An Interpretation, Survey, and Outlook of Microbial Macroecology

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Abstract

The construction of a predictive theory of the dynamics and structure of microbial communities requires the consideration of repeatable, robust empirical patterns. The investigation of such patterns in ecology has historically been the domain of the subdiscipline of *macroecology.* However, the application of macroecology to microorganisms is not straightforward, as there is not a unified view of the subdiscipline. In this Perspective, I start with an *interpretation* of microbial macroecology by mapping the specificities of research in the microbial life sciences to prominent themes of macroecology. The bulk of the remaining manuscript is then dedicated to a *survey* of common microbial macroecological patterns. I begin with a focus on universal patterns that hold regardless of data type before proceeding to identify patterns that reflect temporal dynamics, a major goal being the establishment of a minimal, predictive model of ecological dynamics. I conclude with an *outlook* on the facets of microbial life that remain largely open to macroecological investigation. This Perspective is intended for a range of researchers in the microbial life sciences, both to experimentalists and theorists as well as those from disparate backgrounds.

> *Il mondo è così complicato, aggrovigliato e sovraccarico che per vederci un po chiaro è necessario sfoltire, sfoltire.*
>
> *(The world is so complicated, tangled, and overloaded that to see into it with any clarity you must prune and prune.)*
>
> Italo Calvino
> *Se una notte d'inverno un viaggiatore*
> *(If on a Winters Night a Traveler)*

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Introduction

The characterization of repeatable empirical patterns is an integral activity when developing scientific theory. Therefore, obtaining a predictive understanding of the typical composition and dynamics of microbial communities requires a thorough investigation of ecological patterns. In ecology, such scrutinization generally falls within the purview of *macroecology* [1, 2]. There is no single definition of macroecology, which will be elaborated upon in the subsequent section, though it is often viewed as the study of ecological patterns and processes over large scales. Given the global scale of microbial data collection efforts (e.g., [3]), it is not surprising that macroecological approaches have been increasingly leveraged to investigate macroecological communities (e.g., [4–8]). The sheer number of studies, empirical patterns, and proposed mathematical models warrants a reevaluation of our present understanding of microbial macroecological patterns and how they relate to the development of theory in microbial ecology.

This Perspective is not the first to provide an overview of microbial macroecology [9–12], nor the first to acknowledge the ways in which microbiological approaches shape macroecological investigation [13, 14]. It is also not the purpose of this Perspective to ordain a single definition of macroecology as being the most germane for microorganisms. Rather, an initial goal is to *interpret* prominent macroecological themes through the lens of the microbial life sciences. From there, I provide a *survey* of prominent, repeatable macroecological patterns across cross-sectional data and/or time, highlighting when and how a given pattern can be quantitatively explained by data-driven mathematical modeling efforts. Due to the sequence-based nature of the bulk of microbial data, I will focus on patterns that can be characterized using compositional data. It is also not the goal of this Perspective to prescribe a single model capable of explaining all documented macroecological patterns, though I do not believe this task is insurmountable. Finally, an *outlook* on microbial macroecological investigations is provided, highlighting measurable quantities and biological processes that are likely fruitful targets for future research efforts.

What is macroecology?

It is useful to begin with a brief overview of the historical development and current interpretation of macroecology. The investigation of biodiversity patterns one would now label as "macroecological" have been present since the virtual inception of ecology [15]. The eventual consolidation of macroecology did not occur until the late 20$^{\text{th}}$ century, driven, it has been argued [16], by three historical developments: 1) recognition that processes occurring over larger scales shape communities at the local scale, 2) the accumulation and curation of quantitative biodiversity data, and 3) an increasing acceptance of the limitations of the reductionistic/microscopic approaches that dominated ecological research from the 1970s-1990s (see [17, 18]). These developments lead to the formalization of macroecology in 1989 (using a term first introduced in 1971 [19]) as a research program focused on investigating the relationship between organisms and their environment via statistical patterns over large spatial, temporal, and taxonomic (i.e., # species) scales [1, 2]. This definition has diverged since its inception, though it has been proposed that the various definitions that have since arisen can be coarse-grained into two [16, 20], where macroecology is: 1) large-scale ecology in the sense that practitioners are focused on large scale patterns [21, 22] and 2) the study of recurring statistical patterns of biodiversity over time or across ensembles of communities (i.e., an ecological analogue to statistical physics) [23–26].

While there is no singular, universally accepted definition of macroecology, they all share what has been called an "insistence on empiricism" [20]. Given the plurality of working definitions, instead of attempting to graft microbial particularities onto a single previously established definition it is instead pragmatic to identify empirical themes of macroecological research so that one can examine their relation to microbial ecology. A non-exhaustive list of macroecological themes include:

1. **Scale.** Scale in macroecology refers to both the extent and resolution (i.e., "grain") that a quantity of interest is measured. Scale was originally viewed as constitutive rather than incidental, meaning that macroecological patterns are emergent properties rather than a summation over a large number of communities [2]. The recurrence of patterns across disparate environments and their seeming insensitivity to ecological processes operating within individual communities would then suggest that they are explanatory in their own right [2] (similar to "More Is Different" [27]). Alternative views range from

scale simply being the chosen window of observation [21, 22], to a convenient (though still embraced) property for inference rather than a defining feature [20].

2. **Pattern-first inference.** Empirical patterns remain the primary object of investigation across macroecological definitions despite differences in interpretation. Patterns were originally viewed as higher-level statements about ecosystems, where the investigation of the pattern itself was advocated as the primary strategy of macroecology rather than the reduction of patterns to specific ecological mechanisms. A contrary view is that macroecological patterns are scientifically valuable insofar as they permit discrimination among reasonable ecological mechanisms, where a many-to-one mapping from mechanisms to pattern reflects underdetermination rather than being a justification for viewing the pattern as inherently informative [28, 29].

3. **Non-experimental investigation.** Macroecology was originally envisioned as an explicitly non-experimental research program, the logic of this restriction of scope being that it is often difficult to draw useful ecological generalizations out of the aggregation of results from different experiments [1, 2]. It has been argued that this focus on observation was driven in-part by the ascendancy of small-scale ecological experiments when macroecology was introduced [16, 20].

4. **Reliance on comparative data.** Macroecological research is contingent on the availability of comparable public datasets. This statement was true at the onset of macroecology [1], with the need to ensure the comparability of various sources and types of data becoming only more pressing given that biology has long since entered the era of "big data" [30].

What is microbial macroecology?

Microbial macroecology can be defined as the application of macroecological principles and approaches to microbial systems. Such a definition can be misinterpreted as a tautology, but, as discussed earlier, there are multiple interpretations of macroecology. This plurality, coupled with the particularities of microbiology, can make the application of macroecology appear nebulous from the outset. Below I will examine how the particularities of microbial life science research relates to four previously identified macroecological themes.

1. Scale, *a fortiori*

A characteristic feature of microorganisms is their scale. Between an estimated global abundance of $\sim 10^{30}$ cells [31], global richness ranging from 10^{6} [32] to 10^{12} [6], harboring vast amounts of known phylogenetic and metabolic diversity, and having colonized virtually every environment on Earth [3], microbial life provides the taxonomic, phylogenetic, metabolic, and spatial scales that permit macroecological investigation. Coupled with the comparative ease that timeseries can be obtained for durations far exceeding intrinsic ecological timescales (e.g., division time) [33], microbial communities cover all dimensions of macroecological scale [20]. While scale alone is an insufficient characterization of macroecology, it provides the benefit of permitting one to examine how statistical aggregation may reveal general patterns that might otherwise remain unobservable at smaller scales [20]. An alternative view of scale is that microbial communities are often *high-dimensional*, providing justification for the use of models that seek to capture the *typical* community rather than every possible arrangement [26].

2. The utility of minimal models in microbial macroecological investigations

The application of mathematical models to empirical patterns has increasingly become a defining feature of macroecological investigations [34]. Identifying explanatory ecological mechanisms via modeling is not straightforward, as different mechanisms often have similar explanatory power for a given macroecological pattern [35, 36]. In order to progress it is necessary for researchers to identify the simplest possible model capable of reproducing a given pattern(s), known as *minimal models*, where added model detail acts as a hypothesis that must explain additional features in the data to justify its retention. Such a strategy is consistent with the long-standing spirit of model development in ecology [37], ideally circumventing issues that arise from complex models such as effectively indistinguishable parameter combinations preventing one from differentiating between alternative mechanisms (i.e., "sloppy" models [38]).

The interpretation of macroecological patterns in microbial ecological communities has been greatly aided by the application of minimal mathematical models [4, 25, 26, 39–41]. For example, the simple requirement that a useful ecological model must qualitatively capture macroecological patterns allows one to rule out several candidates (Box 1). Of those models remaining, one can quantitatively predict multiple macroecological patterns where time is not a factor using as few as two free parameters (Fig. 1). Such models provide a foundation for the subsequent identification of minimal models of ecological *dynamics* ([4]; Box 3, Fig. 2) as well as when it is necessary to invoke non-independence between species via the incorporation of explicit ecological interactions (e.g., generalized Lotka-Volterra (gLV)) [42]). This approach does not limit one's modeling efforts to the phenomenological scale of abundances (e.g., logistic growth), as successful minimal modeling efforts have been performed using mechanistic Consumer-Resource Models (CRMs; [8]).

