Title: Diversity is the question, not the answer

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Main Text

"The rock just sits and is." - Albert Markovski

Diversity (the number and/or evenness, and types of taxa within a local community) is arguably one of the most fundamental concepts in community ecology. Ecologists report diversity estimates for a number of reasons, including to ask how patterns in diversity translate to ecosystem function or stability, or to understand how and why diversity changes over space and time. This research is pursued in an effort to build an understanding of the ecological processes of the world and to identify common patterns, with the ultimate goal of improving knowledge of universal mechanisms and building theoretical framework. Once ecological mechanisms are understood, ecologists strive to better predict, conserve, or manage communities to desired outcomes.

Microbial ecologists have a particular interest in diversity, as microbial diversity is expansive, and many microbial communities have near-innumerable membership (Locey and Lennon, 2016). Relative to our planet's better-described communities of macrofauna, microbial communities are

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a trove of untapped and unknown diversity. High-throughput sequencing methods have offered new insight into the extent and limits of microbial diversity, and have spurred research interests, including understanding the rare microbial biosphere (Lynch and Neufeld, 2015) and microbial dark matter (Marcy *et al.*, 2007). High-throughput sequencing combined with cultivation-independent methods continue to reveal a fuller tree of life, expanding our knowledge of evolution and of phylogenetic relationships in biology, which are dominated by microbial lineages (Hug *et al.*, 2016).

With all of the discovery and excitement in microbial ecology about diversity, there often has been an assumption that high diversity is implicitly a good or desirable outcome for communities, and that higher diversity is also somehow more meritorious ecologically. Alas, diversity is not good or bad, it simply "is", much like Albert Markovski's rock. Diversity *is* a property that we observe about microbial communities and measure using statistical indices, and these measurements allows us to develop hypotheses to test the ecological mechanisms driving those communities' dynamics. Diversity is the outcome of ecological processes, and not an ecological process in itself. Thus, a diversity measurement has limited value alone because much context is needed for interpretation. I argue that diversity provides a proxy for comparing communities, and an appropriate starting point for determining underlying ecological causes and consequences in community ecology. Similarly, I suggest that as a field we resist the over-simplification of implicating diversity as a reason for community outcomes or implying that a high diversity microbial community is somehow 'better' than a low diversity community.

Here, I explore the complications and assumptions about microbial diversity and offer suggestions to redirect some of our common misconceptions towards understanding the ecological mechanisms driving patterns in diversity. I focus on within-sample (alpha) diversity of a locality (**Table 1;** see Magurran, 2003 for an excellent primer).

Diversity has many definitions. Which are you using, and why does it matter?

There is a long history of challenge with both defining and measuring ecological diversity (e.g., Ricotta, 2005). An inherent challenge is that there is no universally accepted, absolute value of diversity for a given community. Contrast this to other quantitative measurements considered to have absolutes that are comparable across different methods or scales of measuring. For

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example, whether temperature is measured in Kelvin, Celsius, or Fahrenheit, there is a belief that there is one "true" equivalent value upon which all will scales will agree. Diversity, however, is relative and always constrained by method of measurement. There is not a belief that an absolute diversity value can be determined and compared across methods: each method is a slightly different reduction of multivariate information about a community. If determining an absolute value of diversity were achievable (and it likely is not), it would unite the field of community ecology by ending debate about the merits of different diversity measurements, and instead redirecting focus towards underlying mechanisms.

Thus, "diversity" can refer to be any number of metrics considering any one or number of aspects of a community. Because no absolute value of diversity exists, each method has its own biases and advantages, as discussed previously (e.g., Hill *et al.*, 2003). A lack of specificity about which method is used can lead, at best, to confusion or, at worst, oversimplification or misinterpretation of community outcomes. Thus, the precise method(s) for calculating diversity should be carefully considered and justified either ecologically or biologically according to the scientific question, and then interpreted considering the chosen diversity metric's strengths and limitations. For example, if there is a working hypothesis of differences in phylogenetic breadth between communities in a control and treatment, a diversity metric that incorporates information about the relatedness of taxa may be selected.

