PERSPECTIVE

Dynamics in microbial communities: unraveling mechanisms to identify principles

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Diversity begets higher-order properties such as functional stability and robustness in microbial communities, but principles that inform conceptual (and eventually predictive) models of community dynamics are lacking. Recent work has shown that selection as well as dispersal and drift shape communities, but the mechanistic bases for assembly of communities and the forces that maintain their function in the face of environmental perturbation are not well understood. Conceptually, some interactions among community members could generate endogenous dynamics in composition, even in the absence of environmental changes. These endogenous dynamics are further perturbed by exogenous forcing factors to produce a richer network of community interactions and it is this 'system' that is the basis for higher-order community properties. Elucidation of principles that follow from this conceptual model requires identifying the mechanisms that (a) optimize diversity within a community and (b) impart community stability. The network of interactions between organisms can be an important element by providing a buffer against disturbance beyond the effect of functional redundancy, as alternative pathways with different combinations of microbes can be recruited to fulfill specific functions.
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Introduction

The application of molecular approaches initiated over 25 years ago (Pace *et al.*, 1986) have made it feasible to conduct a census of members of microbial communities from natural and engineered environments, based on their phylogenetic relationships. The enormous advances in DNA-sequencing technology and throughput, in conjunction with gains in computational methods for analysis, have now made it tractable to analyze many hundreds of samples that vary in space or time at a scale where the relative abundance of clades and their co-occurrence patterns can be identified (Ruan *et al.*, 2006; Fuhrman, 2009). New insights beyond inventories of members of microbial communities are being provided using large data sets afforded by high-throughput sequencing such as the use of network analysis of co-occurrence patterns of different taxa. Insights from network analyses include information on relationships and interactions between different organisms in soil (Barberan *et al.*, 2012), inferring ecological traits of soil community members (Williams *et al.*, 2014), and

importance of hydrological controls on benthic microbial biofilms in fluvial networks (Widder *et al.*, 2014). These observations have generated a deep interest by microbial ecologists into the contentious debate within community ecology (Weiher *et al.*, 2011) regarding the principles that underlie the assembly of communities (Nemergut *et al.*, 2013) in the spirit of understanding living systems as complex, dynamic organizations (Woese, 2004). We provide in Table 1 definition of design principles as well as other terms used throughout this article, to assist the reader.

Three areas that have developed intensely over the past few years in microbial ecology include: (a) the relative importance of ecological processes (selection, dispersal, ecological drift and genetic diversification (Vellend, 2010)) in determining microbial community structure (Stegen *et al.*, 2013); (b) the emergent properties of a community such as functional resistance and resilience (Bissett *et al.*, 2013) and the role of diversity in generating those properties (Loreau and de Mazancourt, 2013; Thibaut and Connolly, 2013); and most recently, (c) the concept of synthetic ecology—a philosophical offshoot of synthetic biology, in which the building blocks are not gene modules but mixtures of microbial populations that produce a self-regulating, mutually reinforcing, robust systems engineered for production of a desirable resource or experimental outcome (Wintermute and Silver, 2010; Kazamia *et al.*, 2012).

