Bridging the scales: what can microbial ecologists learn from classic ecology?

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Abstract

The fields of ecology and microbiology have historically developed independently of one another, resulting in each having unique methods, terminology, and concepts. Microbial ecology aims to synthesise these perspectives, merging the molecular and reductionist strengths of the microbiologist with the systems-level viewpoint of the ecologist. However, unifying disciplines with independent histories is not a straightforward task. Ecology is characterised by a series of concepts that aim to explain the diversity and composition of macroscopic ecosystems. Many of these concepts are associated with longstanding controversies surrounding their definitions and application, and these must be taken into consideration when applying them to new, microbial contexts. These concepts and theories from classic ecology also need to be critically evaluated and adjusted to account for the unique characteristics of microbes. Nonetheless, provided that the distinctions between microbial and macroscopic settings are taken into consideration, microbial systems are ideal experimental systems for many of the concepts from classic ecology. Here, we provide a concise and practical guide for microbiologists to five key frameworks from classic ecology—Niche theory, Trophic levels, Keystone species, Succession, and Metacommunities. We discuss the historical context and use of each framework, assess their applications to microbial systems and associated limitations, and offer suggestions for future research to help bridge the gap between the two fields.

Keywords

Niche theory | Trophic levels | Keystone species | Succession | Metacommunities | Neutral theory | Modern coexistence theory | Ecological filters

List of abbreviations

MCT: Modern coexistence theory | PCA: Principal component analysis | NMDS: Nonmetric multidimensional scaling

Note: *Italicized terms in the text can be found in the glossary*

Introduction

The field of ecology has long strived to explain the immense diversity of *species* observed in nature (e.g. Forbes 1925). From this, a rich collection of concepts has emerged that build on species *interactions* and community dynamics to explain what drives *coexistence* and community organization. These ideas in “classic” ecology were first developed and explored mainly with *macro-organisms*, growing out of botanical and zoological research. As these concepts developed through time, their use and meaning have also changed. This has led to decades-long discussions about the utility, meaning and correct application of these frameworks (T. E. Miller and Cooper 2022). The historical depth of these controversies can make it a daunting task for a researcher new to the field to ascertain the use and original context of these concepts, which is often necessary for their appropriate application to new organisms and systems.

While classic ecology was developing, the field of microbiology progressed largely independently with efforts concentrated on understanding basic cellular processes and uncovering the mechanisms of pathogenesis (Kolter 2021). However, recent technological advances have begun to produce an unprecedented amount of data on the global distribution of *microorganisms* and their interactions, leading to a renaissance in microbial ecology. Many researchers have turned to the conceptual and theoretical frameworks from classic ecology to untangle the mechanisms that explain the observed diversity and distribution of microorganisms from this vast amount of information (Costello et al. 2012; Koskella, Hall, and Metcalf 2017; Prosser and Martiny 2020). These concepts have provided insight and helped to advance the field of microbial ecology; however, they must be used with careful consideration of the unique traits and complexities of microbial systems that differ from the macro-systems in which these ideas were developed.

There are fundamental similarities between micro- and macro-organisms that allow us to draw comparisons across scales, including growth constraints imposed by limiting resources and expressed traits such as directed motility (Jarrell and McBride 2008) and phenotypic plasticity (Ackermann 2015). However, micro-organisms also possess unique characteristics not seen in macro-organisms, such as horizontal gene transfer (Brito 2021), dormancy and survival strategies (S. E. Jones and Lennon 2010), and metabolic capabilities such as chemolithoautotrophy (Claassens et al. 2016). Further, microbial systems typically operate on spatial and temporal scales