3. Observational and experimental investigation: *pari passu*

As previously stated, macroecology was originally conceived as an explicitly non-experimental form of investigation [2]. This restriction was in-part motivated by the reality of performing ecological experiments on macroorganisms, as limited observation timescales, replication, and capacity to perform systematic manipulations can impede one's ability to map a given mechanism to a macroecological pattern. Microbial ecology provides a solution, as researchers are increasingly pursuing experimental endeavors that examine microbial dynamics for ensembles of replicate communities [43–47]. This type of experimental design combined with the sheer taxonomic scale typical of microbial communities (i.e., many degrees of freedom) lends itself to the characterization of repeatable patterns typical of macroecological investigations. Indeed, a number of macroecological patterns have been identified in experimental microbial communities [48–51]. A potentially greater benefit is that one can perform systematic experimental manipulations to directly interpret the biotic and abiotic contributors towards a pattern of interest [52]. The microbial macroecological consequences of experimental manipulations have begun to be examined (e.g., [49]), while minimal models capable of explaining patterns in natural communities provide a means to generate novel predictions for future experiments (e.g., [8]).

4. Limitations of microbial measurement

Measurement is not a neutral act. Decisions made by the investigator constrain the set of patterns that can be explored as well as the models that can be tested [53]. Such consequences clearly apply to ecological modeling [54], meaning that it is worth considering how the typical details of microbial community data collection impact subsequent macroecological investigations. A reliance on sequencing is a characteristic of the measurement of microbial communities. While the first sequence-based characterization of microbial diversity relied on Sanger sequencing clone libraries of rRNA genes [55–58], the advent of massive parallel sequencing (then known as "next-generation sequencing") provided an unprecedented means for investigating the composition and structure of large microbial communities, both by targeting 16S rRNA regions [59] as well as entire genomes via metagenomics [60]. The cost of both technologies has long-since decreased to the point where large-scale sampling of communities across space and time is financially feasible. Metagenomics provides an added benefit, as it contains information about the frequencies of genetic variants within community members, permitting the investigation of eco-evolutionary patterns [61]. The need to standardize both the processing of sequence data and the reporting of metadata is well recognized by those in the microbial life sciences [62], ensuring some level of comparability across studies.

Such benefits come with limitations, an example being that units of biodiversity must be gleaned from sequence data [63, 64]. Historically microbial ecologists treated clusters of 16S rRNA barcodes at a given level of sequence similarity as "species" in the sense that they represented the lowest scale of taxonomic resolution, deemed Operational Taxonomic Units (OTUs) [65]. Later microbial ecologists opted for the inference of community members at the level of single nucleotide differences rather than a prescribed level of similarity, referred to as Amplicon or Exact Sequence Variants (ASVs/ESVs) [66]. However, this advancement does not solve the issue that units of diversity inferred from 16S rRNA are ultimately reliant on the degree that a single gene reflects the ecological variation encoded in the entire genome. Metagenomics provides additional information, though sampling effort is more complicated as the number of reads belonging to a given community member is now a composite of coverage values over many genes [67]. Fortunately, many macroecological patterns appear to hold in both barcoding and metagenomic data [67–69]. The increasing momentum towards metagenomics over barcoding provides the added benefit of revealing sub-ASV structure known as "strains", representing the minimal meaningful unit of biodiversity that can be inferred from metagenomic data [70, 71].

An additional, potentially more severe, limitation is that information about absolute abundances (e.g., # cells, # genes) is absent in most sequence data, as the total number of reads is an arbitrary limit set by one's sequencing protocol. This feature, known as compositionality, introduces undesirable statistical artifacts when researchers examine reads as *relative abundances*. Such artifacts can often be corrected through the use of appropriate statistical methods [72–74], while information about absolute abundances remains lost. As there is no widely used sequencing method that preserves the original number of cells, researchers often multiply relative abundances by an externally-obtained measure that is reflective of the total abundance of the community (e.g., quantitative/digital PCR [5, 75], optical density [47], flow cytometry counts [76, 77]). In contrast to *post hoc* rescaling, the scale of absolute abundances can be preserved throughout the sequencing protocol when internal standards are added to samples (e.g., DNA [78–81], cells [82]). These approaches permit the inference of absolute abundances while accounting for experiment-specific statistical artifacts. Fluorescence-based microscopy is a potential alternative for obtaining absolute counts (e.g., fluorescence *in situ* hybridization [83]), though it is more effective for smaller communities where the taxonomic composition is known *a priori*. Such considerations are rarely made for studies with either the temporal or replicative scale necessary for macroecology. As a consequence, the macroecological patterns typically examined in microbial communities are those focused on diversity and composition, with comparatively little known about those that require quantities with *physical dimensions* such as abundance or biomass. This experiment-specific contingency on the existence of information about absolute abundances should be considered when one applies macroecological models where total absolute abundance operates as a community-level constraint (e.g., maximum entropy [23, 84]), providing justification for favoring process-based models over those that are constraint-based [85].

Sample-invariant microbial macroecological patterns

The survey begins by focusing on empirical macroecological patterns that have been documented in both both cross-sectional (i.e., samples from different locations in space or replicate experimental communities) and temporal (i.e., longitudinal) measures of communities. Ultimately, many patterns of historical interest can be quantitatively explained using few free parameters across a range of disparate environments, providing a foundation for building quantitative intuition about the structure of a "typical" microbial community.

Abundance Fluctuation Distribution (AFD)

Understanding how the abundance of a given species is distributed over time or space is a fundamental goal in macroecology. Once this distribution is understood one can leverage its existence to predict community structure if community members are independent. This object is known as the Abundance Fluctuation Distribution (AFD) and has become an object of study in recent years [4]. Such efforts have found that diverse community members tend to have AFDs of the same qualitative shape once rescaled by their mean and variance, a phenomenon known as a *data collapse* [86], that holds both for natural environments and experimental communities [4, 49]. This persistent form is often captured by a gamma distribution, holding both for cross-sectional and temporal data. For the temporal AFD, the gamma distribution can be interpreted as a time-independent probability distribution if certain criteria are met (Box 2). When valid, this interpretation allows one to construct Stochastic Differential Equations (SDEs) comprised of different ecological mechanisms that produce the same stationary AFD. For the gamma AFD, two SDEs are frequently invoked: the Stochastic Logistic Model of growth (SLM) and the Birth-Death-Migration (BDM) model (Box 3; [4, 87, 88]).

The qualitative invariance of the AFD has been documented across taxonomic and phylogenetic scales. Specifically, the abundances of sub-16S rRNA microbial strains inferred using human gut metagenomic timeseries exhibit distributions of the same form as across-host frequencies of the genetic variants that constitute strain differences [89, 90]. Moving from finer to coarser scales, the same form of the AFD has been found to hold when OTUs are merged by taxonomic label or phylogenetic similarity [91]. This operation represents a form of coarse-graining, where the richness of the community reflects the number of degrees of freedom which is then sequentially reduced. The consistent shape of the AFD has been leveraged to investigate the relationship between measures of community biodiversity at different phylogenetic/taxonomic scales (i.e., "diversity begets diversity") [91, 92]).

Taylor's Law

In contrast to the recent focus on the AFD, the power law relationship between the mean and variance of the AFD across community members, known as *Taylor's Law*, has remained an intensely studied pattern for over sixty years [93]. This pattern is virtually ubiquitous in microbial communities, having been characterized both for cross-sectional data as well as over time for disparate environments [4, 8, 16, 48, 49], in both natural and experimental communities [48–50], and the sub-16S rRNA level of strains [89, 90]. An exponent value of two, as is often reported in microbial community data, represents a constant coefficient of variation across community members. Such constancy represents an instance of *scale invariance* of the strength of fluctuations relative to typical abundance.

Taylor's Law represents one of the few law-like patterns in ecology, having resulted in ecologists exerting immense effort to provide mechanistic interpretations of exponent values. Historically such efforts have focused on macroorganisms [16, 94, 95], though in recent years mathematical models have have been developed to investigate Taylor's Law as a reflection of fluctuating resources that shape the dynamics of microbial consumers [8] as well as the sparsity of resource consumption preferences [96]. The CRM has a potentially larger explanatory role to play, as the value of the exponent is associated with the presence of carbohydrate-active enzymes in gut microbiota timeseries [97]. In terms of experimental observation, the (in)variance of the Taylor's Law exponent has been attributed to offspring number correlations [98], competition across space [48], the rate and form of migration as an experimental variable [49], and the application of antibiotics and phage predation [50]. Such experimental efforts confirm when the value of the exponent is and is not a reflection of ecological mechanism, but it is worth stating that the *form* of Taylor's Law is virtually never altered in experiments. Such qualitative invariance in the face of experimental manipulation is consistent with the interpretation that the form of Taylor's Law is a consequence of growth being a multiplicative process [99, 100]. Regarding the contribution of the form of noise towards the form of Taylor's Law (Box 3), environmental noise is sufficient to reproduce observed patterns while demographic noise removes, or even inverts, Taylor's Law for stochastic gLV models [101].