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Table 1 Definitions

Design principles	Fundamental rules and basic underlying concepts governing the function of complex biological systems, which are useful for designing new systems.
Higher-order property	A system behavior that arises from the interaction of 'lower-level' components; in this case, members of a microbial community. Higher-order properties are not predictable from examination of individual members in isolation.
Resilience	The degree to which a system returns to pre-disturbance conditions, in state or function, in response to a disturbance of a given type and magnitude over a certain time period.
Resistance	The degree to which a system's state or function is insensitive to a disturbance of a given type and magnitude.
Dispersal	Movement of organisms across space.
Drift	Stochastic changes in species abundances caused by random birth/death events.
Selection	Deterministic, fitness-based differences in growth or survival between taxa.
Ecotype	A group of bacteria that are ecologically similar.
Endogenous dynamics	Changes in community composition or members' gene expression over time that are caused by interactions among species and occur even under constant environmental conditions (that is, without exogenous perturbations).
Functional redundancy	The number of taxa within a community able to perform a given function.
Interference competition	A type of antagonistic interaction in which one species excludes another from access to a resource or habitat, frequently involving specific physical or chemical mechanisms (for example, production of antibiotics).
Exploitation competition	A type of interaction between species in which organisms compete for a single limiting nutrient.
Niche complementarity	A relationship between multiple coexisting species in which each is limited by different resources, thereby avoiding direct exploitation competition.
Portfolio effect	A condition in which overall ecosystem function is maintained in the face of disturbance because different members are able to perform that function under different environmental conditions.
Press disturbance	A continuous disturbance that may arise sharply but reaches a constant level that is maintained over a long period of time (Lake, 2000). In engineering fields, also termed a 'step disturbance.'
Pulse disturbance	A short-term, often intense disturbance that rapidly decreases in severity over a short period of time (Lake, 2000). In engineering, additionally termed an 'impulse disturbance.'
Synthetic ecology	An approach that uses design principles to engineer communities in which the building blocks are not gene modules but mixtures of cell populations, to produce a self-regulating, mutually reinforcing, robust system that performs a given function.

Principles, properties and dynamics

Although the advances made in the three areas identified above have deepened our understanding of microbial community dynamics, an important gap remains: the identification of broadly applicable principles that can then be used to develop conceptual (and eventually predictive) models of microbial community dynamics (for example, Stein et al. (2013)). Even with the recognition that ecological processes beyond selection are important, what is lacking is an understanding of the mechanistic bases for association (or non-association) of certain ecotypes (Cohan and Perry, 2007) and the forces that maintain community function in the face of environmental perturbation. Note that we are not advocating for a search for 'laws,' the existence of which are contentious in ecology (O'Hara, 2005), but rather for broad generalizations (principles) that describe the interaction between components of the system under study, and which can be assembled into models that test the precision of our understanding of microbial community dynamics. We contend that interactions between members of microbial communities are primary driving forces, and that identifying interaction mechanisms and consequences will provide useful principles for community dynamics, not only for developing a predictive understanding of natural communities but also for the design of robust synthetic communities.

Properties associated with the community, rather than its constituent members (for example, functional stability and resilience), are thought to be consequences of community diversity (Loreau and de Mazancourt, 2013). Note that we emphasize here stability of function, which is distinct from compositional stability (that is, community membership and relative abundance of members). In fact, one reason that properties such as resilience may arise is based on significant changes in relative abundance. If individual populations with shared functions vary in their responses to environmental perturbations, there will be shifts in community composition but retention of functionality. For example, soils across a gradient of Cr(VI) exposure differed in community composition but retained capacity for organic C catabolism (Kourtev et al., 2006). Even pristine habitats never approach the 'steady state' that characterizes a continuous culture (Bull, 2010); therefore, community composition is continuously in flux (Konopka et al., 2007; Lin et al., 2012; Shade et al., 2013). Another consideration is the contribution of various types of experimental errors and analytical limitations in understanding the factors contributing to community stability, a detailed discussion of which is beyond the scope of the article.

Hastings (2010) provided a useful general framework to relate timescales to dynamics, and we believe this framework can be adapted to microbial communities. Even if the physico-chemical environment were constant, the composition of microbial communities would be continuously in flux, due to 'endogenous' dynamics in the relative abundance of

community members and their patterns of gene expression. As environmental factors (that is, exogenous influences) are not constant, these fluctuations further perturb the community's endogenous dynamics. The change in the environmental variable may be short term (for example, a pulse) or continuous over a longer period of time (for example, press disturbance), and recur at either regular periodic intervals (for example, daily, seasonally) or episodically (for example, climatic events). Therefore, microbial communities can be considered complex adaptive systems in which exogenous factors modulate the endogenous dynamics. We hypothesize that endogenous dynamics contribute to a community's resilience in the face of natural or anthropogenic exogenous perturbations. Given that environmental perturbations are inevitable, the key is to focus on identifying the mechanisms of endogenous dynamics and the extent to which they contribute to the formation of a resilient community.

