ESSAY

The role of ecological theory in microbial ecology

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Abstract | Microbial ecology is currently undergoing a revolution, with repercussions spreading throughout microbiology, ecology and ecosystem science. The rapid accumulation of molecular data is uncovering vast diversity, abundant uncultivated microbial groups and novel microbial functions. This accumulation of data requires the application of theory to provide organization, structure, mechanistic insight and, ultimately, predictive power that is of practical value, but the application of theory in microbial ecology is currently very limited. Here we argue that the full potential of the ongoing revolution will not be realized if research is not directed and driven by theory, and that the generality of established ecological theory must be tested using microbial systems.

Bacteria and Archaea have an essential role in earth system processes. They are ubiquitous, possess enormous metabolic and physiological versatility and are essential to virtually all biogeochemical cycling processes — microbial carbon and nitrogen are calculated to be, respectively, equivalent to and tenfold as great as the carbon and nitrogen stored in plants[1]. Although small (~10^{-6} m), they are abundant (>10^{30} individuals globally). Their phylogenetic and physiological diversity is considerably greater than that of animals and plants and their interactions with other life forms are correspondingly more complex.

Understanding the ecology of microorganisms is arguably one of the most compelling intellectual challenges facing contemporary ecology. Although worthy for its intellectual merits alone, developing such an understanding is essential to meet many of the major challenges facing human society today, such as the management of natural ecosystems and the mitigation of climate change. Despite this, the application of theory is severely lacking in microbial ecology where, paradoxically, it is required most. Just as ecological theory arose from natural history to draw generalized conclusions from specific observations of organisms in their environment, so microbiologists need theory to interpret the plethora of observations that have been made since van Leeuwenhoek first saw 'animalcules' more than 300 years ago. With the increasing reliance on specific microbial processes (in, for example, wastewater treatment, industrial chemical production, pharmaceutical production and bioremediation), and the realization that many nonspecific microbial processes such as biogeochemical cycling are essential for ecosystem sustainability, understanding the factors that control these processes is crucial. In our view, this can best be achieved by generating theory that is based on existing observations and subsequent experimental validation.

The importance of theory

Theory is used to classify, interpret and predict the world around us. Without it, microbial ecology is merely the accumulation of situation-bound statements that are of limited predictive ability, providing microbiologists with few insights. Theory has an essential role in developing an understanding of, and explaining the interactions between, microorganisms and their physical, chemical and biological environments. This understanding will be lacking if it is solely qualitative, and a full understanding therefore requires quantitative theory.

Theory generates predictions that can be of practical value for policy makers, stakeholders and society. A striking example is the use of epidemiological models to predict the spread of human and plant pathogens and the use of these predictions to inform and implement control policies[2]. There is similar potential value in applying theory in the many areas in which microorganisms are of environmental and economic importance. For example, improved quantitative theory could increase the efficiency of wastewater treatment processes, through the prediction of optimal operating conditions and conditions that are likely to result in system failure. Quantitative information on the links between microbial community structure, population dynamics and activities will also facilitate assessment and, potentially, mitigation of microbial contributions to climate change, and should lead to quantitative predictions of the impact of climate change on microbial contributions to specific ecosystem processes. Given the high abundance, biomass, diversity and global activities of microorganisms, the ecological theory that has been developed for plants and animals is of limited value if it does not apply to microbial communities. Microorganisms arguably provide much better controlled and more manipulable experimental systems for testing ecological theory than plants or animals, and such testing is essential to establish the generality of theory. The use of better controlled microbial systems might also generate new theory that is relevant to plants and animals.

Two factors limit the development of theory in microbial ecology. The first is a lack of data and associated insights. This is due in large part to the difficulties inherent in observing microorganisms in nature, which often have few distinguishing morphological features and often cannot be cultivated in the laboratory. The application of cultivation-independent molecular techniques and their successors — genomics, metagenomics, transcriptomics and proteomics — has generated a plethora of new and more comprehensive observations of microorganisms in nature, but we still lack the theoretical tools required to detect underlying principles and mechanisms. The second factor is cultural, in that the tools and disciplines of ecological theory are not part of the contemporary mindset in microbiology. Ecological theory and quantitative reasoning typically form only minor components of education in microbiology, and microbiologists have traditionally used a detailed, reductionist approach that is based on understanding physiological mechanisms, with relatively little attention paid to theory. Although the challenge for the microbial ecologist might appear to be the discovery (or recollection) of evermore fascinating details of a given system, the theoretician aims to predict as much as possible about a system using as few of these

details as possible; but the populations and structures of microbial communities, by comparison with those of plants and animals, remain inscrutable. The application of molecular techniques has demonstrated the need for discovery research, but in our view this can only be exploited if it is directed by insights gained from the application of theory.