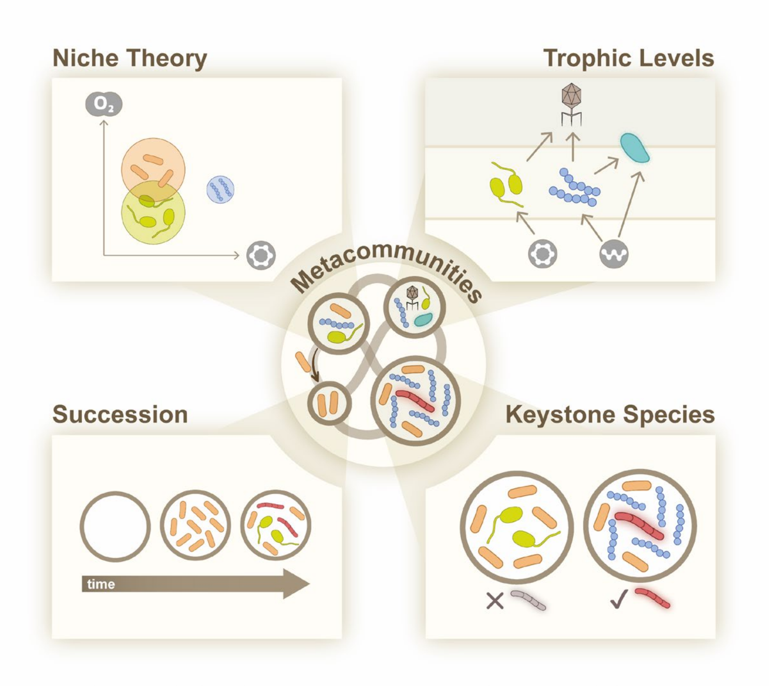

Fig. 1 | Key ecological concepts in microbiology. Niche theory, trophic levels, succession and keystone species are concepts applicable to communities at a given site (or 'patch'). Metacommunities are collections of such communities connected through migration of populations between patches. Grey circles represent resources (*e.g.* oxygen or carbon sources), the red organism is a keystone species, and the uppermost trophic level contains a phage. Design and Illustration by © Maria Carlos Oliveira.

that differ to those in macro-systems resulting in a tighter coupling of eco-evolutionary feedbacks (Hairston Jr et al. 2005) and a lack of a clearly delineated species definition (Hart, Moran, and Ochman 2025) These differences need to be carefully considered when translating ecological concepts from the macro to the micro scale.

Mutual reinforcement between ecology and microbiology holds great promise for the future (Radlinski and Bäumler 2025). This process begins with interdisciplinary conversations that help to integrate ideas from both fields. Here, we aim to provide a guide of how classic ecological theories and concepts can be adapted to microbial systems and show how the dialogue between microbiology and ecology can advance our understanding and steer future research. We focus on five key ecological frameworks that have been major subjects in classic ecology and remain active fields of research: Niche theory, Trophic levels, Keystone species, Succession, and Metacommunities (Fig. 1). For each framework, we discuss the historical context and use in classic ecology, assess applications and limitations and suggest experimental approaches for application to microbial systems (Table 1). Our goal is to provide a clear and concise overview that makes these important frameworks from classic ecology more accessible to microbiologists.

Concept	Features in 'classic' ecology	Applications and extensions in microbial ecology
Niche theory 	• Character displacement/ convergence • Stabilising versus equalising mechanisms • Niche construction	• Neutrality versus niche as determinant of diversity • Effect of environmental fluctuations • Rapid eco-evolutionary feedbacks
Trophic levels 	• Energy flows • Earth is Green • Top-down/Bottom-up processes	• Degradation chains • Cross-feeding (syntrophy) • Trophic plasticity • Microbial predators (phage, protists, predatory bacteria)
Keystone species 	• Keystone predators • Indirect impacts on community structure • Community importance	• Network analyses • Functional keystones
Succession 	• Disturbances • Filters (dispersal limitation, abiotic constraints, biotic interactions) • Trade-offs • Priority effects	• Colonisation of sterile systems • Automated trajectory analyses
Meta-communities 	• Local versus regional dynamics • Patch dynamics/species sorting/ mass effects/neutral dynamics	• Ephemeral patches • Patch nesting • Synthetic landscapes

Table 1 | Summary of key features of concepts from classic ecology and their application to microbial systems. Illustrations by © Maria Carlos Oliveira.

Niche theory

How do multiple species coexist? This is perhaps the most fundamental question in ecology, from which many other ecological concepts arise. The most basic answer to this question is that organisms specialize to specific modes of life in which they do not directly compete, i.e. they occupy separate *niches*. The extensive formalisation of this concept over the previous century has developed into a body of work known as niche theory (see Hutchinson 1957).

One of the simplest examples of niche theory is the R* concept from *consumer-resource models*, which predicts that multiple organisms cannot coexist when limited by a single resource, as the species that can sustain itself at the lowest resource level will outcompete the others and drive them to extinction (e.g. Tilman 1980; MacArthur 1984). Even when extended to multiple limiting resources, this framework results in a hard limit on the number of coexisting species, which cannot exceed the number of limiting factors in the system (also known as the competitive exclusion principle, Gause 1934; Meszéna et al. 2006). Simple niche theory therefore fails to explain the high diversity of ecosystems with very few limiting factors such as tropical forests, phytoplankton communities, or the extraordinary high diversity of some bacterial communities.

