PERSPECTIVE

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Investigating the eco-evolutionary response of microbiomes to environmental change

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Abstract

Microorganisms are the primary engines of biogeochemical processes and foundational to the provisioning of ecosystem services to human society. Free-living microbial communities (microbiomes) and their functioning are now known to be highly sensitive to environmental change. Given microorganisms' capacity for rapid evolution, evolutionary processes could play a role in this response. Currently, however, few models of biogeochemical processes explicitly consider how microbial evolution will affect biogeochemical responses to environmental change. Here, we propose a conceptual framework for explicitly integrating evolution into microbiome–functioning relationships. We consider how microbiomes respond simultaneously to environmental change via four interrelated processes that affect overall microbiome functioning (physiological acclimation, demography, dispersal and evolution). Recent evidence in both the laboratory and the field suggests that ecological and evolutionary dynamics occur simultaneously within microbiomes; however, the implications for biogeochemistry under environmental change will depend on the timescales over which these processes contribute to a microbiome's response. Over the long term, evolution may play an increasingly important role for microbially driven biogeochemical responses to environmental change, particularly to conditions without recent historical precedent.

KEYWORDS
bacteria, eco-evolutionary feedbacks, fungi, global change, rapid evolution

INTRODUCTION

Free-living microbial communities—or microbiomes—are the primary engines of biogeochemical processes (Falkowski et al., 2008) and foundational to the provisioning of ecosystem services to human society (Peralta et al., 2014). Anthropogenic impacts on ecosystems mean that ecological communities—including microbiomes—are increasingly experience conditions that may have no recent (at least 125,000 ya) historical precedent (USGCRP, 2017). Given microorganisms' capacity for rapid evolution, evolutionary processes may thus play an increasingly important role in microbiome responses to no-analogue conditions. Currently, however, few models

explicitly consider how microbial evolution will affect biogeochemical responses to environmental change (but see, e.g. Abs et al., 2020).

Eco-evolutionary dynamics are often defined by timescale, and specifically, that ecological and evolutionary processes both occur in 'contemporary' time (Bassar et al., 2021; Hairston et al., 2005; Hendry, 2017). However, distinguishing between an ecological and evolutionary process can be difficult for microorganisms. Evolution is a change in genetic variation within a population of a species, but defining a microbial species, let alone a population, is arguably less clear than for larger, sexual organisms (Achtman & Wagner, 2008; Fraser et al., 2009; Rosselló-Mora & Amann, 2001).

Furthermore, their relatively high population sizes, rapid generation times and capacity for horizontal gene transfer (HGT) mean that many microorganisms can undergo rapid evolution over days to months (Travisano et al., 1995; Yoshida et al., 2003)—timescales within which ecological dynamics certainly take place. By this reasoning, then, eco-evolutionary dynamics (and likely, feedbacks) are occurring in all microbial systems.

Nevertheless, there remains a disconnect between the fields of microbial ecology and microbial evolution, just as for larger organisms like plants and animals (Yamamichi et al., 2022). With the goal of modelling ecosystem responses to rapid global change, we propose a conceptual framework for explicitly integrating evolution into microbiome–functioning relationships. Adapted from Vellend (2010), our framework builds on evidence that microbiomes respond *simultaneously* to environmental change via four interrelated processes that affect overall microbiome functioning:

1. Physiological acclimation, or changes in the activity of cells/individuals present in the community;
2. Demography, or the differential survival and reproduction of particular taxa;
3. Dispersal, or the colonization of individuals/taxa from other ecosystems that might be better adapted to the new conditions and
4. Evolution, or shifts in the frequencies of particular strains (alleles) within a taxon and/or de novo genetic mutations and recombination, including through HGT.

The question is therefore not *whether* ecological and evolutionary processes are co-occurring, but *how* to quantify their relative contributions and resulting implications for biogeochemistry under environmental change. We conclude that determining the importance of evolution will require investigating the timescales over which these processes impact a microbiome's response.

EVIDENCE FOR ECOLOGICAL RESPONSES OF MICROBIOMES TO ENVIRONMENTAL CHANGE

Currently, most studies that investigate the response of microbiomes to environmental change focus on physiological and demographic responses, or the first two of the four processes listed above. As with larger organisms, changes in environmental variables, such as temperature, pH, and moisture, will affect a microorganism's physiological state, as measured by nearly instantaneous changes in respiration, photosynthesis and/or nutrient uptake rates (Madigan et al., 2018). Where environmental selection pushes microbes beyond their capacity to acclimate physiologically, demographic shifts (births, deaths and dormancy; Lennon & Jones, 2011)

quickly lead to changes in active community composition. Indeed, the taxonomic composition of microbiomes is overwhelmingly sensitive to a variety of perturbations ranging from small-scale manipulations of nutrients and temperature to large-scale disturbances such as deforestation and storms (reviewed in Allison & Martiny, 2008, Shade et al., 2012).