If endogenous dynamics are, in fact, the consequences of biological interactions in microbial communities, there are a rich set of known mechanisms that can produce either negative (for example, exploitation or interference competition) or positive (for example, metabolic coupling) effects on specific populations. Metabolic coupling in microbial communities has been investigated within microbial mats (Visscher and Stolz, 2005), in which highly interactive organisms frequently operate closed biogeochemical cycles within self-organizing structures of micron-to-millimeter scales. One such example is the synergistic growth of cyanobacteria and filamentous anoxygenic phototrophs of the family *Chloroflexaceae*; these phototrophs alleviate the stress induced by photosynthetically produced O_2 and consume glycolate, a product generated at high $O_2:CO_2$ ratios via photorespiration (Bateson and Ward, 1988; Bachar *et al.*, 2007; Polerecky *et al.*, 2007). A consequence of this metabolic coupling is stability in net carbon fixation under high irradiance.

Conversely, interference competition between organisms has also been detected within mat communities (Long *et al.*, 2013) and there is evidence of viral activity that preferentially targets certain species, or ecotypes (Heidelberg *et al.*, 2009). Some of these negative mechanisms (for example, viral lysis and predation) are density dependent, thereby following a 'kill-the-winner' ecological model (Rodriguez-Valera *et al.*, 2009) in which unaffected 'rare' organisms bloom into unoccupied niches and preserve community functional stability. Rare populations may also exert a disproportionately large effect on a community's functional stability if they provide a common good such as secreted extracellular enzymes or essential growth factors that many community members are incapable of synthesizing. Interspecies exchange of growth factors, such as vitamins, provides a good example of this effect; vitamins are necessary in trace amounts, but typically require many enzymes to produce. Therefore, auxotrophies are widely distributed taxonomically. As vitamin concentrations are probably limiting in many environments, maintenance of populations of synthesizers are essential to maintain community function (Sanudo-Wilhelmy *et al.*, 2012). Consequently, comprehension of a community's endogenous dynamics and the interspecies interactions that may drive them will be critical to understand the mechanisms by which communities respond to exogenous perturbations.

Stabilizing diversity

Principles that may follow from the considerations given above include the following: (1) a broad portfolio of organisms with overlapping ecological functions confers functional stability; (2) specific interactions may increase or decrease diversity; and (3) complex interaction networks produce greater stability than simple pairwise interactions.

A central challenge for understanding microbial community dynamics is identifying mechanisms that maximize diversity and interaction networks. Many microbial communities are phylogenetically under-dispersed (Horner-Devine and Bohannan, 2006; Stegen *et al.*, 2012)—thus, it is likely to be that many organisms that serve similar ecological functions coexist. Hutchinson (1961) invoked the 'paradox of the plankton,' specifically in reference to the number of coexisting phytoplankton in competition with each other exceeding that expected from Gause's competitive exclusion principle. Over the last 50 years, a variety of mechanisms have been proposed for coexistence of apparent competitors (Wilson, 2011); both the variability in exogenous factors and endogenous dynamics are important factors that stabilize biodiversity. For example, niche partitioning in space or metabolic specialization/compartmentalization (Johnson *et al.*, 2012) broadens the number of niches that can be occupied by distinct ecotypes, defined as a group of bacteria that are ecologically similar to each other (Cohan, 2006). External selective forces may vary in intensity and duration, with periodicities on differing time scales (Bell, 2010), thereby shifting the directions of selection. For example, one basis for the persistence of rare taxa is that they may be favored occasionally, at a frequency sufficient to retain community membership. Endogenous mechanisms that are density dependent, such as virus susceptibility or grazing by protists (Fox, 2007; Short, 2012) have the effect of, at least temporarily, decreasing the stringency of exploitation competition and provide an opportunity for less-competitive ecotypes to proliferate, thereby enabling coexistence.