Chesson provided an important advancement to solving this problem: modern coexistence theory (MCT) frames the coexistence problem in terms of niche overlaps and *fitness* differences (Barabás, D'Andrea, and Stump 2018; Chesson 2000). When fitness differences are very small ("equivalent species"), the resulting *neutral dynamics* can lead to coexistence, especially when combined with continual evolution or low levels of migration and *disturbance* (Hubbell 2001). An important conclusion of MCT is that the number of coexisting species may not be limited by the number of unique resources or niches. It is instead essential to consider the relative importance of niche differences and neutral processes when attempting to understand coexistence and diversity in a given ecosystem (Adler, HilleRisLambers, and Levine 2007).

In MCT, processes that decrease fitness differences are said to have "equalising" effects while those promoting niche differences have a "stabilising" effect. Research inspired by MCT aims to (1) measure the relative contribution of stabilising and equalising mechanisms in promoting coexistence and (2) predict the effect of environmental changes on species coexistence. Previous work suggests that coexistence is often driven by stabilising mechanisms (Pastore et al. 2021; Buche et al. 2022) but large-scale comparisons are challenging due to the low reproducibility of individual studies (Terry and Armitage 2024). Both experimentalists and theoreticians have used the "invasibility criterion" to provide evidence for coexistence due to stabilising mechanisms. This criterion states that when two or more species coexist, each species must be able to increase in abundance when rare, and thus they are not being driven to extinction (see Barabás, D'Andrea, and Stump 2018; Grainger, Levine, and Gilbert 2019; Clark, Johnston, and Leung 2013). However, this too is often difficult to test empirically in many systems (Siepielski and McPeek 2010). In contrast, microbiomes as model systems are well suited to quantify stabilising/equalising mechanisms as well as the invasibility criterion because they are amenable to high-throughput growth and invasion experiments(Orr, Armitage, and Letten 2025).

Modern coexistence theory changes the way we view the niche, coexistence, and diversity in microbial communities. Some resources may be used equivalently by large numbers of species leading to fitness equality, while others may be subject to more specialised utilisation. Both neutrality and niche may therefore explain different aspects of diversity within microbial communities. However, several gaps remain in our knowledge. Despite the ability of MCT to explain the effect of environmental fluctuations on diversity through so-called 'storage effects' (Barabás, D'Andrea, and Stump 2018), this aspect of the framework has not yet been applied to the seasonal variations to which microbial ecosystems are subject (Orr, Armitage, and Letten 2025). The effect of phenotypic plasticity on niche occupation is likewise underexplored (Orr, Armitage, and Letten 2025). MCT also focuses on qualitative aspects of coexistence (e.g. presence/absence), whereas these traits may be more important for determining quantitative aspects of microbial communities (e.g. relative abundance). Finally, there may be practical difficulties of applying MCT to microbial ecology, including 1) controlling densities of individual species to test concepts such as invasibility, 2) eco-evolutionary feedbacks, which are largely ignored by MCT, involving species evolving on ecological time scales (Hairston Jr et al. 2005), and 3) extrapolating from low-diversity laboratory systems to high-diversity microbial communities in fluctuating environments. Despite these challenges, MCT offers a set of predictions and approaches that can be very useful for microbial ecologists to disentangle the mechanisms of coexistence and explain diversity.

Trophic levels

Niche theory investigates the factors that limit the growth of organisms but often over-emphasizes competition as the dominant force constraining the *realised niche*. Trophic levels provide a more realistic view in which organisms are subject to growth constraints both from ‘below’— their nutritional sources for which there may be competition— and from ‘above’— their predators. The niche of an organism within a trophic level is then defined by the combination of resource availability, competition, and predation.

The concept of “trophic level” has been central to ecology for over 80 years (Lindeman 1942), with Elton (1927) first grouping species with similar diets and predators together. Initially, the primary use was to understand the flow of energy from primary producers to predators, leading to the iconic representation of food chains as ecological pyramids that illustrate the distribution of biomass across levels. The later delineation of *top-down processes* (predation/herbivory/parasitism and trophic cascades) and *bottom-up processes* (nutrient/resource limitation) led to the influential, if overly simplistic "green world hypothesis" that plants are limited by resources, herbivores by predators, and predators by competition for resources (Hairston, Smith, and Slobodkin 1960). However, the relative importance of top-down and bottom-up constraints in community assembly and dynamics remains an ongoing debate (e.g. Sam et al. 2023; Rogers et al. 2024). Some ecologists have even questioned the validity of discrete trophic levels altogether (Polis 1991), suggesting that species positions within food webs are more continuous than categorical. Others suggest that multiple interacting forces make generalities about resource control or trophic cascades impossible (R. O. Peterson et al. 2014; Lynam et al. 2017). Despite these critiques, the concept of trophic levels remains an important heuristic in ecology.