Mean Abundance Distribution (MAD)

The Mean Abundance Distribution (MAD) reflects the degree of variation across community members in typical abundance. The MAD is generally captured by the log-normal distribution for temporal and cross-sectional data from natural communities [4]. A similar result has been found in cross-sectional data from experimental communities [49]. Recent efforts provide a subtler interpretation to the shape of the AFD, where truncating the MAD favors a log-Laplace distribution for low relative abundance thresholds ($\bar{x}_i < 10^{-5}$) while the log-normal is recapitulated for higher values ($\bar{x}_i > 10^{-5}$) [67]. It is essential to note that sampling shapes the empirical MAD and is necessary to incorporate in one's statistical inference [41].

There are interpretive benefits that come from examining the MAD rather than the distribution of species abundances *within* an individual sample. The mean abundance of a given species has historically been an object of interest in theoretical ecology. For example, symmetry in species' birth and death rates under the Unified Neutral Theory of Biodiversity and Biogeography (UNTB) predicts that mean abundances are identical when the species identities are exchangeable [24, 102]. Under this prediction, the MAD is Gaussian for a finite number of independent samples, approaching a single value as the number of samples approaches infinity [4]. More detailed predictions of the form of the MAD can be obtained when interactions between community members are incorporated, as a stochastic gLV model can only reproduce empirical MADs when both the strength and connectedness of interactions between community members is weak [42]. This result was further refined by incorporating Taylor's Law, demonstrating the utility provided by constructing models constrained by multiple macroecological patterns. These results appear consistent with those of a coarse-grained CRM which was able to capture the empirical MAD without fine-tuning [8].

Species Abundance Distribution (SAD)

When Taylor's Law holds and the mean and variance are sufficient to characterize a given AFD, the AFDs of all community members are fully specified once one knows the MAD [4]. These three macroecological laws allow one to predict the shape of the Species Abundance Distribution (SAD) within a given sample, one of the most intensely studied patterns in the history of ecology [28, 103–105]. The resulting SAD is consistent with a prior effort that examined per-sample SADs [7], with the same SAD model being used to generate predictions of global microbial richness by leveraging empirical scaling relationships between the total number of reads and richness [6, 106].

Recently the purported generality of the lognormal has been challenged by a distribution known as the powerbend, a hybrid of a power law and exponential function that often provides greater explanatory power for empirical microbial SADs [107, 108]. This distribution is similar in form to the gamma distribution, which has a history of being invoked to explain empirical SADs [28], differing in that it is a discrete and truncated extension of the gamma. The powerbend is also a generalized distribution, meaning that it can be reduced to simpler distributions often used in ecology (e.g., logseries, power law), potentially applying to microbial communities that display non-lognormal SADs such as those in Tara Oceans data [109]. Notably, the powerbend cannot be reduced to a lognormal, but can qualitatively resemble said distribution in certain parameter regimes.

Similar to its statistical investigation, effort has been expended in the hope of identifying ecological mechanisms capable of generating empirical SADs [28]. For example, CRMs have been largely able to capture empirical SADs in Tara Oceans data when community members belonging to the same taxonomic group have correlated resource preferences [39]. These modeling efforts produce a logseries SAD, rather than the lognormal or powerbend that is most often reported in other environments. However, given that empirical MADs can be recapitulated using certain forms of the gLV model [42], which itself can often be obtained from the CRM [110, 111], it is reasonable to assume that CRMs can be invoked to explain variation in empirical SADs across diverse environments.

Abundance-Occupancy Relationship (AOR)

The relationship between the typical abundance of a community member and its presence across sites is one of the most well-documented patterns in macroecology, known as the Abundance-Occupancy Relationship [112–114]. For microbial communities, this relationship can be qualitatively captured by deriving the predicted occupancy across samples using a gamma distributed AFD and Poisson sampling [4]. This success has significant consequences for our understanding of microbial community data, as it implies that the absence of a given community member in primarily due to sampling effort. Interestingly, the ability to predict occupancy given the mean and variance also extends to experimental communities that exhibit alternative stable-states and does not systematically vary when migration is manipulated [49]. Such a high level of accuracy given the mean and variance alone suggests that occupancy typically contains little ecological information outside of its ability to reflect the form of the underlying AFD. This conclusion relates to the expected occupancy and may not extend to alternative measures such as the joint occupancy between two species, which likely depends on the joint relationship between AFDs. Therefore, while the AOR is a macroecological pattern of historical interest, its ability to provide mechanistic insight into the composition of microbial communities is likely limited.

Temporal microbial macroecological patterns

Timeseries data are fundamentally ordered in a sequence, unlike cross-sectional data, providing an opportunity for macroecological patterns to be investigated as a consequence of temporal dynamics. Below I will summarize temporal macroecological patterns that have been characterized in microbial communities, focusing first on those that examine variables calculated *within* or *across* community members over time before shifting attention to those calculated *between* community members. Contributions are noted from the extensive literature on measures of distance/dissimilarity between the same community sampled at two points in time [33, 115–117] as well as between two communities as a function of time [118–122], though a systematic overview is not provided.

Patterns within and across community members

Discretized growth rates

With temporal data in hand, one can examine how relative abundances change between samples. In macroecology this quantity is often examined using the logarithm, interpreted as the *relative* change in abundance. This is an ecologically meaningful measure as growth is a multiplicative process, allowing for the quantity to be interpreted as a discretized form of the per-capita growth rate which can then be leveraged to test predictions about the role of time-dependent growth within a community [94, 123, 124] (Fig. 2a). Microbial investigations of discretized growth rates primarily rely on sequence data due to the difficulty of directly measuring growth rates in terms of biomass or number of cells in a community-context. Metagenomics can provide an orthogonal source of information on growth, as the degree of bias in the distribution of coverage along the genome due to nested genome replication reflects the growth rate [125, 126], having been leveraged alongside the SLM to provide insight into the relationship between the typical abundance of a community member and its growth rate [127].

In recent years the distribution of discretized growth rates has been an object of macroecological interest (Fig. 2b). Initial investigations found that the distribution was well-described as a Laplace distribution in human and mouse gut microbiota [5] as well as in experimental communities [51]. Later work comparing the explanatory power of minimal models favored demographic noise as an explanation (Box 3) [87], though it is unclear at present how this result relates to analyses that favor environmental noise as an explanation [88, 101]. The latter interpretation is consistent with an alternative measure of fluctuations, the *absolute value* of the change in relative abundance between time points ($|\Delta x_i|$; Fig. 2c), with its dependency on mean abundance being mostly consistent with predictions of environmental noise [128].

Regarding ecological mechanisms, this distribution has been examined as the outcome of density-dependent birth-death processes [129], the niche structure of an environment [130], and the strength of noise in resource inflow [8]. The last explanation is particularly useful in microbial macroecology, as it has been noted that the form of the distribution of discretized growth rates is insensitive to the temporal ordering of observations [131, 132], raising questions about the extent that the distribution reflects temporal dynamics. An answer was found by examining the slope of the relationship between $\Delta \ln x_i(t)$ and $\ln x_i(t)$ through the lens of a CRM (Fig. 2d), as its value was strongly influenced by temporal autocorrelation in resource inflow [8]. Said sensitivity of the joint relationship appears consistent with gLV modeling efforts [101].

Growth rate fluctuations scale over increasing intervals of time, examined as $\mathrm{Var}(\Delta \ln x_i(t)|\Delta t) \propto \Delta t^{2H}$, where H is known as the Hurst exponent (Fig. 2e) [133]. The value of H reflects the direction of temporal correlations, interpreted in physics as anomalous diffusion, with $H < 0.5$ and $H > 0.5$ representing subdiffusion and superdiffusion, respectively. Within human and mouse gut microbiota, values of $H \approx 0.07 - 0.08$ have been reported [5]. The subdiffusive nature of these values is consistent with the view that microbial species are typically driven towards a steady-state. Analytic predictions of $\mathrm{Var}(\Delta \ln x_i(t)|\Delta t)$ can be derived for both the SLM and BDM, with both models predicting diffusion or the absence of scaling (i.e., $\mathrm{Var}(\Delta \ln x_i(t)|\Delta t)$ being constant) when Δt is much smaller or larger than the timescale of growth, respectively. In ecological terms, said saturation reflects community members being driven to their equilibrium abundance over extended timescales [134]. Interestingly, three-member experimental communities in closed phototroph-driven ecosystems displayed exponents ranging from $0.28 - 0.45$ [51]. The cause of this increase is unclear, though plausible explanations include the trophic structure of the community.

Timescales

In natural communities one often finds periods of time where low abundance species remain unobserved. These timescales have been proposed as being informative of the typical turnover time of the community, potentially reflecting ecological forces such as demography [135] resulting in the local extinction of a community member [102, 136]. The timescales when community members are consecutively present or absent are known as residence ($T_{\mathrm{residence}}$; also known as a type of "avalanche" distribution [137, 138]) and return

(T_{return}) times, respectively (Fig. 2f). In human and mouse gut microbiomes the distributions of said variables have been characterized, with the distribution of $T_{\mathrm{residence}}$ tending to follow a power law [5, 8, 138] while that of T_{return} displays a convex shape on a log-log scale [5], though both distributions are sufficiently captured by a power law with an exponential cutoff [5, 8].