In addition, a broad variety of endogenous mechanisms that entail metabolic interactions will increase and stabilize community diversity. Metabolic coupling may entail sequential utilization of organic electron donors such as in the anaerobic degradation of organic

matter (Stams, 1994) or redox reactions involving the coupling of inorganic electron donors and electron acceptors, as in the biogeochemical cycles of Fe, N and S (Burgin et al., 2011; Johnson et al., 2012). The provision of 'public goods' (for example, essential growth factors such as amino acids, nucleosides or cofactors) is another example of metabolic coupling in which a broad diversity of microbes that are deficient in biosynthesis, but capable of assimilation/salvage, are supplied by a smaller number of producing organisms. A key question at the intersection of ecology and evolutionary biology is the extent to which public goods arise passively due to lysis of producing cells versus active excretion. In the case of cofactors, genomic analysis suggests that efflux is a rare (or poorly recognized) trait, although examples of high-level excretion have been reported (Schyns et al., 2005). In marine environments, many microorganisms are known to have specific growth factor requirements, in particular for cobalamin, and analytical techniques have improved to the point that temporal and spatial dynamics in cofactor concentrations can be measured with great sensitivity (down to pM levels) (Sanudo-Wilhelmy et al., 2012). These dynamics are consistent with important metabolic interactions between producers and consumers of these commodities. Furthermore, (meta)genome analysis can putatively identify producing versus auxotrophic members in a community (Swithers et al., 2012; Klein et al., 2013) and potentially even the relative proportions of producers and consumers. Recent advances in the ability to disentangle genomes from even complex communities markedly enhance this potential (Wrighton et al., 2012; Howe et al., 2014).

An extreme example of metabolic interactions enhancing and stabilizing community diversity is syntrophy, in which two or more organisms cooperate to metabolize compounds that cannot be utilized individually. Although the metabolic currencies exchanged in syntrophic interaction studies were largely believed to be H_2 or low-molecular-weight organic acids, electrons may also serve as currency of energy exchange in such interactions (Morita et al., 2011; Shrestha et al., 2013). The extent to which syntrophic interactions occur in complex natural microbial communities remains an underexplored but potentially important type of metabolic interaction contributing to diversity and stability. Other examples of interactions that may stabilize community diversity are those associated with the microbiome that lives in association with lichens. The interactions include metabolite exchange, stress resistance and detoxification of metabolites that collectively are thought to have an impact on the health, growth and fitness of their hosts (Grube et al., 2014).

Beyond the portfolio effect: do networks buffer the system?

One straightforward and intuitive way to rationalize the relationship of diversity to ecosystem properties such as functional stability and resilience is analogous to a diversified portfolio of financial investments—poor performance by one component under a particular condition is more likely to be offset as the number of distinct entities capable of performing that function increase. However, in contrast to a portfolio of financial investments, microbial communities typically possess individual populations that are metabolically versatile, with sets of populations partially overlapping in their potential to carry out specific biogeochemical reactions and resist environmental stresses. In addition, populations can disseminate information, such as genes and chemical signals, throughout the community at relatively rapid rates, and metabolic interconnections and dependencies are common. These characteristics generate a complex network of alternative pathways and diverse microbial catalysts to affect directional flows and fluxes of energy and chemical resources through the community.

A network of multi-functional agents that are similar in some but not all functions is termed functionally degenerate, rather than strictly redundant (Whitacre and Bender, 2010). In such a system (whether in engineering, management or biology), the network provides a buffer against disturbance beyond the portfolio effect, as alternative pathways with different combinations of agents can be recruited to fulfill specific functions. A complex food web represents an ecological example in which complexity is postulated to confer higher-order properties such as stability (Banasek-Richter et al., 2009; Rooney and McCann, 2012). In microbial communities, the physiological response times of microbial populations are generally fast compared with the timescale of perturbations; under those conditions, 'network buffering' is expected to contribute to system robustness.

The concept of network buffering reinforces the assertion that gaining insight into the forces that establish and maintain complex interaction networks in microbial communities is an important research need. Technological advancements in macromolecular sequence acquisition and analysis (Gonzalez et al., 2012), as well as microscale metabolite analysis (Watrous et al., 2012), can be coupled to a set of observational and experimental strategies to address this problem.

