

## Opinion

## Spatial, Temporal, and Phylogenetic Scales of Microbial Ecology

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Microbial communities play a major role in disease, biogeochemical cycling, agriculture, and bioremediation. However, identifying the ecological processes that govern microbial community assembly and disentangling the relative impacts of those processes has proven challenging. Here, we propose that this discord is due to microbial systems being studied at different spatial, temporal, and phylogenetic scales. We argue that different processes dominate at different scales, and that through a more explicit consideration of spatial, temporal, and phylogenetic grains and extents (the two components of scale) a more accurate, clear, and useful understanding of microbial community assembly can be developed. We demonstrate the value of applying ecological concepts of scale to microbiology, specifically examining their application to nestedness, legacy effects, and taxa–area relationships of microbial systems. These proposed considerations of scale will help resolve long-standing debates in microbial ecology regarding the processes determining the assembly of microbial communities, and provide organizing principles around which hypotheses and theories can be developed.

## The Importance of Scale

Microbes, here defined as bacteria, archaea, viruses, fungi, and protists, are the most abundant and diverse organisms on Earth. The number of living microbial cells currently on Earth is estimated to be over  $10^{30}$ , with more than  $10^{29}$  cells in soils alone, giving a global biomass of approximately 400 billion tons of C [1]. The biodiversity represented by microbes is immense, likely orders of magnitude greater than that of plants and animals [2–5]. Commensurate with their ubiquity is the impact of microbes: microbes are central to disease pathogenesis in plants and animals, contribute to biogeochemical cycling, and greatly benefit agriculture, health, bioremediation, and other ecosystem services.

Increasingly it has become evident that these impacts result not only from individual strains and taxa of microbes acting alone, but also from emergent properties of microbial **communities** (see [Glossary](#)) as a whole. For instance, Crohn's disease [6] and other gastrointestinal disorders [7] have been linked to dysbiosis of the human microbiome, while aspects of public health have been tied to soil microbial biodiversity [8]. Carbon and nitrogen cycling can be linked to the structure of microbial communities [9]. In agricultural systems, soil microbial biodiversity can foster improved ecosystem functioning with direct benefits to agroecosystem activity [10]. The structure of bacterial and fungal communities has been tied to their capacity to bioremediate hydrocarbon-contaminated soils [11]. More generally, ecosystem services are connected to microbial taxonomic [12] and functional [14] diversity, as well as the role of microbes in food webs [13]. These and other examples point to the importance of considering not just individual taxa and genes of microbes in isolation, but communities of microbes from a whole systems level perspective.

## Highlights

Understanding the processes that shape microbial communities holds potential to provide important insights into ecology and evolutionary biology, and can enable forecasting and management of microbial ecosystem services.

At least four fundamental processes (selection, dispersal limitation, neutral processes, mutation) may shape microbial communities, but determining their importance has proven challenging.

Ecology has a long history of recognizing that numerous patterns and processes are dependent on spatial, temporal, and phylogenetic scales. Each scale is comprised of two fundamental components: grain and extent.

Recognizing that different processes may dominate at different scales in microbial systems could be instrumental in resolving long-standing uncertainty about which processes are important in shaping microbial communities.

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Understanding the mechanisms shaping microbial communities is hence of critical importance. Such an understanding could help predict the outcomes of interventions to the human microbiome, shifts in biogeochemical cycles in response to environmental change, and alterations in agricultural practices. Furthermore, this knowledge would present opportunities to mitigate microbial disservices and better harness microbial services: it could be used to design better microbiome-based therapies for disease, improve bioremediation strategies, increase agricultural yields, and guide natural products discovery. More generally, it would increase understanding of underlying evolutionary and ecological processes, and illuminate the universality of the functioning of biological systems.

Four mechanisms are generally understood to underlie the assembly of microbial communities [15–17], and indeed the assembly of ecological communities of all organisms [18]. First, communities can be shaped by **selection**. Interactions between taxa, for instance, predation and competition, can affect which species occur (biotic selection), and the physical environment can filter taxa as well (abiotic selection). Second, **neutral assembly processes** can determine the composition of communities. Via processes analogous to genetic drift, the composition of communities can shift and be determined neutrally. Third, **dispersal limitation** can be important: the taxa that occur and are absent from a community can be those that are capable and incapable of reaching it, respectively. Finally, mutation can play a role. *De novo* mutations in microbial genomes can arise to modify community composition and increase diversity. These mechanisms are of course not entirely independent, and they can affect each other.