Given that the typical total number of reads for a barcoding sample ranges from $\sim 10^4 - 10^6$ and the estimated typical number of bacterial cells in e.g. the human colon being $\sim 10^{13}$ [139], the sheer gap between the lower bounds of observation and true abundance suggest that $T_{\mathrm{residence}}$ and T_{return} typically harbor little information about genuine extinction events. This conclusion likely extends to temporal dynamics in general, as distributions of $T_{\mathrm{residence}}$ and T_{return} obtained from timeseries with the temporal order destroyed via permutation are virtually identical to empirical distributions [132]. Instead, these distributions may predominantly reflect the typical composition of a community characterized by the time-agnostic patterns discussed earlier plus sampling. Such generality is supported by both distributions being predicted by coarse-grained CRMs without the use of fitted parameters [8]. It is also likely that this explanation can be extended to the power law relationship between the length of a timeseries and the cumulative richness of the community, known as the Species Time Relationship ($S \propto (\Delta t)^w$), a pattern that can be characterized in any timeseries but has been primarily investigated in industrial wastewater bioreactors [117, 140].

A key feature of microbial temporal dynamics is that community members often fluctuate around a typical value, which can be interpreted as a steady-state. A recent macroecological effort has sought to scrutinize said fluctuations, drawing from efforts in statistical physics to characterize the universal behavior of a random walker destined to return to its origin [141, 142]. The behavior of these deviations can be captured through three patterns: 1) the distribution of the length of the sojourn period (i.e., sojourn time, T_{sojourn}; Fig. 2f), 2) the relationship between sojourn time and the average height under the sojourn curve, and 3) the relationship between the deviation from the steady-state and the time within the sojourn period. Unlike distributions of $T_{\mathrm{residence}}$ and T_{return} mentioned above, distributions of T_{sojourn} appear to reflect underlying temporal dynamics. The third pattern can be rescaled using the second to obtain a universal scaling relation that holds for a variety of stochastic processes, as well as for microbial communities in the human gut [143]. However, zero rescaling was needed in human gut timeseries, potentially due to the timescale of growth in the human gut being close to the lower bound of Δt [144].

Temporal autocorrelation

Temporal autocorrelations are highly useful in that they allow one to evaluate the existence of long-ranged correlations in a community, a form of ecological "memory" [145–147] (Fig. 2g). It is often more convenient to instead examine the Power Spectral Density (PSD), which can be interpreted as the Fourier transform of the autocorrelation function under certain criteria (Fig. 2h). The exponent governing the shape of the PSD reflects the type of underlying noise (i.e., noise color). Exponents within the human gut imply that the underlying autocorrelation function decays as a power law (i.e., exponent of -1, pink noise), indicating that it has no characteristic timescale (i.e., scale-free). In contrast, results from the human palm and oral microbiome imply a lack of temporal structure (i.e., exponent of 0, white noise) [128]. Exponent values from natural communities can reproduced using gLVs, where the product of the strength of self-interaction with the mean abundance serves a key control parameter [128]. Similar results were found in a separate study using gLVs, where experimental mouse microbiomes and marine bacterial communities favored white noise, though in all environments pink noise tended to be found among dominant community members [101]. As a contrasting observation, exponent values in closed phototroph-driven experimental communities indicate the persistence of autocorrelations over extended timescales (i.e., exponent of 2, Brownian noise) [51]. The underlying mechanism responsible for these long-range correlations is unclear, though, as discussed earlier, the trophic structure of the designed community may be a contributor [51].

Despite its advantages, the PSD can only be interpreted in terms of the autocorrelation function when 1) the mean is constant over time and 2) the autocorrelation only depends on Δt (i.e., "wide-sense stationary" [148]). In order to identify community members that are stationary, one can examine the *dissimilarity* between samples to determine whether it saturates with increasing Δt [119] (Fig. 2i). Analyses of the human gut suggest that most community members tend to be stationary, with a minority exhibiting values of $\Phi_i(\Delta t)$ that continue to increase with increasing Δt. The dynamics of this minority cannot be captured by the standard SLM (Box 3), however, modifying the carrying capacity so that there is a large, single change is sufficient to reproduce the lack of saturation. This jump occurs at similar points in time for different community members, suggesting that they are collectively responding to a single, large change in the environment, a phenomenon known as alternative stable states [149–154].

Patterns between community members

Pairwise temporal correlations

Abundance correlations between pairs of species cannot be explained by minimal ecological models that do not explicitly encode interactions, a discrepancy that is often interpreted as a reflection of underlying ecological interactions (Box 3; Fig. 2j; [4]). The distribution of said correlations can be explained using a gLV, where high sparsity in the interaction matrix is necessary to reproduce empirical observations [42]. Regarding explanatory mechanisms, the same distribution can be predicted by fitting a coarse-grained CRM to macroecological patterns that do not explicitly depend on pairwise correlations (i.e., per-sample community richness, Taylor's Law, distribution of discretized growth rates, and the slope of $\Delta \ln x_i(t)$ vs. $\ln x_i(t)$) [8]. The effectiveness of this model suggests that macroecological patterns that do not explicitly depend on quantities calculated from the joint AFD of a pair of species can reflect pairwise correlations due to shared consumption preferences for fluctuating resources. Furthermore, the consideration of correlations is largely sufficient to recapitulate empirical measures of distance/dissimilarity *between communities*[155]. This result extends to the relationship between community dissimilarity and overlap (i.e., probability that a read belongs to a species present in both samples) [155], a macroecological pattern documented in both natural [156] and experimental communities [157].

Moving beyond the shape of the distribution, in recent years it has been reported that the strength of pairwise correlations tends to decline with increasing pairwise phylogenetic distance for both cross-sectional and temporal data [158], a novel macroecological pattern (Fig. 2k). Interpreting phylogenetic distance as a reflection of shared preferences for environmental factors (e.g., resources, temperature), the empirical pattern cannot be recapitulated when competition between community members plays a critical role, nor by fluctuations in the environmental factors induced by community members (e.g., resource consumption). Rather, the environmental factors must be fluctuating independently of species abundances, a scenario known as "environmental filtering" [159]. This macroecological pattern reflects the *expected* pairwise correlation for a given phylogenetic distance, though one can also examine how the structure of the correlation matrix is affected under coarse-graining via phylogeny or taxonomy by examining the distribution of eigenvalues. In general the rank distribution of eigenvalues remains invariant under coarse-graining, as evidenced by its distribution of eigenvalues [138]. Similar results were found when community member pairs were coarse-grained by their strength of correlation [138], a procedure known as the phenomenological renormalization group method due to its utility in investigating the stability of a system [160, 161]. The similar qualitative invariance under these two coarse-graining protocols is unsurprising given the existence of the aforementioned distance-decay relationship, as its validity means that each axis is a function of the other. This inference likely extends to the recently characterized relationship between pairwise phylogenetic distance and the average dissimilarity between all communities that harbor both species [162], as dissimilarities between communities can be largely recapitulated when one considers pairwise correlations between species.

Temporal cross-correlation

Often in ecology one wants to characterize the extent that a pair of community members fluctuate together as a function of temporal displacement. Similar to autocorrelation, one can use the Fourier transform of the cross-correlation function, known as the Cross-Power Spectral Density (CPSD; Fig. 2l,m) [147]. A normalized form of the CPSD, known as coherence, has recently been leveraged to infer resource consumption structure in empirical marine communities via CRMs [163]. Coherence tended to decline with increasing pairwise phylogenetic distance for microbial eukaryotes, an analogous form of the relationship between phylogenetic distance and pairwise correlations [158] (Fig. 2k).

Prospects of microbial macroecology

The preceding sections were concerned with macroecological patterns that can be characterized solely using compositional abundance measurements. While explanatory mechanistic models were invoked (i.e., the CRM), they were used to explain patterns of the only variable that was measured (i.e., relative abundances) rather than all variables in the model (i.e., relative abundances and resources). This approach has changed in recent years, as technological advances and novel experiments provide opportunities to extend macroecological investigations to microbiological phenomena that were previously unobservable. Four potential (non-exhaustive) avenues of microbial macroecological advancement are examined below.

Measuring physiological variables

Microbial researchers have been largely limited in their ability to investigate macroecological laws that depend on variables with physical dimensions measured for *individual community members* (e.g., per-species # cells, biomass), a severe limitation as some of the most impactful results for macroorganisms were gleaned from dimension-based analyses [2]. This limitation does not mean that there is a lack of understanding of physiological macroecological patterns in microorganisms. For example, community-level measurements (e.g., total biomass) have permitted researchers to probe the relationship between community diversity and function [164] and model physiological transitions among community members [165], where physiology acts as a mediator between the environment and the community. Likewise, laboratory measurements of individual microorganisms have provided a quantitative understanding of energy dissipation per-unit biomass across microbial species [166]. Though one can argue that at present the ability to investigate physiological quantities of individual species in a community context is the primary limitation. The continued consideration and measurement of physiological meaningful variables is necessary in that they have repeatedly provided answers for long-standing ecological questions (e.g., empirical scaling laws between mass and growth rate permitting community stability with increased diversity [167]). The quantification of species-level metabolic activity and mass are discussed below, two key physiological quantities in macroecology.