In applying trophic level concepts to microbial communities, two approaches can be taken: microbial communities can be considered a single trophic level within a wider (often macroscopic) ecosystem, or microbial communities can be themselves considered a complete ecosystem, comprised of multiple trophic levels.

Microbial communities as a single trophic level

All microbes can be assigned to a single level in a larger food web, for instance a basal level in which they consume organic matter while being predated upon by phages, protists and metazoans.

This raises the question of whether top-down or bottom-up processes are more important for determining their composition. Bottom-up processes*,* i.e. competition over limiting resources such as nutrients, have generally dominated the thinking of microbial ecologists. However, top-down processes such as protist predation and phages (Szabo et al. 2022; Castledine et al. 2024; Kauffman et al. 2022) can also shape community structure. For example, phages have been shown to increase evenness in abundance between competing *Pseudomonas* species (Brockhurst et al. 2006). Direct manipulation of limiting resources and predation has revealed that bottom-up and top-down processes vary in their importance in different types of communities (Allen et al. 2010; Lucas, McBride, and Strickland 2020) and over time (Tobias-Hünefeldt et al. 2021). In contrast to classic ecology where predator-prey interactions have historically been a strong focus, the influence of predation and parasitism on microbial community structure is comparatively understudied. Incorporation of the growing body of knowledge about bacterial parasitoids such as phages, may overturn our understanding of diversity and traits in microbial systems. Further, quantification of the relative importance of these top-down and bottom-up processes may aid in development of experimental approaches, for instance by predicting whether a community will respond more strongly to changes to its substrate or to the addition of new predators.

Microbial communities as multi-level systems

Microbes possess of a broad range of metabolic pathways making them capable of photosynthesis, heterotrophy, and chemoautotrophy, with the latter unique to bacteria and archaea. Thus, microbial communities can also be viewed as ecosystems with separate trophic levels within themselves. The release of metabolic by-products into the environment can lead to cross-feeding, mutualisms, and even co-regulation where species influence one another's ability to uptake and process resources. For example, primary degraders can break down polymers into monomers that can be utilised by other community members (Pontrelli et al. 2022) whose metabolism releases byproducts, such as organic acids, that can in turn benefit other neighbours (Goldford et al. 2018).These represent classifiable trophic interactions (Gralka et al. 2020). However, two factors challenge our use of the term ‘trophic level’ to describe these relationships: firstly, as discussed above, microbes can exhibit strong phenotypic plasticity and shift roles based on environmental context, thus making their trophic positions dynamic (Daniels, van Vliet, and Ackermann 2023). Second, a high degree of functional redundancy can occur among microbial species making alternative units of study, such as *functional guilds* (groups of functionally similar species), more appropriate (Louca et al. 2018). *In situ,* tools such as metagenomics and metatranscriptomics can be used to predict how genetics and phenotypic plasticity determine a species’ functional guild (Shan et al. 2023). This framework can then be used to help resolve metabolic relationships between functionally related groups to better characterize species interactions and determine community level properties such as *resistance* and *resilience* to disturbances, which can aid in the engineering of synthetic microbial communities.

Keystone species

Interactions between organisms are central to ideas of coexistence, whether they are between trophic levels (predators and prey constraining each other's growth) or within trophic levels (organisms with similar ecological roles competing for limited resources). When a single species has an effect through its interactions with other community members that is disproportionate to its own abundance, this is known as a keystone species. Keystone effects are generally thought to occur through indirect effects involving the rest of the affected community.