Extensive research in microbial ecology has been devoted to understanding the roles of these four processes. For instance, in the human microbiome, selection [19], neutral processes [20], dispersal limitation [21], and other mechanisms [22] have been implicated in the assembly of microbial communities. In marine communities, selection [23] and a lack of dispersal limitation [24,25] can be important. Likewise, in polluted environments abiotic selection has been implicated [26].

These and other examples all point to a heterogeneity of mechanisms of community assembly (selection, neutral processes, dispersal limitation, and mutation) operating across microbial communities. This heterogeneity could be due to many factors, including different mechanisms operating in different environments, different methodologies used to infer mechanisms, and consideration of different groups of microbial taxa. Here, we posit that much of this heterogeneity is due to a factor that has remained relatively unconsidered in microbial ecology: **spatial, temporal, and phylogenetic scale**. We argue that only through an explicit consideration of scale, can a complete understanding of the mechanisms of microbial community assembly be developed.

### Ecology Has a Long Tradition of Considering Scales

Here we will focus on observational studies of microbial ecology, wherein microbial communities are characterized across geographic space, time, or both. These studies, such as the Earth Microbiome Project [27], American Gut Project [28], Human Microbiome Project [29], and Thousand Homes Project [30], have contributed greatly to our understanding of microbial ecology. However, the ideas presented here apply to experimental studies in the field and laboratory as well.

Three scales must be specified, either implicitly or explicitly, for microbial ecology studies [31,32]. First, studies specify a spatial scale. Are samples collected from a single geographic location, or across a city, state, continent, or globally? Second, they specify a temporal scale. Are samples all

### Glossary

**Community:** the set of organisms inhabiting a location or region.

**Dispersal limitation:** the inability of certain organisms to reach certain places.

**Ecological neighborhood:** the region or space that an organism occupies over a set period of time.

**Extent:** the breadth of the whole study.

**Grain:** the breadth of individual units of observations.

**Legacy effects:** the tendency of biological systems to retain antecedent properties after the environment has shifted.

**Nestedness:** the tendency of less diverse communities to be subsets of more diverse communities.

**Neutral assembly processes:** a process of community assembly in which organisms assemble via processes analogous to neutral genetic drift.

**Phylogenetic scale:** the taxonomic groupings under consideration.

**Selection:** the filtering of taxa arriving in a community via biotic and abiotic interactions.

**Spatial scale:** the distance, area, or volume under consideration.

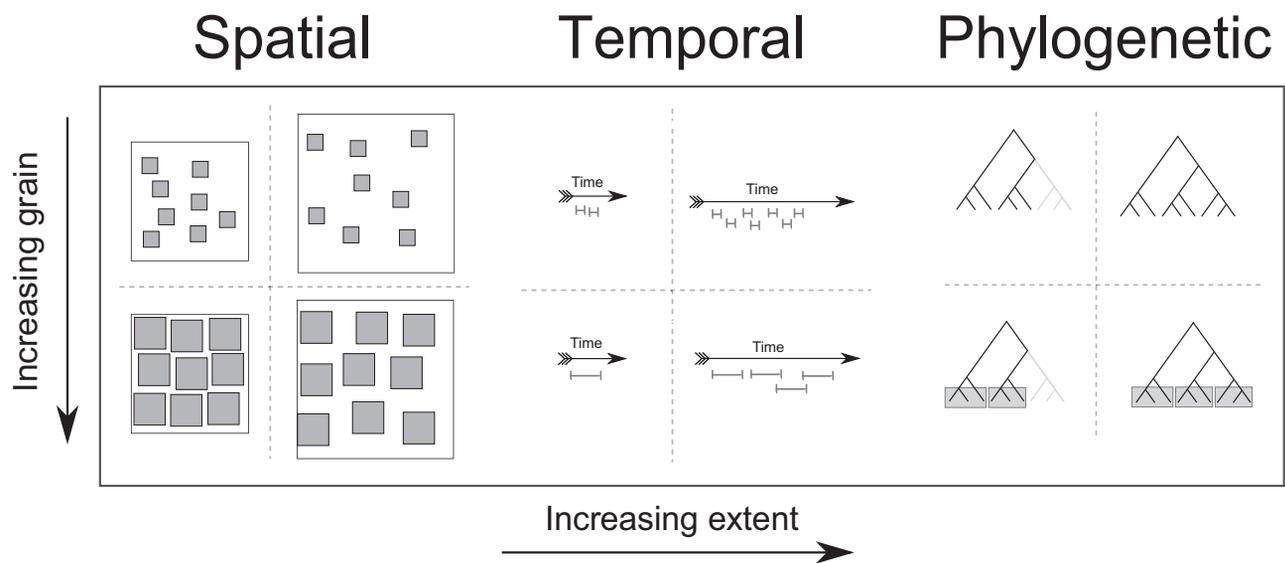
**Taxa–area relationships:** the relationship between diversity in geographic regions and the area of those regions. Taxa–area relationships often follow a consistent form across systems.