The study of metabolism provides a first-principle basis for linking scales of biological organization ranging from cells to ecosystems [168]. However, obtaining per-species estimates of metabolic activity and growth in mixed microbial communities is not straightforward, with the interpretation of "metabolic activity" depending both on what is measured as well as the model used for interpretation [169]. With the measurement of species-level metabolic activity being so difficult, microbial ecologists have leveraged 16S barcoding on reverse-transcribed *RNA* (i.e., cDNA) to identify community members that are actively growing [170]. Taxa deemed metabolically active often display alternative forms of the patterns discussed earlier, such the SAD [171], the spatial distance-dissimilarity relationship [172, 173], and fluctuations in the discretized growth rate [174]. Though this approach may be too coarse a measure to capture variation in the growth rate across species [175] or temporal changes in cell physiology. Analogous approaches are possible for mRNA using metatranscriptomics, potentially providing greater sensitivity to underlying physiological differences among community members [176]. For example, robust relationships between mRNA transcript concentration and carbon biomass have been reported in marine eukaryotic plankton [177]. Given the emphasis in this Perspective on the benefits and drawbacks of sequence-based measurements, it is necessary to note the increasing availability of approaches that do not rely on sequencing. Notable examples include single-cell stable isotope probing and its variations (e.g., Raman microspectroscopy or NanoSIMS) as well as microcalorimetry [178], though difficulties remain in applying such approaches to diverse communities [179].

Biomass is a crucial measure for unifying macroecological patterns [180]. Such unification is possible because the finite supply of resources in a community constrains fluctuations in physiological variables, which are then embedded in empirical scaling relationships [181]. One such pattern that has been difficult to obtain for microorganisms is the distribution of biomass values within a community, known as the Community Size-Spectrum (CSS) [182]. Recent technological advances now permit the measurement of the mass of individual cells by combining microfluidics with a cantilever [183]. This innovative approach has since been used to investigate the relationship between the mean mass and growth rate across bacterial strains [184], an allometric scaling relationship of historical interest in macroecology [168, 185, 186]. While this approach has only been applied to populations of single species, it could theoretically be used characterize the CSS (Fig. 3a). However, there remains the need for a method to distinguish cellular mass estimates by species identity. Such a tool could provide the means to probe patterns *in situ*, such as the scaling relationship between per-species biomass and the basal metabolic rate (i.e., Kleiber's Law) [187] or population density (i.e., Damuths Law) [188].

Resources as mechanisms

Throughout this Perspective empirical macroecological patterns have been primarily interpreted through the lens of *phenomenological* models (e.g., SLM, gLV; Boxes 1 and 3). While this approach is useful, it is ultimately limited in that it does not provide insight into the underlying mechanisms that shape microbial communities. Given that growth requires resources of some kind, researchers have increasingly viewed consumption as a mechanism that shapes the process of community assembly and final composition, for both experiments and theory. Potential resources can be measured in natural communities (e.g., metabolomics) and coupled with sequence based measures of abundance, providing a novel means to infer the dimensionality of a community in terms of a CRM [189]. To list just a few experimental examples, a resource-centered view of microbial life has been leveraged to investigate how community composition depends on the availability of carbon sources [43, 190], the exchange of excreted resources (i.e., cross-feeding) [191, 192] and the impact of environmental fluctuations [193].

Additionally, increased attention towards the ecological role played by resources has spurred the experimental investigation of novel macroecological patterns. A notable example is the dependency between the number of substitutable resources supplied to an environment and the diversity of the assembled community, a novel empirical pattern known as the *resource-diversity relationship* [194] (Fig. 3b). The slope of this relationship deviates from what is expected under strict competitive exclusion [195], but can be explained once one incorporates cross-feeding. However, this relationship is unlikely to exist as a single, universal form across environmental scenarios. Additional experimental investigations report relationships ranging from the absence of the relationship [196, 197] to its eventual reversal [198]. Mathematical models have the potential to validate the range of documented relationships as well as generate novel forms (e.g., reversal of the relationship when metabolic trade-offs are imposed [199]).

Spatial patterns as the outcome of physical processes

Patterns of diversity and abundance over space have historically been objects of interest in macroecology [13, 102, 200]. However, identifying the ecological mechanisms responsible for near-ubiquitous spatial patterns in natural communities is challenging, particularly for microorganisms (for notable exceptions, see [201–203]). This difficulty arises in-part due to the minuscule spatial scale that cells typically traverse over their lifespan [204–206]. Given that the movement of microbial cells over space is effectively a physical process, experimental efforts in defined environments provide a novel approach for connecting microbial movement to spatial community-level patterns. Using such an approach has allowed researchers to characterize community-level spatial patterns as the outcome of negative interactions [207] and resource exchange [208, 209] (Fig. 3c), as well as how coexistence can be mediated by mechanical interactions between species [210]. Leveraging physical similarities can then provide general explanations for spatial patterns. One key consideration is spatial dimensionality, as environments can be modeled as having one (e.g., xylem), two (e.g., human skin) or three spatial dimensions (e.g., soil aggregates). Within a spatial dimension one can then identify environments with similar geometries. For example, diverse microbial communities are found in porous soils, plant apoplasts, and crypts in host intestines, all of which can be viewed as small physical cavities. Microbial growth in these seemingly disparate environments may be unified by recognizing how increased cellular density results in a buildup of mechanical pressure, a determinant of the outcome of competition [211] that can ameliorate competitive exclusion for slow-growing microbes [212]. A similar emphasis on physical structure can be applied to highly spatially-structured communities such as biofilms, which can be understood as a type of physical matter, the constituents of which require energy consumption to move and reproduce (i.e., living matter) [213, 214]. A greater emphasis on microbial spatial macroecology as the outcome of movement in a physically-defined environment has the potential to establish stronger conceptual links between mechanisms and patterns.

Phage as trophic structure

While the mechanistic origin of ecological interactions has not been extensively discussed throughout this Perspective, when they have been invoked it has been at the scale of resource competition. This is a limited view of microbial life, as it ignores the possibility of predation. For bacteria, a major source of predation-induced mortality is bacteriophage, responsible for 10-40% of daily bacterial biomass turnover in marine systems [215, 216]. This sheer impact on microbial death suggests the existence of macroecological patterns that reflect underlying predator-prey dynamics, analogous to biomass scaling relationships documented in macroorganisms [217, 218]. Indeed, the co-occurrence of phage and bacterial taxa [219, 220], the correlation in their relative abundances [220], and the relationship between the phage and bacterial diversity has been investigated in natural environments [221].

Regarding absolute counts as a potentially more macroecological measure, scaling relationships between the total cellular abundance of a community and the total number of phage particles have been repeatedly reported [222, 223] (Fig. 3d). Such information has the potential to act as a constraint on minimal mathematical models. For example, the ratio of phage and bacteria in the human gut was recently leveraged as a constraint alongside sequence and microscopy count data to investigate the balance between phage life-history strategies (e.g., cell lysis vs. remaining in the host genome) [224]. It is also possible that a macroecological view of phage is amenable to experimental manipulation, as phage diversity can be reliably maintained in replicate experimental microcosms harboring a single bacterial strain [225], analogous to the maintenance of microbial diversity on a single carbon source [43]

Summary

This Perspective provides an overview of the objects of study, approaches, and goals of microbial macroecology. Despite its length, an exhaustive catalog of microbial macroecological patterns was not provided. Rather, an emphasis has been placed on intensely studied patterns that can be connected to minimal mathematical models, providing a basis for microbial ecologists to determine whether a pattern in their system of interest represents a truly unique feature.

While this Perspective ends with an advocation to increase the microbiological domain of macroecology, efforts have been made throughout to identify limitations. Individual macroecological patterns rarely reflect a single ecological cause. Evaluating the explanatory ability of sets of patterns is a needed, though not necessarily sufficient, step in the process of winnowing down potential mechanisms. Coupling minimal models with observational patterns is not a panacea for all inferential ills. Sampling is rarely complete, data is imperfect, and the act of measurement often aggregates separate communities. Such concerns are valid and are well-stated in the literature (e.g., [35, 226, 227]). Experimental approaches to macroecology alongside additional consideration of the limitations of microbial measurement has the potential to provide partial amelioration. Regardless, scientists are not going to stop looking for patterns in their data nor stop considering potential explanations. This reality means that it necessary for microbial ecologists to maintain a baseline understanding of the (dis)advantages of macroecological approaches.

I end by emphasizing the interdisciplinary and collaborative nature of the research that has shaped our macroecological understanding of microbial life. This assessment is based on contributions made by microbial ecologists from different backgrounds (biologists and physicists) as well as those that take different investigative approaches (experimentalists and theorists). Such empirical and theoretical developments often occur in parallel, but become expedited when cross-communication and collaboration is encouraged among researchers of diverse backgrounds. Continued close collaborations are needed to not only identify novel macroecological patterns, but to also identify *how* they can be measured and subsequently incorporated into systematic theory.