While concepts similar to keystone species were described by early ecologists, the term was first coined when describing the effect of predatory *Pisaster* sea stars on the composition of tide pool communities. Since then, "keystone predation" has been commonly used to describe increases in community diversity caused by an apex predator through regulation of interactions among prey species(Robert T. Paine 1966; R. T. Paine 1969; Estes and Palmisano 1974; Naiman, Melillo, and Hobbie 1986). The use of "keystone" then spread to include keystone mutualists, modifiers, herbivores, guilds, and resources(Terborgh 1986; Owen-Smith 1987; Rainey et al. 1995; Daily, Ehrlich, and Haddad 1993). The broad use of the term led to inconsistencies in the use and definition of "keystone" that persist today(Mills, Soulé, and Doak 1993; Cottee-Jones and Whittaker 2012). A wide range of both qualitative and quantitative effects have been attributed to keystone species across many different ecosystems (see Power et al. 1996), and related concepts arose, such as *foundation species* (Dayton 1972) and *ecosystem engineers* (C. G. Jones, Lawton, and Shachak 1994). To streamline the definition of keystone species, Power and Mills proposed a useful and quantitative measure, in which the community importance of a community member is determined by the ratio of its effect to abundance (Power and Scott Mills 1995; Power et al. 1996).

Keystone species have often been identified through observational studies (R. T. Paine 1969). However, these do not account for confounding factors, such as unmeasured *abiotic* variables that affect species abundances and community dynamics, and thus obscure true ecological relationships(Gotelli, Ulrich, and Maestre 2011). While species removal experiments provide stronger evidence, they are often labour intensive and can have issues with controls and scale effects (Mills, Soulé, and Doak 1993; Menge et al. 1994; Christianou and Ebenman 2005). Despite this, there are well-documented examples of keystone species, including apex predators, that have advanced our understanding of species interactions and their potential effects on community dynamics (Langendorf et al. 2025).

In microbial communities, keystone predators can occur, for instance when metazoans consume bacteria (e.g. C. N. Peterson et al. 2008) or when bacteria, such as myxobacteria and *Bdellovibrio*, act as bacterivores (Petters et al. 2021). Yet the concept can be difficult to apply to microbial systems, where species can rapidly adapt to changing conditions at both the physiological and genetic level. Further, microbial species can act as keystones under one set of abiotic or *biotic* conditions and not another, making their identification context dependent and difficult (Weiss et al. 2023; Daniels, van Vliet, and Ackermann 2023; Bittleston et al. 2020).

Microbial keystone species have been identified based on patterns of co-occurrence ((Berry and Widder 2014; Tudela, Claus, and Saleh 2021); however, these approaches do not capture interspecies interactions or species' ecological roles. This can be addressed by using microbial network analyses (Banerjee, Schlaeppi, and van der Heijden 2018; Matchado et al. 2021) or by directly mapping interaction patterns (Venturelli et al. 2018). It is important to note that the keystone species definition used in these network-based studies (i.e. a species that interacts with many other species) differs from its initial, abundance or biomass-based definition. This may be due to the difficulties in obtaining absolute abundance data and inferring interactions from sequencing approaches, as well as the lack of clear trophic structure in many communities. An alternative application of the keystone concept for microbial systems is to determine functional keystones whose metabolic roles are critical for maintaining a function of interest (Gunderson 2000; Cottee-Jones and Whittaker 2012) (Gunderson 2000, Cottee-Jones & Whittaker 2012).

The prevalence and importance of keystone species in microbial communities remains an open research question for the future. A recent study by Mizrahi et al. (2025) challenges the occurrence of keystone species in microbial communities by using a quantitative definition that identifies keystone species through effects on community diversity. While this approach provides a more comparable measure, it does not account for keystone effects on functional roles or the proportion of the effect relative to the species abundance. To address this question in future work, the quantification of keystone species and their definition in microbial systems needs to be unified. Additionally, computational and empirical approaches that capture fine scale spatial and temporal dynamics across environmental contexts are needed to properly assess the concept of keystone species in microbial communities.

Succession

The ecological theories above generally assume that communities are at or near equilibrium, with no long-term change in the composition of the system over time. However, many systems undergo frequent changes in environmental conditions. Fast and disruptive environmental changes, known as *disturbances*, can open new niches resulting in changes to both the composition of a community and the environmental context in which they interact. Succession describes compositional changes in a community over time from a disturbed starting point towards a potential equilibrium 'climax' state.