**Temporal scale:** the time period under consideration.

collected over an hour, day, season, or decade, and how do these durations relate to replication rates and asynchronous properties such as dormancy? Finally, they specify a phylogenetic scale. For example, are all microbes considered, or are just bacteria, archaea, or fungi considered, and are they identified to the operational taxonomic unit (OTU) level or a coarser taxonomic resolution?

Each of these scales, spatial, temporal, and phylogenetic, are composed of two components: **grain** and **extent** [31]. Grain is defined as the breadth of individual units of observations. For example, if multiple soil cores from within 10 m quadrats are mixed prior to sequencing, then the spatial grain is 10 m. Likewise, if ocean water is filtered for 12 hours and then sequenced, then the temporal grain is 12 hours. And if reads are clustered at the OTU level (but not the strain level, for instance), then the phylogenetic grain is at the OTU level. In contrast to grain, extent is defined as the breadth of the whole study. A study of human gut microbiomes from across the contiguous USA would have a spatial extent of approximately 4000 km. A study of airborne microbes sampled throughout 2012 and 2013 would have a temporal extent of 2 years. A study that considered all archaea but no other microbes would have an extent limited to the domain archaea. Grain and extent circumscribe scale. Figure 1 diagrams the components of ecological scale.

Ecology has a long tradition of recognizing and leveraging the importance of spatial, temporal, and phylogenetic scales. As Levin [33] eloquently stated, ecology, and indeed most science, seeks to build models or theories to explain the mechanisms generating patterns. The best models omit unnecessary details and include just the components and processes that are necessary for making useful predictions. We do not want models that predict every detail of a pattern, that model would be the system itself, but rather a model that can predict its key features. But most ecological patterns vary depending on grain and extent. (The exception being scaling laws and fractal or scale-invariant patterns.) So by necessity, our conceptual models and the mechanisms that we identify as being important will often vary across scales concomitantly.



Trends in Microbiology

**Figure 1. Scale in Microbial Ecology.** Ecological scale has three axes: space, time, and phylogeny. Each of these has two components: grain, the scope of the unit of observations, and extent, the scope of the entire set of observations [31,32]. Ecological processes and patterns often depend on spatial, temporal, and phylogenetic grain and extent.

In this way, scale is at the heart of understanding the mechanisms of assembly of microbial communities.

Among macroorganisms, it is well established that different mechanisms dominate community assembly at different grains and extents. For instance, interspecific interactions (biotic selection) often dominate at small spatial scales, while environmental filtering (abiotic selection) often dominates at larger spatial scales [34]. In other systems, neutral processes dominate at small spatial scales, while other processes such as dispersal limitation dominate at larger spatial scales [31]. The effects of anthropogenic disturbance can also be highly scale-dependent [35]. Numerous other examples abound for temporal and spatial scales (reviewed in [32]). A heterogeneity of mechanisms and scale-dependence is the norm rather than the exception. Microbes show extensive variation in mechanisms of community assembly, but the role of scale in generating this variability remains largely unexamined.

We suggest that there are two main interrelated questions concerning scale in microbial ecology. First, which microbial patterns and processes are scale-dependent and which are scale-independent? Although the thesis of this opinion article is that scale affects many microbial patterns and processes, this scale-dependence may not always be the case: there may be patterns and processes that are scale-independent and universal [33]. Identifying such universal patterns and processes is of high utility toward building a causal and predictive understanding of microbial ecology. Second, when patterns and processes are scale-dependent, what is that scale-dependence? Microbial ecology should seek to assess the prevalence of scale-dependence, which patterns and processes dominate at which scales, and the causes of this variability.