Key knowledge gaps for elucidating design principles

Any effort to identify principles that lead to assembly of communities with particular emergent properties must be considered in the context of the historical debate (Justus, 2007) about whether and how biological diversity fosters functional stability in dynamic environments. As most empirical studies have found that diversity increases the stability of ecosystem function (McNaughton, 1977; Mori et al., 2013; McIntire and Fajardo, 2014), ecologists

are now confident that diversity begets functional stability in ecosystems (Hooper *et al.*, 2005). Two significant general knowledge gaps that arise are:

- What are the mechanisms that optimize diversity within a biological community?
- What are the mechanisms by which diversity imparts community stability?

As mentioned earlier, the first question has been of intense interest in aquatic and plant ecology for the last 50 years and was articulated as the paradox of the plankton (Hutchinson, 1961). Many theories have been put forward to explain the paradox (Wilson, 2011), but these are often difficult to experimentally test in non-microbial systems. Our contention is that it is microbe–microbe interactions within a feedback-regulated microbial network (that is, the endogenous dynamics of the system) that are important in optimizing diversity. However, it is the second question that is more intriguing and remains a central knowledge gap in ecology (Loreau *et al.*, 2001; Hooper *et al.*, 2005). Two overarching mechanisms for optimizing diversity are frequently proposed. The first is that the presence of functionally redundant community members that differ in some ecologically important traits provides insurance, which allows selection from a pool of functionally equivalent populations for those that are best adapted to changing environmental conditions. The second mechanism involves functionally distinct members that occupy a network of complementary niches with interactions between them buffering environmental variation and conferring gains in productivity and efficiency (known as 'niche complementarity'). These two mechanisms are not mutually exclusive and are increasingly seen as opposing ends of a spectrum (Loreau *et al.*, 2001). We would add network buffering as a third mechanism in which the interconnections among constituent members of the community lead to functional stability beyond the 'portfolio effect.' Attempts to disentangle the relative contributions of each mechanism are frequently thwarted, because natural systems are highly complex and exhibit variable environmental conditions and diversity over time (Hooper *et al.*, 2005). For example, experiments with plant communities produced results consistent with sampling mechanisms in some years and niche complementarity in others (Tilman *et al.*, 2001). This suggests that elucidation of the principles governing the relative contributions of portfolio effects, network buffering and niche complementarity to stability in ecosystem properties must involve systems for which both environmental conditions and biological diversity can be simultaneously controlled. Constructed microbial communities (Cook *et al.*, 2006; Brune and Bayer, 2012) or consortia derived from native communities (Cole *et al.*, 2014) can provide such laboratory-based experimental systems.

As assays of functional stability tend to measure either whole-community properties or enzymatic activities that are functions possessed by many members of the community, it is frequently impossible to correlate member relative-abundance changes in response to environmental perturbation to the specific physiological state of each member. Hence, parsing out the effects of environmental selection and interspecies interactions in imparting functional stability will require species-resolved functional studies in communities (Hooper *et al.*, 2005). Advanced technologies such as metatranscriptomics or metaproteomics allow species-resolved analysis of the adaptive responses made by individual community members to environmental perturbations (Konopka and Wilkins, 2012), and thereby gain insights into the contributions made via different mechanisms to functional stability of the community. Although the application of such techniques to microbial communities requires accurate assignment of genome fragments to specific organisms, recent developments provide the necessary computational tools (Sharon and Banfield, 2013).

The above approach would lend itself to viewing microbial communities as compartmentalized networks of genomes and associated functions (Shade *et al.*, 2012), from which emergent community properties arise through interactions between components. In principle, even minor perturbations to community composition or the functional activity of specific community members can significantly reorder the functions of each member and the network of interactions between them. Responses of communities to variations in the type, magnitude, duration and periodicity of environmental perturbations often appear idiosyncratic (Shade *et al.*, 2012). Elucidation of principles will require quantitative metrics applied to a matrix of experimental conditions.