The concept of succession was initially developed to describe the dynamics of plant communities on sand dunes (Cowles 1899) and then was widely used in many systems from abandoned agricultural fields (Pickett 1982) to tropical forests (Hubbell 1979). This led to considerable controversy over the underlying concepts, including the degree of determinism in successional dynamics and the validity of the climax community concept (Whittaker 1953). Our contemporary understanding of succession describes compositional changes in terms of a series of filters operating through time (Kraft and Ackerly 2014), integrating the long-standing discussions on successional mechanisms (Connell and Slatyer 1977) with the closely related field of community assembly (Chang and HilleRisLambers 2016). In this view, an initial *dispersal*-based filter is applied to a larger, regional species pool that determines which species will be able to disseminate to the disturbed site. Then, an environmental filter determines which of the resulting species will be able to grow and reproduce. These two filters tend to select for organisms with similar traits, being capable of both dispersal to and establishment at the site. Competition between established organisms, represented by a final biotic filter, then reduces species similarity, especially if survival is dependent on *niche* separation. The biotic filter also includes interactions from other trophic levels, including predation and herbivory. This filter-based view means that organisms with different strategies tend to dominate at different points throughout succession, with rapidly dispersing organisms giving way to effective colonisers and finally strong competitors (McCook and Chapman 1991). Longer-term, further compositional change may occur as slow environmental modifications by the community allow invasion of specialists better suited to the new conditions (Chapin et al. 1994).

When exploring succession in microbial communities, a good starting point is to identify a reproducible temporal pattern of organismal abundances in the system of interest. With the advent of metagenomics and high-throughput sequencing, the standard approach to this problem is to measure relative or absolute species abundances at different timepoints and display these data with ordination plots using eigenanalysis-based methods or distance-based methods, e.g. principal component analysis (PCA) or nonmetric multidimensional scaling (NMDS) (Gonze et al. 2018). Successional dynamics can then be identified from clear temporal sequences on these axes (e.g. Koenig et al. 2011; Zhong et al. 2018; Rao et al. 2021). When designing such experiments it is important to clearly identify the event that acts as the beginning of the successional sequence. Separately from the disturbance-based starting point of classic succession, many studies focus on *de novo* community assembly in a new sterile environment such as the neonatal gut (Rao et al. 2021). A second factor to consider is the sampling timescale necessary to capture the successional dynamics, which are generally much faster in microbial than macroscopic ecosystems.

Despite the growing prevalence of large sequence-based datasets, little work has been done to develop protocols for the detection of succession. We suggest using machine learning tools, such as trajectory inference (Saelens et al. 2019), to automatically infer multi-dimensional successional pathways from noisy and incomplete abundance data. This may also allow successional dynamics to be inferred when abundance data is only available from single time points for multiple communities at different stages of development.

Once a reproducible successional pattern has been observed, the next step is to determine what mechanisms drive it. Due to the importance of metabolic *trade-offs* to microorganisms (Giovannoni, Thrash, and Temperton 2014; Huelsmann, Schubert, and Ackermann 2024) many previous studies of microbial succession have attributed community changes to metabolic specialisation, such as replacement of chitin degraders by cross-feeders on marine snow (Datta et al. 2016). Microbial succession based on a colonisation/competition trade-off has also been described (Wetherington et al. 2022).

Successional dynamics can also be explored by manipulating the ecological filters in the ecosystem. *Priority effects* (Debray et al. 2022) — a component of the biotic filter — describe the effects of early-arriving species on the growth of later species and can be measured by artificially controlling the introduction times of different species. For instance, if changes to the environment by one species are necessary for a second to establish, this mechanism may be revealed by showing that the facilitated species fails to establish if introduced before the facilitator. The effects of dispersal and growth abilities on community composition and diversity can also be manipulated in the lab and *in situ* (e.g. Albright, Chase, and Martiny 2019) making microbial communities excellent systems to test successional dynamics.

Metacommunities

In addition to the temporal dynamics introduced by succession, communities can also be shaped by spatial dynamics; for example, a species that goes locally extinct in one region may be reintroduced through migration from another region. Metacommunity theory offers a framework to incorporate both space and time into community models by building on classic ecological theories including succession, niche theory, and trade-offs (Leibold et al. 2004).