Current ecological theory

An established body of theory exists for plant and animal ecology but the differences between microorganisms and 'large' organisms, and the extent to which these differences restrict the applicability of existing theory to microbial ecology, often form an impasse that is tacitly accepted and seldom questioned. Commonly cited differences include the small size of microorganisms, high rates of population growth, high rates and extent of dispersal, the vast abundance of microorganisms, and the unique aspects of their biology (such as parasexuality or extremely hardy resting stages). However, the breadth of distribution of many of these traits among microorganisms in nature is not known. Furthermore, the existence of these traits does not necessarily prevent the application of existing ecological theory to microorganisms (see later discussion of spores and seed banks). Also, the relatively large scales of time and space over which most microorganisms are studied does not necessarily preclude the application of existing theory; theory related to the subdiscipline of ecology called macroecology was developed specifically to further the understanding of ecology on large scales of space and time (see below). The challenge facing microbial ecologists, and indeed all ecologists, is to match the appropriate theoretical approach to the organism, system, scale and question of interest.

Microbial model systems have played an important, although often underappreciated, part in the development of existing ecological theory (reviewed in REF. 3), demonstrating its general applicability to microorganisms. However, it is less common for existing theory to be applied to microorganisms in nature despite the fact that this would be valuable. It would be extraordinarily inefficient to attempt to reinvent existing theory for application to microorganisms. Furthermore, the application of existing theory would afford ecologists the opportunity to test the true generality of ecological principles and to create a synthetic ecology that spans all organisms. This would greatly increase our understanding of ecological systems and allow the much more effective management of the natural world.

In the following sections we discuss examples of areas of ecological theory that might be particularly valuable in microbial ecology. In doing this, we attempt to determine whether the particular characteristics of microorganisms present difficulties in applying ecological theory that has been developed for plants and higher animals. We consider whether and where new theory might be required for microorganisms to enhance or replace established ecological theory. We also identify conceptual and practical challenges faced by microbial ecologists in applying quantitative ecological theory.

Ecological species concepts

Most ecological theory depends on a concept of species: population ecology counts individuals within species whereas community ecology and macroecology count the number of species. Species are most commonly defined through the biological species concept promoted by Mayr[4]. This is a genetic definition that envisages a species as a group of interbreeding individuals that is isolated from other such groups by barriers to recombination. If genetic exchange within a species is sufficiently extensive, and that between species is sufficiently low, species will be relatively homogeneous in themselves and ecologically distinct from other species. Unfortunately, prokaryotes (and some eukaryotes) are asexual, thereby violating these assumptions, and do not form species in this genetic way. An alternative, the ecological species concept, defines a species as a set of individuals that can be considered to be identical in all relevant ecological properties. Cohan[5] has argued that bacteria have ecological species ('ecotypes'). He postulates that bacteria occupy discrete niches and that periodic selection will purge genetic variation within each niche without preventing divergence between the inhabitants of different niches. So, genetically and ecologically distinct species will arise, provided there is little or no recombination, and ecological theories that assume such species should apply to bacteria. This also predicts that molecular diversity should relate directly to ecological diversity.

Cohan's ecotypes depend on discrete niches but speciation is more difficult to envisage when the relevant environmental variables are continuous. Bacterial speciation in these situations could be explored using the theory of adaptive dynamics[6,7], but this might not lead to simple mapping between molecular markers and an ecological niche. More crucially, speciation, and ecological species definitions, must consider bacterial gene-transfer processes, which are erratic and transfer only a small part of the genome. They provide a potential mechanism for maintaining biological species in Mayr's sense[8], because an incoming gene can replace the homologous copy in the genome, maintaining the genetic cohesion of the species. In addition, these processes can also result in the horizontal transfer of genes with no counterpart in the recipient that can be maintained on a plasmid or integrated by non-homologous recombination. However, the importance of homologous recombination and horizontal transfer varies widely among well-studied bacterial species, and perhaps even more so among the uncultured masses in the environment. This heterogeneity is one reason why we are still far from a consensus on the nature of bacterial species, as revealed at a recent Royal Society discussion meeting[9].

A consequence of gene transfer is that the bacterial genome is thought to consist of two distinct parts, the core genome and the accessory genome[10]. The core genome comprises genes that are essential in most circumstances and might form the basis for Mayrian species that maintain coherence through homologous recombination. The accessory genome encodes special ecological adaptations in genes that are readily gained and lost. Strains that belong to the same species, as defined by their core genome, can differ in the presence and absence of hundreds of accessory genes, and consequently can have different ecological capabilities. According to this view, Cohan's ecotypes are merely temporary lineages with particular constellations of accessory genes, and the ecological niche cannot explain the apparent cohesion of species that are defined by the phylogeny of core genes[11].