We consider as an example an experimental approach for identifying a design principle that mechanistically addresses the link between community diversity and functional stability. Unimodal relationships between species richness and productivity, such that maximum richness is correlated with intermediate productivities, are commonly found in many communities (Graham and Duda, 2011). However, it is very difficult to draw a mechanistic link, as species richness could be driving productivity, or, conversely, productivity may drive species richness, or both. One hypothesis that could be proposed is that more highly productive ecosystems exhibit reduced species diversity, because their environments are more stable. As such, the functional diversity and redundancy required in variable environments will not be required and, consequently, a community is optimized for increased yield under these more stable conditions by reducing its functional redundancy (and, therefore, network complexity). Attempts to test related hypotheses using variable-diversity combinations of plant species in the field have

yielded inconsistent results (Tilman *et al.*, 2001) as significant, year-to-year environmental variation and intrusion by invading species are confounding variables. By using consortia or synthetic communities of microbes in the laboratory, both environmental constraints and species richness can be controlled. Furthermore, large numbers of potential combinations of members with diverse physiologies can be examined. A hypothetical outcome from such a set of experiments is provided in Figure 1. In this example, the average productivity (that is, total biomass yield) of communities of diversity $1 < n < 4$ (composed of an autotroph and up to three heterotrophs, chosen either at random or by phenotype) is compared with that of the autotroph alone. These communities are then subjected to environments in which salinity stress is varied in magnitude and/or duration to differing degrees. Such microbial experiments could be performed using a large array of different heterotrophic partners, such that the effect of network complexity can be separated from the specific traits of individual members in ways that are very difficult in macroorganisms. In this contrived example, the addition of a single heterotroph tends to increase total community productivity, as the heterotroph recycles fixed carbon back to CO_2. Addition of a second heterotroph provides additional efficiency by providing functional degeneracy; each species can specialize in consuming different compounds. This gain in productivity holds as long as the environment remains sufficiently stable to permit both heterotrophs to perform a distinct function. Inclusion of a third heterotrophic species, however, tends to reduce productivity under stable environmental conditions due to the decreases in efficiency required to maintain organisms that are increasingly functionally redundant. Yet, they outperform the lower diversity communities where environmental conditions are
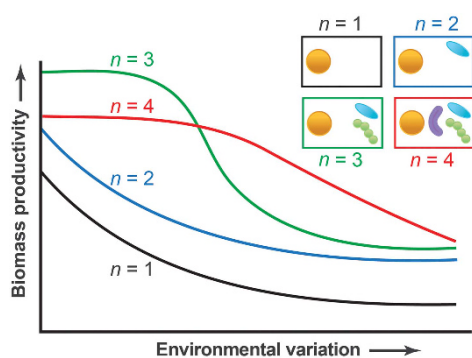
more variable, as the members tend to better buffer against environmental stress due to their functional degeneracy. If such a relationship were found to apply to microbial communities in general, a candidate design principle could be proposed: 'The optimal species diversity for maximum community productivity increases with the degree of variation in environmental conditions that a community experiences.' Technological developments in not only 'omics but also in high-throughput cultivation and analysis (for example, Wittebolle *et al.*, 2009) increasingly make such approaches tractable in microbial systems.

By addressing these scientific gaps, we believe that design principles for microbial communities can be defined. This would move the field from correlations based on observations to mechanisms and entail substantial refinement over our current level of understanding, which can be encapsulated as:

- a broad portfolio of distinct ecotypes with overlapping ecological functions confers stability on an ecosystem
- specific biological interactions can increase or decrease diversity
- complex interaction networks produce greater stability than simple pairwise interactions

We believe that deeper principles of design are discoverable, because the challenges and trade-offs faced by microbes recur in many disparate communities; the challenge is to design strategies to make the complexity of microbial communities comprehensible. Although exceptions do occur in biology, general rules advance prediction by suggesting probable behavior when applied to a novel system or environmental perturbation. Infusing design principles into simulation models, whose aim is to synthesize current mechanistic understanding of microbial community dynamics, will increase the generality of those models, permit testing the limits of design principles and suggest strategies to exploit them to better control the properties and behavior of microbial communities.

Conflict of Interest

The authors declare no conflict of interest.

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Figure 1 Hypothetical data from a theoretical experiment to identify a community design principle relating community biomass productivity and species diversity (*n*) to the degree of environmental variation to which the community is exposed. Inset boxes depict communities of varying species diversity. This experimental data would lend support to the following design principle: the optimal species diversity for maximum productivity increases with the degree of variation in environmental conditions that a community experiences.

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