Diversity metrics are, by design, flexible, and thus can be calculated from any type of community dataset. Because it is difficult to observe individual microbial cells and distinguish among microbial taxa, microbial ecologists use many inexact methods for observing communities, including cell morphology or probe binding with microscope counts, fingerprinting, colony phenotypes, and sequencing. Each of these methods produces a differently biased perspective of the community. Thus, due to methodological differences, diversity often is not comparable directly across studies even if the same metric is calculated. This results in vagueness and does not promote a deeper understanding of microbial community ecology. It also means that diversity cannot be "important" in itself because much context is needed for interpretation.

The temptation of diversity: it is easy to calculate, but let's not forget limitations

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For a high-throughput sequencing dataset, diversity is straightforward to determine, perhaps in part because popular sequence analysis pipelines automatically output these calculations. The ease of diversity calculation may tempt us to indiscriminately report them or to assume that they are informative for our study. However, for sequencing methods, there are a range of analysis choices regarding the operational taxonomic unit (OTU) definition (Rideout *et al.*, 2014; Schloss, 2016; Preheim *et al.*, 2013; Eren *et al.*, 2013). The taxonomic unit is whatever is appropriate to the scientific question (or, as it often happens, default in the sequence analysis pipeline), as chosen by the researcher. This is an important consideration because OTU definitions will impact our perspective of diversity, and some OTU-defining methods consistently over- or under-inflate the number of taxa observed (e.g. Edgar, 2013), which directly impacts diversity calculations.

There are also inherent diversity biases resulting from cultivation-independent methods. Diversity metrics may be inflated by the DNA of inactive or dormant organisms (Jones and Lennon, 2010). DNA extraction protocols can bias against lyses of certain groups, skewing their representation in the community (e.g., Gram positive bacteria). Co-extraction of relic or taphonomic DNA can overestimate standing diversity (Carini *et al.*, 2016). There is also primer bias in amplicon sequencing, which can underestimate diversity by omitting or under-representing certain microbial lineages (Klindworth *et al.*, 2013). For some marker genes, like the 16S rRNA gene, bacterial and archaeal taxa may have very different copy numbers (Stoddard *et al.*, 2015), which complicates our perception of their relative contributions to the community. For taxon-rich microbial communities, like soils, and especially for highly uneven, rich communities that are dominated by a few very abundant taxa (Adams *et al.*, 2013), under-sampling of the community is an additional consideration (e.g., Gihring *et al.*, 2012). Increasing the amount of sequences generated for under-sampled communities resulted in continued increase in diversity estimates, with particular sensitivity in the performance of non-parametric estimators that extrapolate absolute community diversity based on the number of singletons and doubletons (Gihring *et al.*, 2012).

Of course, no method is without bias. However, due to our inexact methods for observing communities, microbial diversity calculations in particular have so many biases that they may be considered as rough approximations. Efforts should be made to standardize biases across samples prior to making diversity comparisons, and, even then, to interpret results with care.

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High diversity isn't necessarily "better" or "healthy."

If higher diversity were universally better for communities, why devote resources to understanding ecological mechanisms? If it were true that higher diversity is always an improvement, we could manage microbial communities by simply making them more diverse.

There are countless examples of ecosystems in which higher diversity is not more meritorious. As a simple example, a rainforest harbors more plant species per hectare than a temperate forest, but it is not interpreted that the temperate forest is a less important or less-thriving ecosystem. These two ecosystem are different, and for many abiotic or biotic reasons that could be uncovered and investigated further. Similarly, vaginal microbial communities exhibit a range of diversities across healthy women, including some communities that are dominated by lactobacilli and others (reported as 20-30% of asymptomatic individuals) that have less lactobacilli but more diverse membership (Ma *et al.*, 2012). As another example, high-fat and low-fat diets had comparable levels of Shannon diversity, Chao diversity and richness (though, different taxonomic compositions) in humanized mouse models (Turnbaugh *et al.*, 2009). These studies and others demonstrate that lower diversity is not necessarily indicative of a worse community or ecosystem and lower diversity does not necessarily imply less stable or less 'healthy' communities.