Data and code availability

Data were obtained from the following previously published studies: Fig. 1 from Table S1 in [4], Fig. 2 from host M3 [33] reprocessed in [143], Fig. 3 from [183, 194, 209, 222]. All code is available on GitHub under a GNU General Public License: `micro_macro_perspective`

Acknowledgments

I thank Á. Sánchez for the invitation, J. Grilli for their mentorship, and K. J. Locey for introducing me to macroecology. I thank E. Pigani and M. Sireci for their feedback. Conceptual diagrams were created in BioRender under a CC BY 4.0 license.

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Boxes

Box 1: Null vs. Neutral models

Macroecologists often evaluate empirical patterns by comparing them with statistical baselines that preserve certain features in the data while removing others that reflect an ecological mechanism(s) of interest. This approach provides *null* models for hypothesis testing and *predictive* models for hypothesis generation, respectively. In macroecology, models that assume equivalence among community members (i.e., equal birth, death, and immigration rates) are often invoked, the bulk of which follow the Unified Neutral Theory of Biodiversity (UNTB) [102]. The UNTB and its variations have made considerable contributions to our understanding of macrobial communities and represents a genuine advancement in theoretical ecology (see [24] for an overview and [228] for a recent summary). For microbial communities the UNTB has been applied both as a null [92, 229–231] as well as to generate predictions [231–234]. However, for microbial communities the UNTB generally fails to recapitulate regularly occurring macroecological patterns (e.g., the shape of the MAD) [4]. One can argue that this lack of correspondence can be looked past, as there is no universally accepted procedure for identifying the "correct" null model, a perennial issue in community ecology [84, 235–238]. As a counterpoint, a rigorous null is one that is not easy to "break", meaning that it should capture qualitative features of the data while its quantitative validity remains an open question. The lack of correspondence between UNTB and baseline macroecological patterns can obfuscate why the model failed to capture a more involved pattern. This gap is possibly reflected by the recurring interpretation that deviations from UNTB necessarily arise due to the existence of interactions between community members. In reality, the UNTB does not exclude the possibility of interactions (and its success does not necessarily mean the community is truly Neutral [239]), only that intra- and interspecific interactions be equivalent. In this sense, one can understand the difference between UNTB and alternative approaches, where the minimal model capable of capturing macroecological patterns (e.g., the MAD) is the one that emphasizes *non-equivalence* among community members (Fig. 1).

Box 2: Interpreting temporal vs. cross-sectional comparisons

Microbial community data can often be classified by sampling strategy, where collection occurs: 1) over time within a single community or 2) across multiple communities at a single point in time (i.e., cross-sectional). Given the increasing availability of high-replication community assembly experiments [240], it is worth reflecting on the relation between macroecological measures taken *across communities* vs. *within a single community over time.* For instance, say one is interested in the typical value of some observable that is a function of abundance and can be calculated using either sampling strategy ($\mathcal{O}(x_i(t))$). If both 1) the distribution of abundances approaches stationarity ($P_{\mathrm{AFD}}(x_i, t) \xrightarrow[t\to\infty]{} P_{\mathrm{AFD}}(x_i^*)$) and 2) the system explores all possible states of $\mathcal{O}(x_i(t))$ as time goes to infinity, then the expected value of said observable calculated over an ensemble of communities will be equal to that calculated over time within a community

$$\langle \mathcal{O}(x_i) \rangle \equiv \int O(x_i) P_{\mathrm{AFD}}(x_i) dx_i = \lim_{T\to\infty} \frac{1}{T} \int_0^T O(x_i(t)) dt \equiv \overline{\mathcal{O}(x_i)}$$

This relationship holds when the system is *ergodic*, providing a powerful tool for relating community data [241] as well as testing predictions from theory, as often it is more analytically tractable to calculate the expected value over an ensemble than over time. It is essential to note that ergodicity is a *property of the specific observable.* For example, an observable that is sensitive to community members switching between alternative stable states, a behavior that has been observed microbial communities [47, 119, 154], is unlikely to be ergodic. The existence of ergodicity has been explored in ecological models of microbial communities [242] and properties related to ergodicity have been empirically investigated, such as the time required for community members to return to a given abundance (i.e., *recurrence* or *sojourn time*) in marine plankton communities, a necessary, but not sufficient, condition [143, 243]. Fortunately one can now begin to test the existence of ergodicity in microbial communities thanks to the increasing number of well-controlled microbial community assembly experiments, where measurements are taken both over time as well as over a large ensemble (e.g., [47]). For example, it has been found that after the cessation of migration that fluctuations in the discretized growth rate remain constant over time *within* a community while the same observable calculated *across* communities tended to increase with time, a violation of ergodicity [49].

Box 3: Identifying noise source via data-driven minimal modeling

Noise source is an important consideration when constructing ecological models. Theoretical ecology is often concerned with population size fluctuations arising due to 1) demographic (i.e., endogenous) or 2) environmental (i.e., exogenous) sources. These can be mathematically interpreted as fluctuations scaling with $\sqrt{x_i}$ for demographic noise, as they are a consequence of the *number* of demographic events (e.g., birth, death), whereas environmental noise scales with x_i due to environmental variation typically acting on the *rate* of growth. Given that empirical AFDs tend to be captured by a gamma distribution, researchers have focused on two Stochastic Differential Equations (SDEs) that differ in their encoded source of noise but return the same stationary probability distribution. These models are the Birth-Death Model (BDM; more commonly known as the Cox–Ingersoll–Ross model) [244] and the Stochastic Logistic Model (SLM) [4, 128].

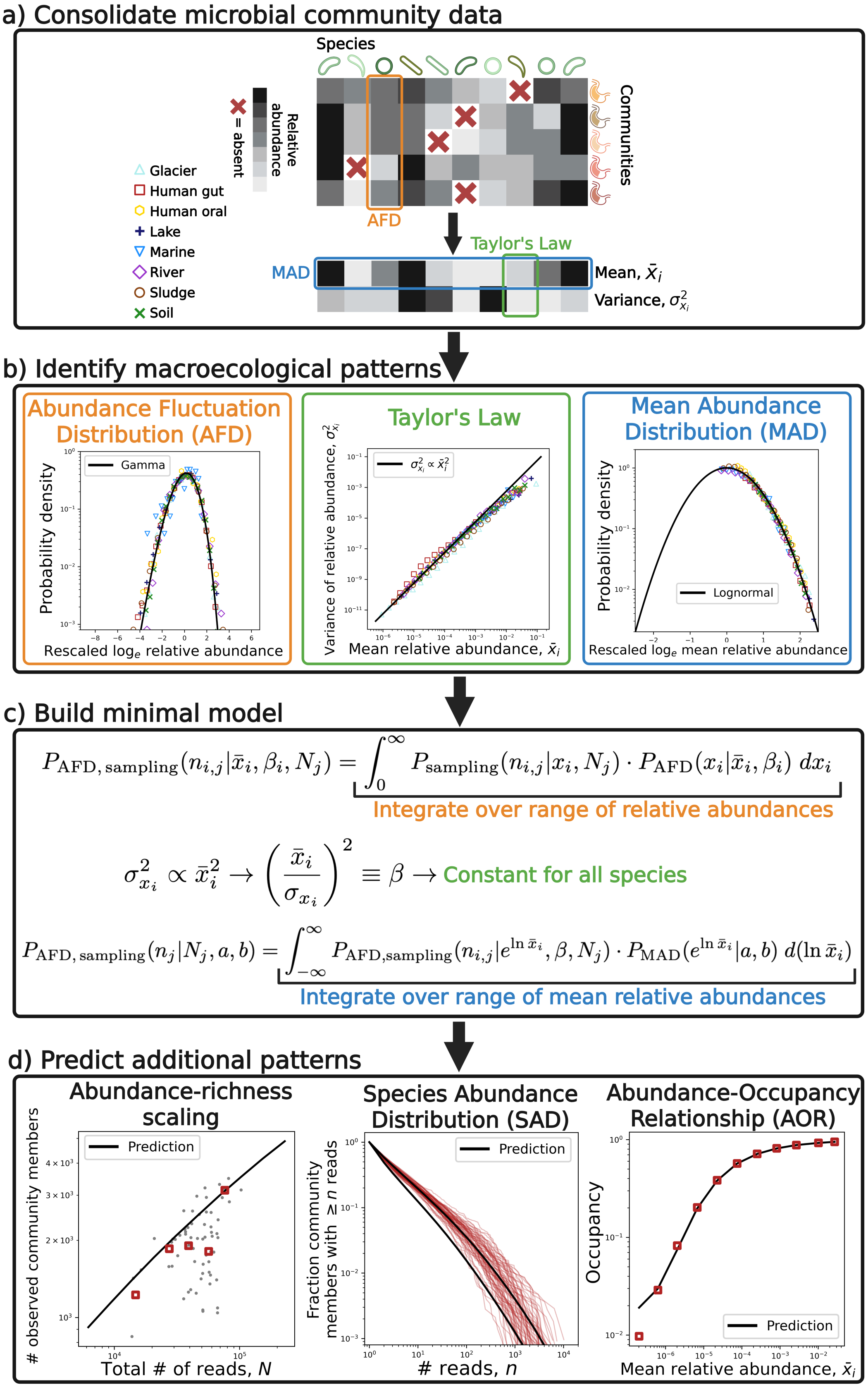
$$\left.\begin{array}{lclcl} \text{SLM}: \frac{dx_i}{dt} & = & \overbrace{\frac{x_i}{\tau_i}\left(1-\frac{x_i}{K_i}\right)}^{\text{Logistic growth}} & + & \overbrace{\sqrt{\frac{\sigma_i}{\tau_i}}x_i \cdot \eta_i(t)}^{\text{Environmental noise}} \\ \text{BDM}: \frac{dx_i}{dt} & = & \underbrace{m_i + x_i(b_i - d_i)}_{\text{Migration + linear growth}} & + & \underbrace{\sqrt{(b_i+d_i)x_i} \cdot \eta_i(t)}_{\text{Demographic noise}} \end{array}\right\} \xrightarrow[t\to\infty]{} P(x_i^*) \sim \text{Gamma}(\bar{x}_i, \beta_i)$$

