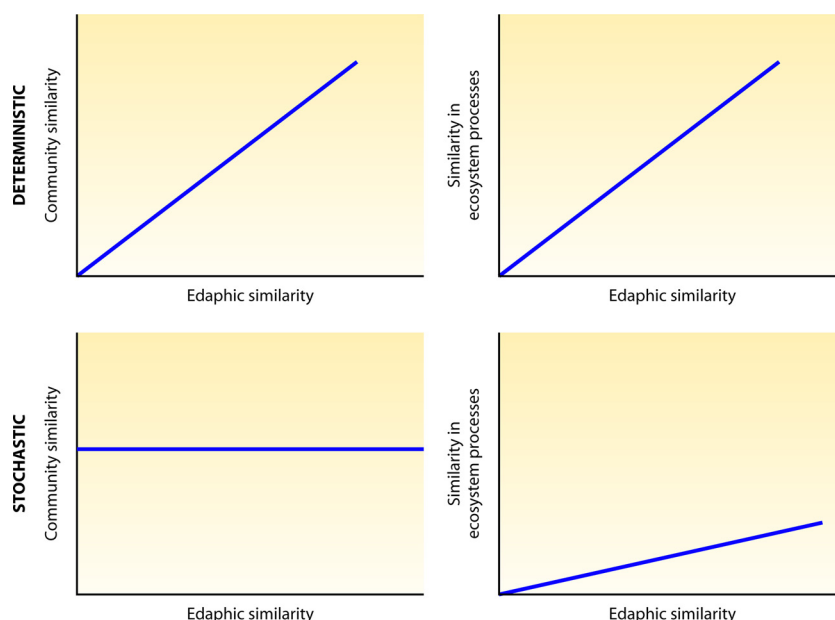


FIG 4 Conceptual model outlining the relationship between edaphic factors, soil microbial community composition, and ecosystem processes for deterministic and stochastic assembly mechanisms.

closely related taxa (79, 157). In total, an understanding of the relationship between patterns of microbial diversity and community assembly demands the implementation of a framework that accounts for the unique biology and scales of microbial ecology to properly discern meaningful patterns in microbial communities, as opposed to patterns that are artifacts of sampling methods.

While high-resolution data on microbial communities are increasingly revealing a multitude of patterns which suggest that various mechanisms in community assembly are at work across different environments and scales, Vellend's framework provides a foundation to unify wide-ranging observations in the context of fundamental, testable ecological processes. The framework described here will help microbial ecology to move from a largely observational and correlative field to one with more mechanistic insights. If executed with the proper experimental approaches, this effort will not only advance ecological theory but also take a major step forward in demystifying microbial communities and therefore the building blocks of ecosystems, our environments, and even ourselves.

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Diana R. Nemergut is an Associate Professor at the University of Colorado in the Environmental Studies program and the Institute of Arctic and Alpine Research. She is currently serving as a Program Director in Antarctic Organisms and Ecosystems at the National Science Foundation. Her research focuses on the evolution and ecology of environmental microbial communities. She received her Ph.D. from the University of Colorado and was a postdoctoral fellow at Rutgers University. She was inspired to go into microbiology after working as a technician in Dr. Joan Bennett's laboratory at Tulane University in 1997.



Steven K. Schmidt is Professor and Chair of the Department of Ecology and Evolutionary Biology, University of Colorado, Boulder. His research interests include biogeochemistry of extreme ecosystems, fungal ecology, soil microbiology, and microbe-plant interactions. Dr. Schmidt has published extensively on the biogeochemistry and microbial diversity of high-mountain ecosystems around the world, including the High Himalayas, the Andes, and many other ranges. His latest research projects focus on the function and diversity of microbes found on the Earth's highest volcanoes (Llullaillaco and Ojos del Salado) and the microbes that are endemic to high-elevation snow packs.