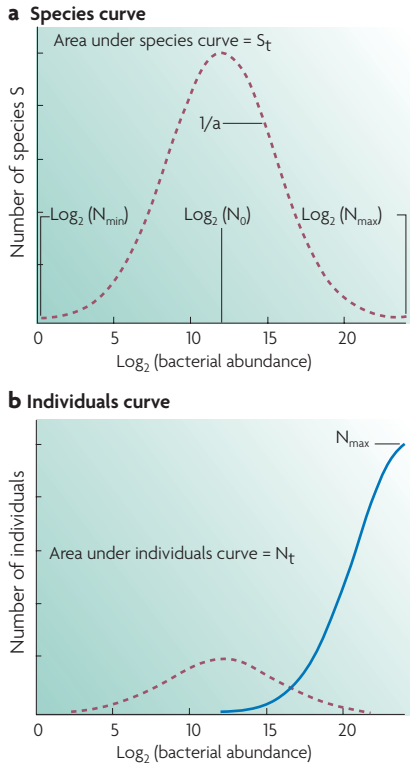
Surveys of 16S ribosomal RNA (rRNA) gene sequences have demonstrated the huge diversity of bacterial communities, but if much of the interesting ecological adaptation is conferred by the accessory genome then the true ecological diversity exists in the rich brew of catabolic plasmids, resistance transposons and pathogenesis islands. These can be shared among disparate bacteria in an environment that favours them, but can be absent in the 'same' bacterial species growing elsewhere. The methods of evolutionary ecology have been applied to the interaction between these accessory elements and their host bacteria. For example, Bergstrom and

Box 1 | **Theoretical approaches for estimating diversity in a sample**

A species abundance curve is simply a graph in which the abundance of a particular species is plotted on the *x* axis and the number of species at that abundance is plotted on the *y* axis (see figure). The observation and contemplation of these distributions is supported by a rich literature in conventional ecology in which some research, but not all, has imbued such distributions with some ecological meaning. However, microbial ecologists have an interest in species abundance curves because the area underneath a species abundance curve is the total diversity. This presents us with a 'catch 22' situation: we cannot measure abundances, so do not know the species–area curve, so we cannot estimate diversity.

In the absence of data, we can assume that a particular distribution, for example a log-normal distribution, applies. We can then make an estimate on that basis. Guessing distributions is not a wholly satisfactory procedure. Consequently, others have sought to fit a line to, and extrapolate from, abundance data (typically clone libraries) available to them[17].

Unfortunately, clone libraries in microbial ecology are so small ($<10^3$) and microbial communities so large ($>10^{15}$) that the sample distribution is unlikely to look like the community from which it was drawn. An alternative approach to estimating species abundance curves is to examine the reassociation kinetics of DNA extracted from an environment[17]. This approach involves denaturing DNA, separating the two strands of the DNA molecule, and then allowing them to reassociate. The most abundant sequences should reassociate first and the reassociation kinetics therefore reflect the underlying distribution of similar sequences and, consequently, the genomic diversity. However, for experimental reasons, only the reassociation of a small proportion of the diversity can be observed. Consequently, the bulk of the curve is extrapolated from a few taxa. It can be plausibly argued that this means that there is a great deal of uncertainty about the unobserved portion of the species abundance curve.



The figure shows a log-normal species abundance curve and corresponding cumulative individuals curve. 1/a is the width of the species curve, where a is the spread parameter. N_{min} is the abundance of the least abundant species; N_{max} is the abundance of the most abundant species; and N_0 is the modal species abundance. Figure reproduced with permission from REF. 16 © (2002) US National Academy of Sciences.

colleagues[12] discussed the conditions for plasmid maintenance, and a recent theoretical exploration concludes that the 'evolutionary arms race' between bacteria and bacteriophages can result in speciation of the host[13]. This presents a major challenge to those studying prokaryotic population and community ecology. The current solution is to use operational definitions of taxonomic units but we are a long way from a coherent body of theory that relates the fluid nature of bacterial genomes to the ecology of bacterial communities.

Measuring diversity and species richness

Since the estimation of substantial microbial diversity within soils[14], microbial ecologists have yearned to quantify and describe microbial diversity within any given environment. The sheer complexity of most environments, and the rapid realization that collector's curves of cloned environmental 16S rRNA gene sequences would give complete coverage only in the very simplest ecosystems, has necessitated the development of a more theoretical basis for estimating prokaryotic diversity. To this end, Dunbar and colleagues[15] and Curtis and colleagues[16] pioneered the use of species abundance curves that use log-normal relationships (which will include some taxa that are rare and others that are present in high numbers) to provide theoretical estimates of prokaryotic diversity, yielding diversity estimates that are similar to those derived by Torsvik and colleagues[14] using DNA–DNA hybridization (BOX 1). Gans and colleagues[17] highlight the requirement for collector's curves of in excess of one million PCR-derived clones to ensure coverage of 80% of bacterial species within a 1-g soil sample. Without screening large numbers of clones, sampling low-abundance species remains a matter of chance.

16S rRNA gene sequences provide an operational measure of species. High-throughput sequencing[18] or SARST (serial analysis of ribosomal sequence tags)[19] are currently the best suited techniques for estimating prokaryotic diversity. However, strains or isolates with identical 16S rRNA gene sequences can have different physiological characteristics of ecological importance and methods with greater taxonomic resolution are therefore required. Approaches such as pyrosequencing[20,21], which address diversity across entire metagenomes, might be appropriate and could suggest alternative conceptual approaches to diversity. Many ecological questions require information on specific phylogenetic groups or functional groups, such as rhizobia or ammonia oxidizers, which might increase tractability.

Many of the key questions in microbial community ecology require reliable estimation of species richness. Analysis of species abundance curves and the lack of a universal definition of species highlight the practical and conceptual difficulties associated with such estimates. The analyses described above provide the basis for quantifying species richness and for assessing the cost and feasibility of quantification.