There is a recent example in which we do overwhelm microbial communities with more and different diversity in an effort to manage them: fecal transplants after an opportunistic infection by *Clostridium difficile* (Kassam *et al.*, 2013). Not all fecal transplants are successful, despite the apparent deluge of additional diversity to the community. It would be a misinterpretation to suggest that the diversity in itself is the answer to the frequent success of fecal transplants in mitigating *C. difficile infection*.

Notably, microbial ecologists have borrowed value-laden terms from traditional ecology to describe diversity, which may be one historical reason for the persistence of assumptions that higher diversity is better. For example, ecologists use *richness* to refer to the number of species, and *depauperate* to describe communities with low diversity. This terminology was used in the literature as early as the 1920's (e.g., Wheeler, 1926), but seems to have become more prominent by the 1940's (e.g., Hubbs and Lagler, 1949). Thus, microbial ecologists perhaps have intuited value from legacy jargon without reconsideration of its merit.

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Diversity only has value in a comparative context

Except in the context of informing study design and approach (e.g., how many sequences are needed for exhaustive coverage of a community?), there is little ecological value in reporting that a community has ten-thousand taxa or ten. The insight emerges when comparing that community to another situation or community of interest, and then asking what is the difference observed and why. This could be in the context of an experimental design between control and treatment conditions, over a natural or controlled environmental gradient, over time, in response to a disturbance or stressor, or over geographic space.

Comparative microbial diversity, especially when multi-layered community and functional measurements are applied, has provided key insights into underlying processes. For example, two sets of replicated methanogenic bioreactors responded differently to a pulse glucose shock: one set was stable, while the other decreased in performance (Hashsham *et al.*, 2000; Fernandez *et al.*, 2000). It was discovered that the sets harbored very different microbial compositions, measured using several complementary methods, including cell morphology, fingerprinting, and rRNA probes, which allowed the researchers to delve more precisely into the comparative mechanisms of functional stability. In particular, the bioreactors with less diverse membership had an ability to perform parallel substrate processing during the glucose shock to maintain performance. One important conclusion from this study was that communities with higher diversity were not necessarily more functionally stable in the face of disturbance.

Because of all of the nuances in calculating diversity, comparing diversity within a single study or across a series of related studies (often by the same researcher) provides situation-specific insights and modest advances. For understanding larger scale patterns in diversity over space or time or across many ecosystems, researchers often have to spend much time curating disparate datasets for meta-analysis, and re-defining taxonomic units across studies to be maximally comparable. Even then, due to methodological differences, each dataset sometimes must remain as a distinct unit and quantitative cross-study comparisons are limited. Though quantifying large-scale patterns in microbial ecology is challenging, one of the scientific reasons for doing so is to test ecological theories established in traditional ecology for microbial communities. Calculating diversity for microbial communities and analyzing their overarching patterns using methods directly comparable to studies in traditional ecology pushes forward our pursuit of a unified ecological theory. For example, studies have considered latitudinal gradients

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of diversity (e.g., Chu *et al.*, 2010), and species-area and species-time relationships (e.g., Bell *et al.*, 2005; Shade *et al.*, 2013). In some cases, microbial diversity exhibits similar large-scale patterns to communities of larger organisms ("macroorganisms", e.g., Locey and Lennon 2016), and in some cases, they are distinct (e.g., Fierer *et al.*, 2011). Understanding these points of distinction for microbial diversity will allow us to delve deeper into the ecological mechanisms driving their patterns, and better place them in the context of a grander view of biology. To provide specific example of how comparisons of large-scale patterns in diversity can uncover common underlying ecology, a recent meta-analysis used species richness, observed community size, and maximum community size of both macrobial and microbial communities to discover a universal scaling law relationship between the size of the community and its evenness (inclusive of dominance and rarity), where larger communities exhibit lower evenness and a larger "rare biosphere" (Locey and Lennon 2016).