A metacommunity is a set of communities that occupy distinct habitat patches that are linked by dispersal of multiple, potentially interacting species (Leibold et al. 2004). In this framework, diversity and composition of communities can be understood through the interplay between dispersal rates, competitive exclusion and patch heterogeneity. Historically, metacommunities were classified into four paradigmatic types to classify dynamics: patch dynamics, species sorting, mass effects, and neutral dynamics (Leibold et al. 2004). In patch dynamics, occasional local disturbance creates heterogeneity among patches in terms of patch age. Local successional dynamics result in different communities in each patch as newly colonized patches allow for persistence of good colonizers, while older patches are dominated by competitively dominant species. Regional diversity of connected patches is thus controlled by disturbance and dispersal rates. Species sorting describes the dynamics in which patches that differ in resources and abiotic conditions favour different species. Thus, diversity is controlled by among-patch heterogeneity and the dispersal ability of species. Mass effects describe the situation in which high dispersal rates dominate local patch dynamics and have a higher contribution to the community composition than local birth and death dynamics. This can result in high abundances of species that are poorly adapted to local conditions. Lastly, neutral dynamics occur when all species have small or zero fitness differences, acting as a null model to study how species distributions are influenced solely by stochastic events (see MCT above). While a useful heuristic, the utility of these four metacommunity paradigms has since been questioned as natural communities often do not fit neatly into one paradigm(Winegardner et al. 2012).

The basic concept of metacommunity theory may initially appear highly applicable to microbial communities, as dispersal, competition/colonization trade-offs, and local habitats with patch dynamics are common features of microbial habitats. Further, empirical tests of the metacommunity framework have been outlined with both macro and micro systems in mind (Grainger and Gilbert 2016; Logue et al. 2011). However, several features of microbial communities often make the original metacommunity framework difficult to apply. Natural habitat patches can vary in their characteristics (Logue et al. 2011): patches may have boundaries but be ephemeral (e.g. marine snow particles) or be more permanent but with indistinct boundaries (e.g. zones along plant roots). Further, microbial communities often exhibit hierarchal structures with different spatial scales creating different kinds of patches and potentially patches within patches (e.g. the microbiome of the oral and nasal cavities within the human body, Proctor and Relman 2017). In these cases, rather than the four paradigms, microbial community dynamics may be better described directly by the birth, death, and dispersal processes that are responsible for the spatiotemporal changes in both species density and the local environment. Meta-ecosystem theory expands on classic metacommunity theory to include the flow of energy and resources which captures the spatiotemporal fluxes in patch dynamics and abiotic conditions ((Massol et al. 2011; Gounand et al. 2018) and thus may also be better suited to capture microbial community dynamics.

The metacommunity and meta-ecosystem frameworks remain underutilised with relatively few studies applying these concepts to microbial systems (e.g. Livingston et al. 2012; Limberger et al. 2017; E. T. Miller and Bohannan 2019). Microbial communities offer highly manipulable systems in which the mechanistic processes driving metacommunity and in-patch dynamics can be controlled. Dispersal, key to metacommunity theory, can easily be adjusted with appropriately designed transfers of cultures between microcosms (allowing the testing of metacommunity dynamics), while chemostats and microfluidic chips allow for the microorganisms' feedback with the environment to be controlled (allowing the testing of meta-ecosystem predictions). Microfluidic chips, artificial soil, and droplet-based experiments (Krishna Kumar et al. 2021; Wetherington et al. 2022; Batsch et al. 2024; Čaušević et al. 2022) also create semi-realistic spatial habitats which allow for the effects of landscape heterogeneity and fragmentation to be compared with theoretical predictions (Mony et al. 2020). Microbial systems are particularly well-suited for testing metacommunity and meta-ecosystem theories, and, in turn, these frameworks can further advance our understanding of the mechanisms and processes driving microbial species distributions and densities at the single patch and regional scales.

Microbial ecology: new insights from old ideas

Microbial ecologists have access to a level of detail about their experimental systems that earlier ecologists would have only been able to dream of. High-throughput techniques allow us to measure microbial populations with unparalleled temporal and spatial resolution, abiotic conditions can be precisely manipulated and monitored, and even the physiological states of interacting organisms can be accessed in real time with microscopy. These experimental advances now allow us to test theories that were originally formulated in a much more data-poor era, much as modern genome sequencing has revealed the intricacies of the evolutionary relationships posited by Darwin.

The need for structured theoretical and conceptual frameworks will continue to grow with the accelerating generation of ecological data. Concepts such as trophic levels and keystone species can, for example, help us resolve the increasingly apparent role of phages in structuring bacterial communities (Castledine et al. 2024). Classic ecology may also provide conceptual tools to help us understand the role of scale in microbial ecosystems. At the largest scales, microbial communities are incredibly species rich, often surpassing the community diversity observed in macroscopic systems. However, this coarse-grained sampling neglects the microscopic scale of microbial interactions and the heterogeneity of the micro-environment. Concepts from classic ecology can inform our understanding of how the processes underpinning microbial ecology interrelate across scales, as well as help us identify the scales that must be sampled to explore these relationships (Levin 1992). These ideas will allow us to refine our view of what constitutes a cohesive community in microbial systems.