Spatial scale

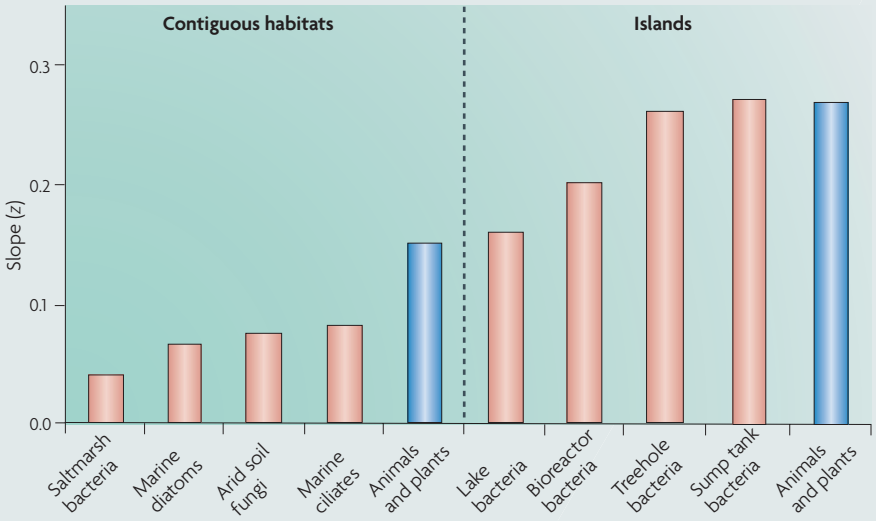
The pivotal role of spatial patterns and processes in ecology is widely recognized. Many systems, such as fragmented habitats and populations, cannot be studied without a serious consideration of space. This has generated the subdiscipline of landscape ecology (which has recently been applied to ecological aspects of antibiotic resistance in bacteria[22]), the metapopulation paradigm and metacommunity theory[23,24]. Other research areas focus directly on the role of spatial scaling in ecological patterns. For example, species–area relationships (SARs) have a long history in ecology (see for example REFS 25–27). A SAR describing areas with relatively few species in common has greater species turnover[28] and is steeper than a SAR with more species in common; steepness therefore describes how quickly local assemblages of species differentiate in space.

The spatial scaling of microbial diversity is now being addressed by coupling the molecular characterization of microbial communities with macroecological theory[29]. Compared with plants and animals, few SAR studies have been published for microorganisms, making a balanced comparison of SAR patterns between the different groups difficult. The SAR is commonly assumed to follow a power-law of the form $S \propto A^z$, where S is species richness, A is area and z is the slope of the curve. Empirical evidence suggests that for animals and plants within contiguous habitats, z is generally in the range of 0.1 to 0.2, and for discrete islands z is steeper ($0.2 < z < 0.39$) (REF. 27), although a new meta-analysis of SAR slopes suggests that this difference might not be as pronounced as previously thought[30] (BOX 2). This study also confirmed a general trend in the increasing steepness of z with increasing body size from ciliates to large mammals. Recent research has documented power-law species–area (or more generally, taxa–area) relationships in fungi and bacteria[31,32] and bacteria in 'island' habitats[29,33–36]. The z values estimated in studies of contiguous habitats were much lower than those of island habitats, but island z values were similar in magnitude to those observed for plants and animals. More research is required to establish whether microorganisms are distributed spatially in ways that are similar to plant and animal species, but one study indicates that soil community composition is non-random at a continental scale, and that soil community composition and diversity at large scales can be predicted primarily on the basis of a single variable (pH)[37]. Such patterns differ from those of plants and animals, the biogeographical distributions of which are influenced by site temperature and latitude.

Diversity–energy relationships

In addition to relationships between diversity and area, common patterns have been described between diversity and energy. For example, primary productivity (the rate of energy capture and carbon fixation by primary producers) is thought to be a key determinant of plant and animal biodiversity[27,38]. A positive quadratic or hump-shaped relationship is frequently observed between productivity and diversity, in which diversity peaks at intermediate productivity[27], although other patterns have also been observed[39,40]. Bacterial communities also exhibit such diversity–energy relationships. Horner-Devine and colleagues[41] observed that increasing productivity both increased and decreased taxonomic diversity of bacteria in aquatic mesocosms and that the shape of the relationship between productivity and diversity differed between bacterial taxa. These initial results suggest that bacterial diversity can vary with energy and that the nature of the relationship can in some instances resemble that of plants and animals. Further studies are required to determine the mechanisms underlying microbial species richness and the influence of nutrient supply (for example, that associated with eutrophication) on microbial species richness and diversity.

Box 2 | **Theoretical approaches for estimating microbial species–area relationships**



Despite the theoretical and practical importance of species–area relationships (SARs), which relate an area (A) to the number of species (S) found within this area, they are difficult to quantify directly at ecologically relevant scales (see figure for a comparison of some microbial SARs from different contiguous habitats and islands). For organisms with the extraordinary abundance and diversity of microorganisms, this poses a challenge even at the scale of a single environmental sample. Microbial ecologists (and plant and animal ecologists) must therefore use theoretical approaches to estimate SARs.