### Consideration of Scale Is Less Pervasive in Microbial Ecology

For the most part, the interplay between scale and mechanisms has received little attention in microbial ecology [36–38]. This oversight may be due to at least two factors. First, many microbial ecologists may be unaware of the role that scale plays in macroorganism ecology and its potential for microbial ecology. Indeed, a recent opinion by Shade and colleagues calls for the union of macroecological patterns and principles across all systems [39]. Second, many microbial ecologists may not fully consider the **ecological neighborhoods** of microbes. An ecological neighborhood is defined as the region that an organism occupies over a set period of time [40]; it constrains the spatial grains and extents that are relevant to the assembly of communities. Many microbes have been assumed to interact with their environment only at microscopic scales, making larger grains and extents seemingly irrelevant. However, extensive evidence indicates that microbes often quickly disperse great distances and persist for long periods of time. Hence, the ecological neighborhoods of many microbes are likely larger than those of macroorganisms. We suggest that there is no reason to expect that scale should be less of a consideration in the microbial world, at least from the perspective of ecological neighborhoods, and that it should actually be more of a consideration. Furthermore, studying the microbial world may be complicated by a disconnect between the scales at which microbial communities can be sampled and the scales at which microbes act.

### Explicitly Incorporating Scale in Microbial Ecology

With increasingly large data sets, scale can be incorporated in microbial ecology in much the same way that it has been incorporated in macroorganism ecology. Here we present three examples.

#### Nestedness of Microbial Communities

Recently, Thompson *et al.* [27] showed that when considered at coarse taxonomic grains (e.g., the class level), communities of microbes tend to be nested within each other: that is,

communities with fewer taxa tend to be subsets of communities with more taxa. This **nestedness** holds globally across a wide array of environments, with, for example, at the phylum level, soil communities from around the world being nested within each other, and marine communities generally being nested within soil communities. In macroorganisms, nestedness can point to ordered extinctions or colonization events [41], raising the possibility that such events may be widely involved in the assembly of microbial communities. Thompson *et al.* [27] investigated how nestedness varies with phylogenetic grain, and found that it is strong at coarse grains and weakens with increasingly fine grains, until at the OTU level it is almost entirely absent (for instance, the human microbiome and marine microbial communities share many phyla but few OTUs). This analysis of phylogenetic grain could be expanded to cover phylogenetic extent and also spatial and temporal scales. How do patterns of nestedness vary for different groups of taxa, for instance, are families of just Alphaproteobacteria or Gammaproteobacteria nested? And how does nestedness vary depending on the extent of the geographic region considered or time period (temporal extent) over which samples are collected? Finally, how does spatial and temporal grain affect patterns of nestedness? If samples from a geographic region are merged (coarse grained), does that change patterns of nestedness? An example of a path to investigate these questions has been shown through reanalyzing data from three studies [42].

In addition to investigating how patterns of nestedness vary with scale, the key element here is linking those patterns to mechanisms of community assembly [43]. As discussed above, patterns that vary with scale can point to effects of mechanisms varying with scale, but that linkage must be established. Thompson *et al.* [27] hypothesized several mechanisms that could account for the microbial nestedness patterns, but additional analyses (testing independent predictions from hypothesized mechanisms) would be necessary to link process to pattern, and its interrelationship with spatial, temporal, and phylogenetic scale.

#### Legacy Effects in Microbial Communities

Understanding **legacy effects** in microbial communities is an active area of research. Legacy effects occur when ecological communities lag behind shifts in the environment [44]. For instance, a legacy effect would occur if agricultural practices change but communities of plants in agricultural lands remained unchanged. Legacy effects also occur widely as a result of climate change. *A priori*, microbial communities might not be expected to show legacy effects extensively because microbes often have short generation times, individually respond quickly to environmental shifts, and disperse readily (but see [45], for instance). However, mounting evidence points to legacy effects spanning months to several decades in microbial communities, particularly in soils, potentially mediated by lags in vegetation, other environmental characteristics, and hysteresis in microbial communities themselves [46–48].

The question of legacy effects can be thought of as a question of temporal extent: what temporal extents of environmental conditions are relevant for predicting distributions of microbes? These effects are necessary for large temporal extents of environmental conditions to be important in determining the distributions of microbes [49]. As usual, the duration and strength of legacy effects may vary with temporal grain (the length of time communities are sampled), spatial grain and extent, and phylogenetic grain and extent. Understanding how legacy effects vary across these scales will help elucidate their relevance and importance to microbial systems.

To evaluate the importance of legacy effects in microbial communities, predictive models can be constructed using not just environmental conditions at the time of sampling, but also environmental conditions from the past (as reviewed in [50]). Legacy effects can be indicated when historical

conditions are found to be predictive using model selection techniques. In addition, when available, historical data on microbial communities can be very useful; for instance, samples collected from decades ago that have been preserved can be sequenced and utilized.

### The Taxa–Area Relationship

The **taxa–area** (or species–area) relationship is a fundamental pattern in ecology. It quantifies the manner in which the number of taxa or species in a region scales with the size of that region [51]. As such, it quantifies how diversity scales with spatial grain, and can be used to understand and predict the distribution of biodiversity. Broadly, the taxa–area relationship typically follows an s-shape: increasing steeply at small local spatial grains, leveling off at regional grains, and again increasing steeply at continental and larger grains [52].