Where for the SLM K_i represents the carrying capacity, σ_i the strength of environmental noise, and τ_i the timescale of growth. For the BDM m_i, b_i, and d_i represent rates of migration, birth, and death, respectively. The term $\eta_i(t)$ introduces stochasticity as white noise [245]. There exists an additional model with the same form as the BDM where the deterministic component represents deviations from an equilibrium abundance that are then subject to a linear restoring force, known as the Stochastic Linear-Response Model [246]. These models are *phenomenological* in nature, in that they do not provide explanations of *how* a given parameter depends on some detail of the environment. They also do not explicitly encode interactions between community members (e.g., gLV), though this omission does not mean that interactions are absent in the real community. Rather, their success implies that any underlying interactions implicitly impact a given pattern as a single collective impact, known in physics as a mean-field effect [247]. The two SDEs can be reparameterized as:

	SLM	BDM
$\bar{x}_i$	$K_i\left(1-\frac{\sigma_i}{2}\right)$	$\frac{m_i}{d_i-b_i}$
$\beta_i \equiv \text{CV}_{x_i}^{-2}$	$\frac{2-\sigma_i}{\sigma_i}$	$\frac{2m_i}{b_i+d_i}$
Timescale	τ_i	$(b_i-d_i)^{-1}$

allowing researchers to generate predictions that hinge on the *dynamics* of the system while ensuring equivalent stationary behavior. This consideration means that the ability to differentiate between models depends on the underlying timescale of growth being larger than that of sampling, a limitation that holds severe consequences for investigating microbial dynamics. For example, in environments such as the human gut microbiome the time between fecal sampling is expected to be similar to the timescale of growth ($\sim$ 1 day). While temporal dependence can be found in certain microbial macroecological patterns (see Temporal Microbial Macroecological Patterns) and recent rigorous BDM vs. SLM model comparisons suggest a slight preference for environmental noise [88], it is worth emphasizing that one must consider both sampling and biological timescales in the design and analysis of temporal ecological studies.

Figures



$$P_{\mathrm{AFD,\,sampling}}(n_{i,j}|\bar{x}_i,\beta_i,N_j) = \underbrace{\int_0^\infty P_{\mathrm{sampling}}(n_{i,j}|x_i,N_j)\cdot P_{\mathrm{AFD}}(x_i|\bar{x}_i,\beta_i)\,dx_i}_{\text{Integrate over range of relative abundances}}$$

$$\sigma^2_{x_i} \propto \bar{x}_i^2 \rightarrow \left(\frac{\bar{x}_i}{\sigma_{x_i}}\right)^2 \equiv \beta \rightarrow \text{Constant for all species}$$

$$P_{\mathrm{AFD,\,sampling}}(n_j|N_j,a,b) = \underbrace{\int_{-\infty}^\infty P_{\mathrm{AFD,sampling}}(n_{i,j}|e^{\ln\bar{x}_i},\beta,N_j)\cdot P_{\mathrm{MAD}}(e^{\ln\bar{x}_i}|a,b)\,d(\ln\bar{x}_i)}_{\text{Integrate over range of mean relative abundances}}$$

Figure 1: **The path from data →patterns →minimal model →predictions in microbial macroecology. a)** In microbial ecology one often consolidates their samples as a sample-by-species matrix of relative abundance, consisting of samples from different sites (as illustrated) or timepoints. Using statistical moments calculated from empirical data, one can establish the existence of macroecological patterns. **b)** Three macroecological laws exist across disparate environments [4]: 1) abundances across sites/over time for a given community member tend to follow a gamma distribution (AFD), there exists a power law relationship between the mean and variance of abundance (i.e., Taylor's Law), and 3) the distribution of mean abundances of all community members follows a lognormal (MAD). **c)** These three empirical laws provide the means to construct a minimal model of microbial community composition. Namely, using a form of the AFD that accounts for sampling (i.e., # reads) and recognizing that Taylor's Law with an exponent value of two implies that the coefficient of variation of abundance remains constant across community members (i.e., a function of β), one can integrate over the MAD to obtain a probability distribution for the number of reads requiring only the total number of reads in a sample and the two fitted parameters of the lognormal MAD (i.e., a and b). **d)** With this distribution in-hand, one can then evaluate its predictive capacity by deriving additional macroecological patternsa and comparing them to empirical data.