The most straightforward analyses of microbial SARs are direct plots of sample data (see for example REF. 35). These analyses assume that the slope of the observed sample SAR parallels the slope that would result from a complete census. For a power-law SAR (in which the number of species is a constant power of the area ($S \propto A^z$; where z is the slope of the curve)), this translates to an assumption that the observed species richness in a sample is a constant proportion of the total species richness in the area from which it was sampled, and that this constant proportion is not affected by scale.

Parametric approaches are also commonly used to estimate the increase of species richness with sample size (or sampling area) (BOX 1). In short, sample data are fitted to models of relative abundance (or assumed on theoretical grounds), and this sample frequency distribution is projected to estimate the number of unobserved species in the community[70]. Parametric approaches assume that the sample frequency distribution is a truncated version of the community-level distribution, which in turn assumes that individuals are randomly sampled from the community. In many studies this assumption can be seriously violated. Microbial communities are commonly investigated by identifying individuals from soil or sediment cores across a landscape. Even if these environmental samples are randomly distributed in space, spatial aggregation in microbial populations will result in a non-random sample of individuals from the community.

An alternative approach to estimating SARs is to examine patterns of community turnover across a landscape (the distance–decay relationship). This method has been applied to estimate SARs at local, regional and global scales (reviewed in REF. 29). Recent studies have shown that distance–decay methods underestimate SAR slopes[71], which suggests the need for further theoretical work in this area.

The figure shows the slopes of the SARs for contiguous habitat studies of saltmarsh bacteria[32], marine diatoms[72], arid soil fungi[29], and marine ciliates[72] compared with the slopes of the SARs for island habitat studies of lake bacteria[36], wastewater treatment bioreactor bacteria[34], treehole bacteria[35] and coolant sump tank bacteria[33]. The blue bars show typical values for studies of animals and plants in these two habitats[26].

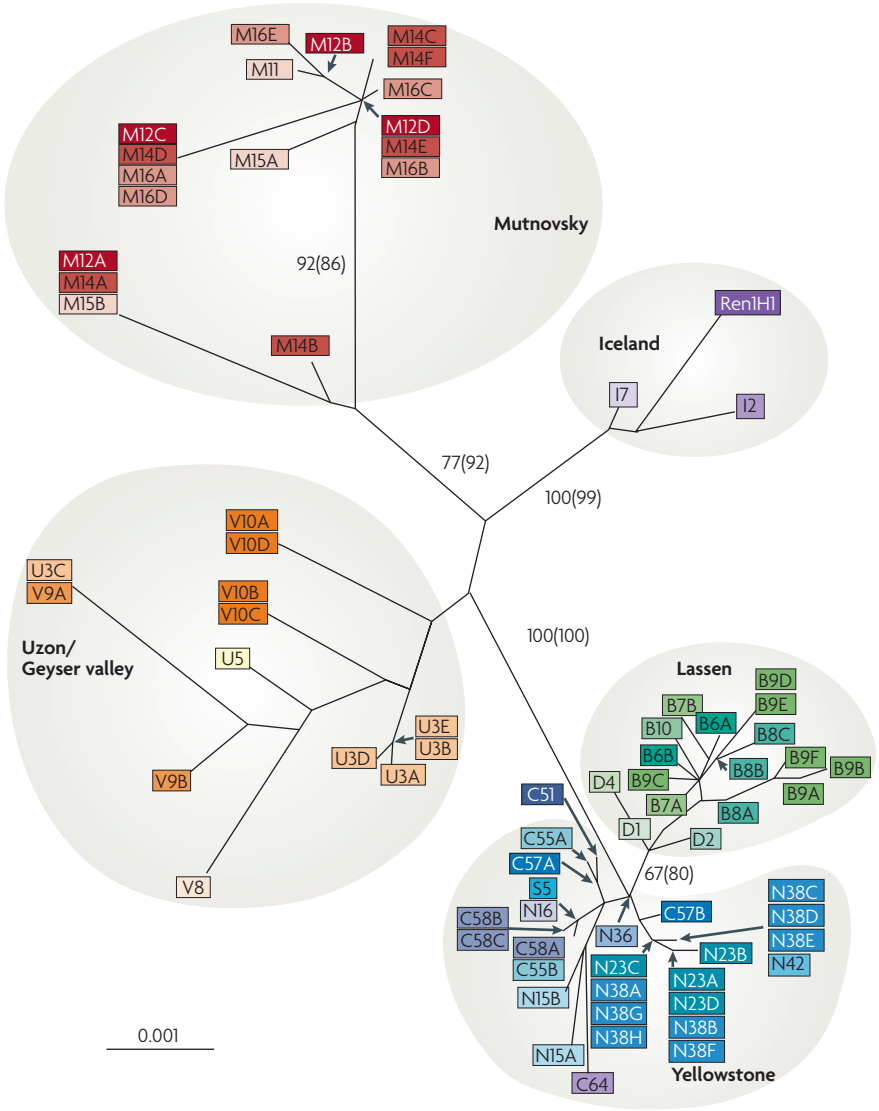


Figure 1 | **Evidence for endemicity in prokaryotes.** The phylogenetic analysis of sequences of nine genetic loci from *Sulfolobus* strains, isolated from water and sediment samples collected from a nested hierarchy of five geographical locations, is shown. Clades correspond to the five geographical regions, showing that strains within a region share a common evolutionary history that is distinct from strains found in other regions. Strains from the same sample are depicted in the same colour. The scale bar represents 1 substitution per 1,000 sites. Modified with permission from REF. 45 © (2003) American Association for the Advancement of Science.