For bacteria, archaea, and fungi, the taxa–area relationship has been widely measured across ecosystems using high-throughput 16S ribosomal RNA gene sequencing. Evidence indicates that microbes exhibit taxa–area relationships in much the same way that macroorganisms do [53–55]. However, many key scale-related facets of the microbial taxa–area relationship remain unexamined. For instance, how does diversity vary jointly with spatial and temporal grain? This latter relationship, the species–time–area relationship (STAR), can reveal much more about the processes underlying the distribution of biodiversity than the taxa–area relationship alone [56]. Furthermore, how does the microbial taxa–area relationship and STAR depend on spatial and temporal extent? In macroorganism communities, evidence suggests that the taxa–area relationship exhibits universal behavior at continental spatial extents, but is more unpredictable at smaller spatial extents. Finally, how does phylogenetic grain and extent affect the properties of the taxa–area relationship and STAR for microbes? Hence, in the context of scale, microbial taxa–area relationships can be viewed dually as fundamental objects of interest, describing how diversity varies with spatial grain, and as objects that can vary with other axes of scale. Answering these scale-related questions will lead to a deeper understanding of one of the most fundamental scaling relationships in microbial ecology.

Many of the key studies examining the large-scale taxa–area relationships in macroorganisms have relied on range maps of their distributions to assess diversity at different granularities [57]. Such range maps have begun to be developed for microbes [23], but more thorough databases of microbial ranges will be important in developing a scale-dependent understanding of taxa–area relationships for microbes. Additional sampling of microbial communities, both in time and space, coupled with the application of novel computational tools, will likely be central in moving this area of research forward.

### Concluding Remarks and Future Perspectives

Moving forward, we advocate that an explicit consideration of spatial, temporal, and phylogenetic grain and extent would lead to an improved understanding of the mechanisms of community assembly among microbes (see Outstanding Questions). Such an understanding would both aid in predicting microbial systems and their functions, and help to design interventions to microbial systems to improve human health, agriculture, and the environment. There is a long tradition of explicitly considering scale in macroorganism ecology, from which microbial ecology will be able to draw on to great effect.

How can scales be more explicitly considered in microbial ecology? First, observational data can be collected in such a manner as to allow analyses at different scales. Nested spatial sampling designs and accompanying time series allow both spatial and temporal grain and extent to be varied (e.g., [45]). Similarly, accurate phylogenetic trees allow phylogenetic scale to be varied. Second, analyses can be performed at different scales. Rather than choosing just one grain

### Outstanding Questions

Which microbial diversity patterns and ecological processes are dependent on spatial, temporal, and phylogenetic scales, and which are scale-independent?

When microbial patterns and processes are scale-dependent, what is the nature of that dependence?

Which of the four general processes of community assembly (selection, dispersal limitation, neutral processes, mutation) dominate microbial community assembly at which spatial, temporal, and phylogenetic scales?

Do the ecological neighborhoods of microbes predict their scale-dependence?

How do patterns of microbial nestedness depend on scale?

How does the taxa–area relationship for microbes depend on scale?

How do microbial legacy effects depend on scale?

How do scale-dependencies vary with the two axes of scale, grain and extent?

How do scale-dependencies for microbial communities differ from those of macroorganisms?

and extent (e.g., the minimum spatial grain across all sampling locations), analyses can be conducted at varying grains and extents, implemented by merging samples and considering just samples from subsets of the geographic region sampled, time course sampled, or taxa that were classified. Finally, and perhaps most difficult, patterns varying across scales should be connected to processes. With observational data, applications and advances in models and theory are necessary to achieve the latter.

While this opinion article has focused on observational data, the ideas presented here apply equally well to experimental systems. Manipulative experiments can help test hypotheses generated from analyses of observation-based data, particularly hypotheses about underlying mechanisms. If a microbial system is manipulated experimentally, it is equally important to consider how the effects of those manipulations vary across spatial, temporal, and phylogenetic scales. Moreover, if an experiment is designed to test for a particular mechanism, then that mechanism may suggest a relevant scale for the experiment; for instance, the spatial scale of ecological neighborhoods, which may be difficult to define for many microbes and one of the key underlying challenges. Careful consideration of scale in microbial ecology can both inform the design of experiments, analysis of observational data, and interpretation of mechanisms underlying the assembly of microbial communities, ultimately yielding a more accurate, useful, and complete picture of the microbial world.

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