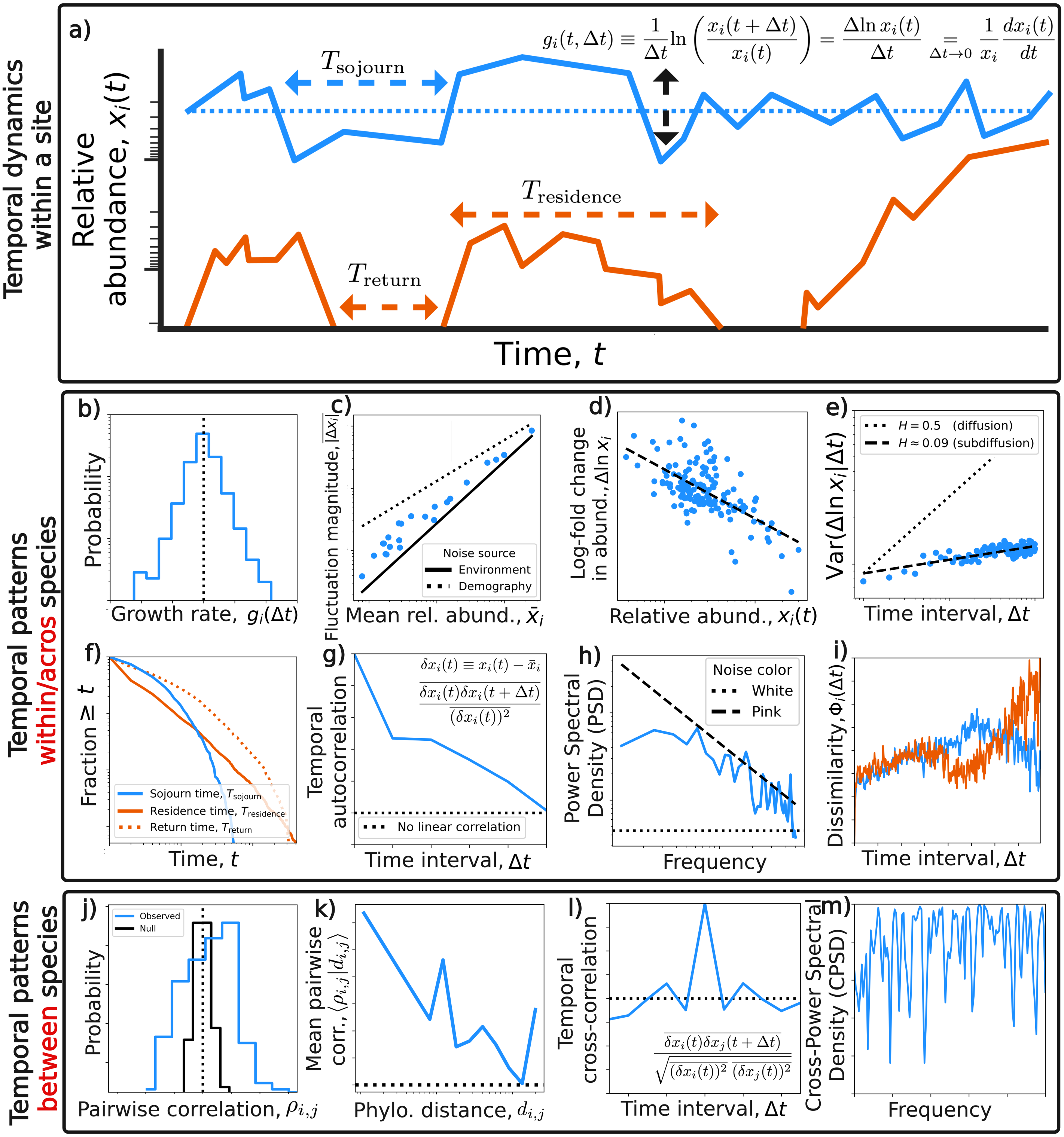

Temporal dynamics within a site
a)
Relative abundance, $x_i(t)$
$g_i(t,\Delta t) \equiv \frac{1}{\Delta t}\ln\left(\frac{x_i(t+\Delta t)}{x_i(t)}\right) = \frac{\Delta \ln x_i(t)}{\Delta t} \underset{\Delta t \to 0}{=} \frac{1}{x_i}\frac{dx_i(t)}{dt}$
T_{sojourn}
$T_{\text{residence}}$
T_{return}
Time, t
Temporal patterns within/acros species
b)
Probability
Growth rate, $g_i(\Delta t)$
c)
Fluctuation magnitude, $\overline{|\Delta x_i|}$
Mean rel. abund., $\bar{x}_i$
Noise source
Environment
Demography
d)
Log-fold change in abund., $\Delta \ln x_i$
Relative abund., $x_i(t)$
e)
$H = 0.5$ (diffusion)
$H \approx 0.09$ (subdiffusion)
$\mathrm{Var}(\Delta \ln x_i|\Delta t)$
Time interval, Δt
f)
Fraction $\geq t$
Sojourn time, T_{sojourn}
Residence time, $T_{\text{residence}}$
Return time, T_{return}
Time, t
g)
Temporal autocorrelation
$\delta x_i(t) \equiv x_i(t) - \bar{x}_i$
$\frac{\overline{\delta x_i(t)\delta x_i(t+\Delta t)}}{\overline{(\delta x_i(t))^2}}$
No linear correlation
Time interval, Δt
h)
Power Spectral Density (PSD)
Noise color
White
Pink
Frequency
i)
Dissimilarity, $\Phi_i(\Delta t)$
Time interval, Δt
Temporal patterns between species
j)
Observed
Null
Probability
Pairwise correlation, $\rho_{i,j}$
k)
Mean pairwise corr., $\langle \rho_{i,j} | d_{i,j} \rangle$
Phylo. distance, $d_{i,j}$
l)
Temporal cross-correlation
$\frac{\overline{\delta x_i(t)\delta x_j(t+\Delta t)}}{\sqrt{\overline{(\delta x_i(t))^2}\ \overline{(\delta x_j(t))^2}}}$
Time interval, Δt
m)
Cross-Power Spectral Density (CPSD)
Frequency

Figure 2: **Temporal macroecological dynamics. a)** The temporal relative abundance trajectory of a community member determines the macroecological patterns that can be examined. When a community member is consistently sampled over time (blue), it is possible to calculate the discretized per-capita growth rate $g_i(t, \Delta t)$ as well as quantities such as the length of fluctuations around steady-state abundance (i.e., sojourn time, T_{sojourn}). In contrast, when a community member is periodically unobserved (orange), one can calculate the residence ($T_{\mathrm{residence}}$) and return times (T_{return}). These two cases have the potential to reflect different ecological dynamics and the corresponding patterns can be broadly grouped into two categories: those calculated **b-i)** within/across or **j-m)** between community members. All patterns are obtained from host M3 in [33].

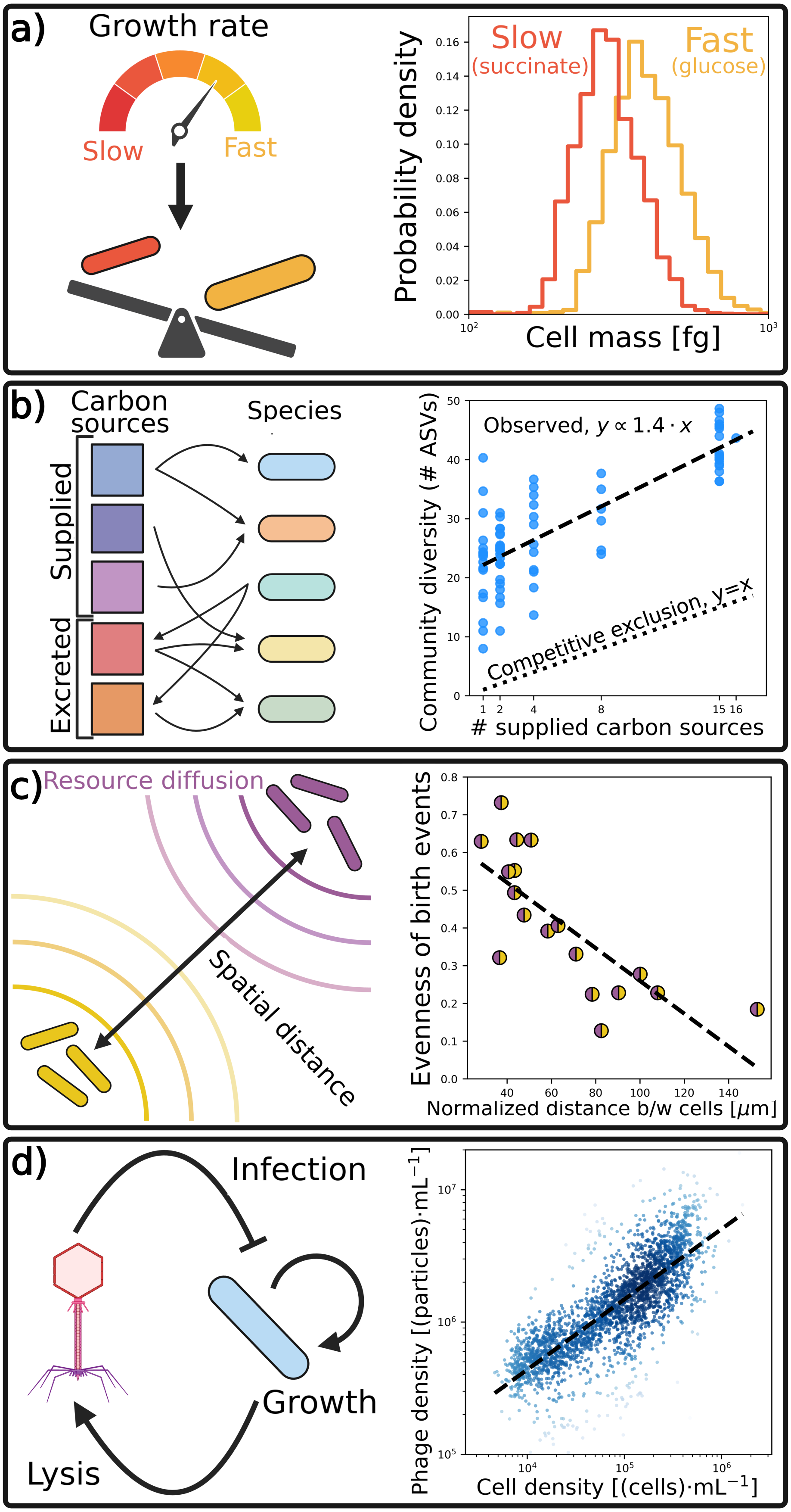

a)
Growth rate
Slow
Fast
Probability density
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Slow
(succinate)
Fast
(glucose)
10^2
10^3
Cell mass [fg]
b)
Carbon sources
Species
Supplied
Excreted
Community diversity (# ASVs)
50
40
30
20
10
0
Observed, $y \propto 1.4 \cdot x$
Competitive exclusion, y=x
1
2
4
8
15
16
supplied carbon sources
c)
Resource diffusion
Spatial distance
Evenness of birth events
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
40
60
80
100
120
140
Normalized distance b/w cells [μm]
d)
Infection
Growth
Lysis
Phage density [(particles)·mL^{-1}]
10^7
10^6
10^5
10^4
10^5
10^6
Cell density [(cells)·mL^{-1}]

Figure 3: **Novel and underutilized microbial macroecological patterns. a)** Physiological measurements have played a crucial role in the maturation of macroecology. Recent technological advances permit the measurement of *per-cell mass* in microbial populations [183], allowing one to investigate how mass as a dimension relates to other key quantities such as the population-level growth rate. **b)** The supply of *resources* can be viewed as an experimental variable that permits the manipulation of microbial communities, revealing novel macroecological patterns that allow one to identify explanatory CRMs [194]. **c)** While spatial metadata is often provided alongside environmental samples, it is difficult to establish robust spatial patterns in microbial macroecology, much less connect them with ecological mechanisms. Defining space as a physical aspect within experiments allows one to investigate the spatial dependency of ecological mechanisms. For example, cross-feeding as the consumption of excreted resources diffusing over space shapes the reproductive success of a two-member community [209]. **d)** Phage plays a crucial role in the global turnover of microbial biomass and is conceptually similar to predator-prey scaling relationships often examined in macrobial macroecology. This illustrated minimal (and almost certainly unrealistic) conceptual model of phage infection can be mathematically formalized and potentially coupled with scaling relationships as empirically-informed constraints [222].