Tadashi Fukami is an Assistant Professor in the Department of Biology at Stanford University. He studies how species assemble into ecological communities, focusing on historical contingency, or when and why the structure and function of communities are contingent on the history of species immigration. He earned a bachelor's degree from Waseda University in 1996, a master's degree from the University of Tokyo in 1998, and a Ph.D. from the University of Tennessee, Knoxville, in 2003. After postdoctoral work at Landcare Research, New Zealand, he was an Assistant Professor at the University of Hawaii at Manoa before moving to Stanford.



Sean P. O'Neill is an M.A. student in the Department of Ecology and Evolutionary Biology at the University of Colorado, and he is affiliated with the Institute of Arctic and Alpine Research, both in Boulder, CO. His current research is focused on the role of neutral and niche processes in microbial community assembly as well as the role of microbial communities in landscape ecology and ecosystem management practices. He earned his bachelor's degree at the University of Colorado in 2008 and has been engaged with research in microbial ecology since 2006.



Teresa M. Bilinski is a Ph.D. student in the Institute for Arctic and Alpine Research and the Department of Ecology and Evolutionary Biology at the University of Colorado in Boulder. Her dissertation research focuses on the role of bacterial community ecology in groundwater arsenic cycling. She earned a bachelor's degree at the University of Oregon and a master's degree from the University of Colorado. She will begin a position as an Assistant Professor at St. Edward's University in the Fall of 2013.



Lee F. Stanish is a postdoctoral researcher in the Chemistry and Geochemistry Department at the Colorado School of Mines. Her research focuses on differentiating the relative importance of physical, biogeographic, and biological processes in structuring microbial communities, with a focus on finding common patterns in the ecological responses of phylogenetically diverse microorganisms. She earned a Ph.D. from the University of Colorado at Boulder, where she explored the role of hydrology and species interactions in structuring microbial mat communities in Antarctic streams. Her current research applies ecological principles to engineered systems for enhancing the productivity of algal biofuels.



Joseph E. Knelman is a Ph.D. student at the University of Colorado, Boulder, at the Institute of Arctic and Alpine Research and in the Department of Ecology and Evolutionary Biology. His research interests center around the ecology of plant-soil microbe interactions from natural to agricultural systems. His past work has examined the impact of plant colonization on microbial communities and nitrogen fixation in early successional soils. He received a bachelor's degree from Northwestern University and a master's degree from the University of Colorado.



John L. Darcy is a Ph.D. student in the Department of Ecology and Evolutionary Biology at the University of Colorado, Boulder. He is interested in many aspects of microbiology and ecology, especially microbial phylogenetics and phylogeography. His work seeks to understand which factors aid microorganisms in attaining their spatial distributions and to what extent taxa differ in this regard. He earned his bachelor's degree at the University of Colorado.



Ryan C. Lynch is a Ph.D. candidate at the University of Colorado in the Department of Ecology and Evolutionary Biology. He is a member of the Schmidt Laboratory, where he studies desert soil *Actinobacteria*. He uses experimental and comparative population genomic approaches to seek to uncover both novel adaptive bacterial traits and underlying evolutionary processes. He earned his bachelor's degree at the University of Colorado.



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Philipp Wickey is a bachelor's student with a dual major in Physical Geography and Environmental Studies at the University of Colorado, studying the interaction between humans and the environment. Specifically, he is interested in disturbance ecology and restoration. His experience also includes research in forest fire ecology in the American West, megafauna extinction in Australia, and arthropod recovery in Costa Rica.



Scott Ferrenberg is currently a doctoral candidate in the Department of Ecology and Evolutionary Biology at the University of Colorado. His research focuses on understanding how disturbance events influence species' interactions and how phenotypic variation within populations affects processes within the larger biological community. He earned his M.S. in 2002 from the University of Maryland Department of Entomology. Among various positions, he spent 2 years as a fire ecologist with the U.S. Geological Survey and 3 years as an associate research scientist with the University of California's Sierra Nevada Research Institute, studying the potential for species' range shifts under climate-warming scenarios.