A final consideration is whether a given diversity comparison is ecologically meaningful. For example, can any insight be gleaned to consider that an acid mine drainage community is much less diverse than a soil (or, to be a bit facetious, that a mammal gut has different diversity than the surface of a kitchen counter)? In these examples, there are very distinct ecosystems with fundamentally different drivers and constraints. We do not need to calculate diversity in each to be led to hypotheses as to why they are different. An exception to this is in questions concerning source tracking of specific community members (e.g., Knights *et al.*, 2011) where disparate but connected ecosystems or regional metacommunities may be implicated in seeding each other's diversity.

If diversity is not the answer, what is?

There are many ecological mechanisms that underpin patterns in community diversity, and they are inherently difficult to unravel. The most commonly studied mechanisms are deterministic processes. For instance, abiotic drivers and constraints, like environmental filters and carrying capacity of an ecosystem, limit the type and number organisms capable of exploiting the habitat. Abiotic disturbances may disrupt resource availability and make new niche space available, driving replacement or proportional changes in communities. Disturbances sometimes impact specific members rather than the whole community, driving selection or release from competition or predation. Biotic interactions are also important drivers of diversity, and the nature and strength

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of interactions like antagonism and synergism can result in complex and non-intuitive multi-member interactions (e.g., Tilman, 1994) Thus, our ultimate understanding of diversity requires more than measurements of diversity; we also need contextual data and sufficient numbers of community observations for thoughtful comparisons that test specific hypotheses about how diversity may, or may not, change across sample categories or gradients.

Suppose a hypothetical study used marker gene sequencing to uncover evidence that a certain pathogen is more successful in invading a host-associated microbial community that has relatively lower diversity as compared to a higher diversity community. The researchers may then report that high diversity prevents pathogen invasion, and then attribute this to an underlying higher functional diversity in that community.

The question to consider is: what about the ecology of the more diverse community is inhibitory towards the pathogen, and what about the less diverse community is permissive? Perhaps it is that there is a direct competitor of the pathogen in the more diverse community. Or, perhaps there is a mutualist of the pathogen in the low-diversity community that promotes its growth. Perhaps the higher diversity community has lower pH, and the pathogen is sensitive to this specific abiotic driver. Perhaps it is because a subset of community members has stimulated the host immune response in the higher diversity community. Perhaps it is because the higher diversity community is at carrying capacity, and there are no available niches for the invading pathogen. Perhaps the pathogen acquired a beneficial gene, via horizontal gene transfer, from a member of the lower diversity community that improved its success. (Also, without directly measuring function or functional potential, it is a conceptual leap to move from the observation of high compositional diversity to the assumption of high functional diversity.)

The mechanisms maintaining or changing microbial diversity are many and complex. Understanding how these mechanisms collectively contribute to community outcomes is of great importance for the goals of predicting, conserving, and managing microbial communities, and reporting diversity without underlying hypotheses, contextual data for interpretation, or useful comparisons does not advance our understanding towards these goals. Furthermore, common assumptions that “higher diversity is better” oversimplifies complex mechanisms and can sidetrack progress. There is a lot of work to be done, and measuring diversity is the first step in a rich line of scientific inquiry. Measurement of diversity should serve as a starting point for further inquiry of ecological mechanisms rather than an “answer” to community outcomes.

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Conflict of interest

There author declares no conflict of interest.

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352 **Table 1**. Different aspects of within-sample (alpha) diversity. One or more of these aspects are
353 incorporated into common diversity estimates, like Shannon Diversity, Faith's phylogenetic
354 diversity, etc.
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Aspect of diversity	Notes
Community size	The total number of individuals observed in a locality
Number of taxa (richness)	Summarizes the total number of taxa, where taxon is counted as an equivalent unit
Equitability of taxa (evenness)	Summarizes how evenly distributed are relative contributions across taxa
Composition of taxa	Accounts for the number of unique taxa and their identities, which can be taxonomic or operational
Relative contributions of taxa	Accounts for the proportional contributions of each taxon to the total count of all individuals observed
Phylogenetic relatedness of taxa	The evolutionary breadth represented by taxa given a phylogenetic tree

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