While we have focused here on ideas that can be imported from classic ecology, the unique characteristics of microbial ecosystems is also rich territory for new concepts. For example, the leakiness of bacterial metabolism combined with their rapid rates of evolution have led to the black queen hypothesis (Morris 2015), which posits that metabolic interdependencies between microbes should be widespread. The extremely high levels of relatedness between members of a clonal microbial population also favour ecological strategies that would not be feasible in typical macroscopic ecosystems, such as adaptive suicide (Humphreys and Ruxton 2019). Development of these novel, scale-specific ideas, combined with the appropriate application of classic concepts, will allow us to develop a more comprehensive view of microbial ecology. In turn, the inclusion of microbial data can advance these classic frameworks by offering ideal experimental settings and broadening the range of organisms to which they apply. This further integration of classic ecology and microbiology will continue to drive both fields forward in their quest to explain the distribution of species across scales.

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Data availability statement

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

<u>Glossary Terms (Box 1)</u>

Abiotic components- all non-living environmental factors which influence the survival and distribution of organisms within an ecosystem (e.g. temperature, water availability, pH, soil quality, nutrient levels).

Biotic components- the collection of living organisms within an ecosystem or community.

Coexistence- long-term maintenance of different species in a given environment without extinction of community members.

Competition- interaction where organisms use the same limiting resource, such as space, food, or light, which often leads to reduced growth, survival and reproduction. Both *interspecific* (competition between organisms of different species) or *intraspecific* (competition between organisms of the same species) can occur.

Consumer-resource models- mathematical frameworks used to describe reciprocal interactions between a community of consumers and a shared pool of resources. Interactions between consumers are solely mediated through competition for resources.

Cross-feeding (syntrophy)- interaction where one organism consumes the metabolic byproducts of another facilitating mutual growth and survival. Commonly found in microbial communities.

Dispersal- settlement and successful reproduction of individuals away from their place of birth

Disturbance- an event (abiotic or biotic) that causes minor to severe changes to community composition and the surrounding environment. Classic examples of disturbances include forest fires, flooding, invasive species, antibiotic treatments, and hurricanes.

Facilitation- positive interaction where at least one species benefits, and no species are harmed.

Fitness- a quantitative measure of the contribution of an individual to the gene pool of the next generation.

Functional guild- a group of organisms that acquire and process resources similarly and which have overlapping functions within an ecosystem (*e.g.* the same ability to break down a specific polymer). Guild members may be taxonomically distinct.

Interactions- relationship between organisms within an ecosystem where one species impacts the survival, growth, or reproduction of the other and vice versa. Types of interactions include facilitation, mutualism, commensalism, cross-feeding, predation, and competition.

Macro-organism- organism that can be observed with the naked eye. Most commonly refers to multicellular species with specialized organs and tissues within the animal and plant kingdom.

Microorganism- biological agent smaller than the acuity of the human eye ($\lessapprox$50 μm). May include multicellular organisms (*e.g.* filamentous fungi), protists, bacteria and archaea, as well as non-living phage.

Mutualism- interaction where both species benefit and enhance each other's survival, growth, and reproduction.

Neutral dynamics- a 'null' theory of ecology which assumes that all species are functionally and competitively equivalent. Community structure under neutral dynamics is purely driven by stochastic processes such as random birth, death, dispersal, and speciation.

Niche- the range of factors required by a species for its persistence within an ecosystem. The *fundamental niche* of a species denotes the range of resources and abiotic conditions that a species could use, while the *realised niche* consists of the actual set of resources and conditions that the organism uses which is determined by limiting factors such as interspecific competition.

Resistance- the ability of a community or population to remain unchanged in response to disturbance.

Resilience- the ability of a community or population to recover after a disturbance event.

Species- in macro-organisms, a group of individuals capable of interbreeding to produce fertile offspring. In microorganisms, a heuristic term based on varying degrees of genetic similarity determined using full-genome sequences, operational taxonomic units (OTUs), or amplicon sequence variants (ASVs).

Trade-off- a constraint that causes an increase in a trait or function to result in the reduction of another (e.g. the limits set on total investment into different tissues by nutritional and energetic constraints).

Top-down/bottom-up processes- directional regulation within a trophic-structured ecosystem, whereby species occupying higher trophic levels exert control over the composition of lower trophic levels and vice versa.

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