Temporal scales

Microorganisms have the potential for rapid growth and short generation times, relative to those of plants and animals. This potential is often not realized in natural environments, where nutritional and physicochemical conditions can limit growth but, under favourable conditions, it can lead to varying patterns of microbial diversity over different temporal scales. Evolution in microorganisms can occur rapidly, particularly under strong selective pressures, potentially leading to convergence of ecological and evolutionary timescales. This fundamental property can be exploited to examine contemporary issues in ecology, such as climate change, in which anthropogenic forcing might have an evolutionary effect on organism–environment relationships. When Dykhuizen[8] asked 'Why are there so many species of bacteria?', he contemplated factors such as low extinction rates and high speciation. He reasoned that bacteria have been able to avoid mass extinctions over geological time, unlike some larger organisms (such as the dinosaurs), owing to their ability to withstand rapid changes in environmental conditions. Unusually high speciation rates would be a more likely dominant factor in influencing temporal diversity patterns, and laboratory studies of experimental evolution demonstrate that speciation is 'easy and likely' for bacteria through niche and environmental partitioning[42,43]. This might not occur in nature for many microorganisms, for which growth can be limited by access to resources or other aspects of the environment. Nevertheless, this property of microbial systems provides unique opportunities for theoretical ecologists that have not been fully exploited.

Most larger organisms have a limited distribution range that is due to physical barriers such as lakes, mountain ranges or seas. The chances of allopatric speciation in microorganisms can be reduced by high abundance and greater dispersal[44]. A constant influx of immigrants into a given habitat would negate the probability of speciation. However, there is increasing evidence of endemicity for some prokaryotic populations (see for example REFS 45,46) (FIG. 1). Many pressing questions in microbial ecology require the consideration of both spatial and temporal scale. Growth rates can vary over several orders of magnitude depending on environmental and nutritional conditions, and speciation will depend on both growth and dispersal. Analysis of the combined effects of these factors on microbial community structure, evolution and ecosystem function requires quantitative modelling.

Variable activity in microorganisms

Early molecular studies did not differentiate between active and inactive microorganisms but a large proportion of the cells in a given environment are inactive at any one time[47]. Several bacterial genera form resistant spores, but non-sporulating bacteria can also switch to slow-growing or dormant vegetative forms that are resistant to environmental stress[48]. Inactivity in microbial communities will affect many aspects of their ecology, including population dynamics and diversity, and it complicates the application of ecological theory, which usually focuses on living and active individuals. Existing theory on the role of seed banks in plant ecology might be applicable. The seed bank is important, as germination will cause temporal variation in the observed plant diversity. Dormant seeds have an important role in the succession of plant communities, but the diversity of the seed bank (potential diversity) and that of the established vegetation (realized diversity) often differ considerably[49]. Inactive microbial cells and seeds do not contribute directly to ecosystem processes but are important for the resilience of a community to perturbation and might

become important when environmental conditions change. Inclusion of inactive community members therefore requires the consideration of the nature of the study.

Competitive strategies

Considering all aspects of ecological theory is beyond the scope of this article, but competition theory provides an example that has already been applied to microbial populations. Competition theory is particularly well developed and tested for plants[50,51]. The introduction by Grime[50] of a continuum between three competitive strategies of plants provided a conceptual breakthrough and could offer a useful starting point in describing competitive strategies of microbial populations.

In terms of the three CSR strategies identified by Grime (competitor–stress tolerator–ruderal), competitors are adapted for rapid resource utilization and long-term site occupation, stress tolerators are adapted to persist in low-resource environments and ruderals are adapted to highly disturbed sites by growing and reproducing quickly. The C and R axes can relate to zymogenous microorganisms (for example, pseudomonads growing on readily used organic substrates released into the rhizosphere), having a high maximum specific growth rate (μ_{max}), persistence and rapid colonization when substrate appears intermittently at high concentrations (for example, animal excreta, rhizodeposits or leaf litter). The S axis can relate to autochthonous organisms (such as cellulolytic bacteria) with low μ_{max} and high substrate affinity (equivalent to a low Monod saturation coefficient, K_s), ensuring survival when there is low substrate flow. These analogies are useful, and experimental studies in batch and continuous culture have explored the mechanisms that control competition and other microbial interactions in terms of growth parameters (see for example REFS 52,53), but the relationships often break down because of the complexities of life in environments such as soil or sediments. These mechanisms include the remarkable physiological flexibility of many microorganisms to micro-environmental changes and their genetic flexibility (for example, through horizontal gene transfer).

More direct analogies have been drawn between Monod growth kinetics and logistic growth of plant and animal populations, described in terms of the intrinsic rate of increase (r) (equivalent to μ_{max}) and the carrying capacity (K). Concepts of selection that are based on r and K have been used to describe bacterial growth under different substrate-supply conditions (see for example REF. 54), although the K and K_s concepts are not directly equivalent. A further example is the use of predator–prey models in epidemiology, which predict cyclical changes in predator and prey abundances. These models form the basis for mathematical approaches to understanding the transmission of infectious disease[55,56], in which the infectious agent is treated as the predator and the host as the prey, but with modifications describing, for example, heterogeneous exposure and behaviour of host and pathogen.

Behaviour

It is often thought that behaviour is a cognitive process and therefore is not applicable to microorganisms. However, this is an area in which theory and experimental microbial ecology are closely linked, as changes in cellular processes that occur in response to external signals can be considered 'behaviour', including those that are triggered by environmental stimuli, such as chemotaxis, spore germination and quorum sensing. Genomics has revealed a vast array of regulatory systems in even the simplest organisms, highlighting their ability to process many simultaneous signals[57] to optimize performance. Tools that are used by behavioural ecologists, such as game theory[58], dynamic programming[59] and optimization theory[60], could be used to improve our understanding of microbial behaviour and responses to changes in resources or temperature. The broad applicability of behavioural theory is highlighted by using microorganisms to study the evolution of sociality[61].

The factors that determine microbial characteristics such as the timing of cell division or the allocation of resources to alternative life forms such as spores or other persistence states[48] can be investigated using life-history theory, which traditionally addresses the trade-offs between growth, differentiation and reproduction. Furthermore, existing theory predicts how organisms combine different life-history traits such as sexuality and parasexuality[62] and the combination of different components of competitive fitness (for example, growth rate, starvation survival or the transition from low- to high-resource conditions)[63] to form life-history 'strategies'.

Similarly, chemotaxis (the sensing of, and movement towards, a higher concentration of a required resource) could be scrutinized to determine the relative benefits of expending energy to seek a more favourable patch, using optimal foraging models with a high concentration of an inferior resource or a lower concentration of a preferred resource. Although the ecological role of energy taxis is often discussed[64], the wealth of existing theory in this area is largely ignored. The molecular mechanisms of chemotaxis in microorganisms are well understood, but a theoretical framework would undoubtedly improve its understanding in an ecological context. One example is the application of optimal foraging theory in modelling the bacteriophage exploitation of bacterial hosts[65].

The recent application of ecological game theory (a mathematical approach used

Box 3 | **Areas with potential for the application of ecological theory**

- Population ecology, including epidemiology.
- Interactions of microorganisms with plants, animals and other microorganisms. For example, prediction of the influence of microorganisms on the distribution of plants is essential, but current approaches such as climate envelopes ignore the effects on microorganisms.
- Community ecology and community assembly. A central question is why so many species can coexist when there are apparently so few different niches. This problem is potentially more tractable for microbial communities for which generation times can be shorter, spatial scale poses less of a problem and diversity is comparable with, if not greater than, that of plants and animals.
- Biodiversity–function. The dependency of ecosystems on microbial organisms implies that the effects of declining microbial diversity will be of significance to the functioning of these systems. Studying artificial microbial communities, with defined levels of 'species' richness and measurement of ecosystem function, has been attempted[73–75], but the contribution from microbial ecologists to biodiversity–function analysis is currently in its infancy.
- Macroecology. The identification of patterns is particularly relevant to microbial ecology as it is frequently difficult to identify individual species or their functions. The influence of climate change on the distribution of species is another area of macroecology that has great potential.
- Biogeochemical cycling. Biogeochemical cycling process models traditionally treat microbial communities as a black box, ignoring both biomass and diversity. The establishment of quantitative links between microbial diversity and ecosystem processes is essential, and requires scaling from the micron level, at which mechanisms controlling diversity can operate, through to landscape and global levels, at which important effects are considered.

to model situations in which two or more organisms interact) to microorganisms significantly affects our understanding of positive interactions, such as cooperation, among microorganisms[66,67]. In any system in which members of a population cooperate there is potential for defection, which can lead to the coexistence of multiple behavioural strategies. The coexistence of individuals that display different strategies can be explored readily in microbial populations using game theory models that were generated for similar phenomena in multicellular organisms[68,69].

Conclusions

The questions that microbiologists are asking are inherently quantitative and advances in theory require a collaboration with other disciplines, including ecology. Some of the main areas with potential for the application of ecological theory are listed in BOX 3.

Microbial ecology is said to be driven — but also limited — by techniques. However, we propose that advances in microbial ecology are limited by a lack of conceptual and theoretical approaches. This restricts the synthesis and integration of data that are generated by the plethora of techniques available, prevents the introduction of new ideas that transcend our experience, prevents the identification of, and focus on, fundamental questions, novel approaches and critical techniques, and restricts our ability to predict. This has implications for the basic science of microbiology and for its practical applications. New technologies will increasingly lead us down blind, non-generalist and expensive alleyways if studies are not directed and driven by theory.

The relevance and importance of microorganisms in natural ecosystems are self-evident, but stakeholders and end-users require predictive modelling. Practitioners and policy makers must make decisions about microbial communities and processes, but in the absence of a theoretical framework, many decisions rely on a combination of empiricism and intuition. This can deliver successes, but solutions are often partial and situation-bound and the failure of empirical and intuitive decision making can be baffling and counterintuitive. Fear of failure promotes conservative decision making, leading to excessive use of resources (for example, environmental engineers use too much power and medics overprescribe). Furthermore, empirical problem solving is inevitably subject to the law of diminishing returns: the increments delivered by each item of research get smaller and smaller each year.

In many cases we might be able to borrow and adapt ecological theory that has already been developed for plants and animals. Conversely, existing ecological theory must be tested and novel theory generated in microbial systems. Indeed, the greater control and manipulation provided by microbial experimental systems facilitate more rigorous and thorough tests of ecological theory. In other areas, new theoretical and conceptual approaches might be required to deal with the smaller size, faster growth, greater dispersal and asexuality of microorganisms. It is certain, however, that the central and global importance of microorganisms in natural ecosystems necessitates the acceptance, development and application of ecological theory.

Glossary

Adaptive dynamics
Adaptive dynamics links evolutionary dynamics and population dynamics and emphasizes ecological interactions in describing the evolution of a population.

Allopatric speciation
Speciation that is due to the physical isolation of populations by an extrinsic barrier, which results in (genetic) reproductive isolation of the populations, such that if the barrier between the populations breaks down individuals from each population can no longer interbreed.

Autochthonous organisms
Autochthonous organisms are adapted to a regular supply of substrate at low concentration and have a relatively low maximum specific growth rate and high substrate affinity.

Climate envelopes
The range of climatic conditions under which a population of a species can persist. In reality, climate envelopes are an abstraction and species distributions are constrained and explained by a number of factors beyond climate, such as habitat availability, historical events, dispersal limitation and interspecific interactions.

Community
Broadly, this is a collection of populations of different species that occur together in space and time. The definition of a community varies. One definition includes all species (that is, across all trophic levels). A less inclusive definition includes all trophically similar species (for example, all the plants in a rainforest).

Eutrophication
The enrichment of a water body with nutrients, leading to excessive growth of algae and other photosynthetic organisms, the subsequent decay of which results in the depletion of oxygen.

Macroecology
The study of broad-scale patterns in ecology. These include the patterns in, and relationships between, key ecological variables (such as population size and population occupancy), as well as life-history parameters that are important in determining ecological niches and responses to ecological changes (for example, body size, metabolic rate and growth rate).

Metacommunity
Metacommunities are large-scale regional assemblages of trophically similar individuals and species, each of which is perceived to exist as a series of local communities, linked by the dispersal of potentially interacting species. The dynamics that arise within metacommunities consist of spatial dynamics and community dynamics (multispecies interactions or the emergent properties arising from them within communities), and the interaction between them.

Metapopulation
A group of populations that are perceived to exist as a series of local populations that are linked by migration between them. However, the rate of migration is limited, such that the dynamics of the metapopulation should be seen as the sum of the dynamics of the individual subpopulations. Specifically, the size of the metapopulation is determined by the balance between extinction and colonization.

Monod growth kinetics
Monod growth kinetics describe the influence of the concentration of a growth-limiting substrate on the specific growth rate of microorganisms, in a form similar to the Michaelis–Menten equation. Kinetics are determined by two growth parameters: the maximum specific growth rate (achieved at high, non-limiting substrate concentration) and the saturation coefficient, which is the substrate concentration at which the specific growth rate is half of the maximum specific growth rate.

Niche
The particular set of resources and environmental conditions that an individual species exploits. This includes food, shelter and climatic tolerances. Basic ecological theory predicts that no two species can coexist if they have the same niche, unless they are identical in all respects.

Optimal foraging models
Optimal foraging models aim to describe and quantitatively predict behaviour decisions by animals to optimize foraging, particularly with regard to energy intake and expenditure.

Population
A group of individuals of one species in an area that is separate from other groups apart from rare migration events. In practice, the size and nature of the area is defined, often arbitrarily, for the purposes of the study being undertaken.

Pyrosequencing
A method for DNA sequencing, in which the inorganic pyrophosphate that is released from a nucleoside triphosphate during DNA chain elongation is detected by a bioluminometric assay.

SARST (serial analysis of ribosomal sequence tags)
A high-throughput method for characterizing microbial diversity that is based on cloning and sequencing short 16S ribosomal RNA gene sequences linked into concatamers.

Seed bank
A store of viable seed buried and dormant within the environment.

Zymogenous microorganisms
Zymogenous microorganisms are adapted to growth on an intermittent supply of substrate at high concentrations and have a relatively high maximum specific growth rate and low substrate affinity.

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doi: 10.1038/nrmicro1643

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Acknowledgements
This article arose from a workshop supported by UKPopNet, and funding is gratefully acknowledged.

Competing interests statement
The authors declare no competing financial interests.

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