Importantly, these demographic responses capture ecological processes of distantly diverged taxa (over geological timescales) and are not the result of rapid, contemporary evolution. Microbial communities are typically characterized using operational taxonomic units (OTUs) that are based on the sequence similarity of marker genes such as the 16S rDNA region. While it is difficult to directly compare the taxonomy of microorganisms to that of larger organisms, it is enlightening to frame this sequence divergence in macroevolutionary terms. Based on the rate of bacterial 16S rRNA evolution (Ochman et al., 1999), a back-of-the-envelope calculation indicates that a 1% nucleotide sequence difference reflects a divergence time of roughly 50 million years ago, or about when primates evolved (Figure 1). A 3% difference thus corresponds to a divergence of roughly 150 mya, or the origination of birds as evidenced by *Archaeopteryx* fossils. Even the more recently proposed use of amplicon sequence variants (ASVs) captures taxa
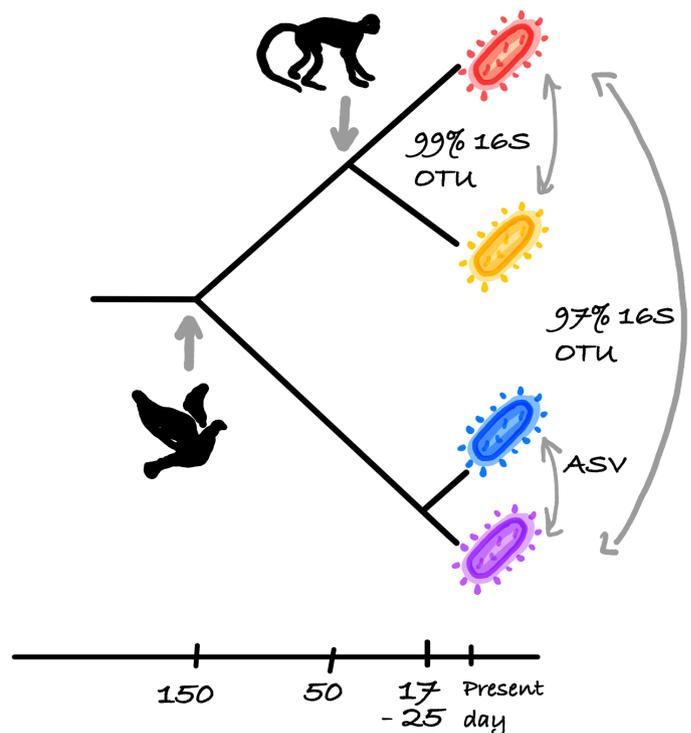
FIGURE 1 A rough estimate of the temporal divergence of 16S-based taxonomic units based on nucleotide sequence differences. A 1% nucleotide difference between 16S rRNA sequences corresponds with a rough divergence time of 50 million years ago, and a 3% difference, ~150 million years ago. OTU is operational taxonomic unit, and ASV is amplicon sequence variant. The sequence difference between ASVs depends on the sequence length.

that diverged ~17–25 mya (assuming a typical 200–300 bp amplicon region). While these comparisons to animal evolution are certainly imperfect, they highlight the tremendous potential for trait divergence within bacterial OTUs/ASVs. We also note that metagenomic sequencing offers a more resolved picture of microbial diversity and therefore the potential for inferring evolution (Denef & Banfield, 2012; Shoemaker et al., 2022), but these approaches are still being developed. Thus, our current understanding of microbiome responses to global change is based on broad characterization of microbial taxa, certainly above the species level and in macro-organism terms, more akin to major lineages of vertebrates.

EVIDENCE FOR EVOLUTIONARY RESPONSES OF MICROBIOMES TO ENVIRONMENTAL CHANGE

The very nature of microorganisms—with their relatively high population sizes and rapid generation times—provides the opportunity for rapid evolution in response to new environmental conditions. Laboratory studies of bacteria, fungi and other microeukaryotes demonstrate that some microorganisms can adapt quickly to selective pressures on timescales relevant for global change. Perhaps most famously, *E. coli* adapts to increased temperatures through mutations in regulatory genes (Bennett et al., 1992; Tenaillon et al., 2012). Similarly, the marine bacterium *Roseobacter* evolved genetically and phenotypically in response to elevated temperature within just a few months (Kent et al., 2018), and the fungus *Neurospora* adapted to higher temperatures by altering its carbon metabolism and allocation to reproductive spores (Romero-Olivares et al., 2015). Such rapid evolution is not only restricted to temperature; for instance, marine bacteria and eukaryotic algae adapted to increased CO_2 within 2–4 years (Hutchins et al., 2015; Tong et al., 2018). However, it is unclear how to translate these results into natural settings, as evolutionary outcomes may differ under more realistic conditions in a complex community (Scheuerl et al., 2020) and in populations with longer generation times.

A handful of studies demonstrate that free-living microbes, including fungi, bacteria and archaea, are locally adapted in nature (e.g. Belotte et al., 2003; Cadillo-Quiroz et al., 2012; Johnson et al., 2006; Leducq et al., 2014; Moore et al., 1998). The time frame of such adaptation is unclear, however. At least two studies provide direct evidence that free-living microbes have the potential to evolve as quickly in the wild as in the laboratory. In an acid mine drainage, *Leptospirillum* evolved over 5 years through both single nucleotide substitutions and recombination of bacteria strains (Denef & Banfield, 2012). In a less extreme environment, a strain of *Curtobacterium*, dominant in surface leaf litter, was inoculated into microbial 'cages' and transplanted into

five sites across a temperature and precipitation gradient (Chase et al., 2021). After just 6 months in the field, the strain accumulated genomic mutations. Some mutations occurred in parallel within sites, indicating that they were likely adaptive to the new conditions.

Together, these results suggest that both ecological shifts in microbiome composition and rapid evolution of microbial populations can occur in response to environmental change at the same time. However, the above examples reflect the extremes that occur along a continuum (Figure 2). In between broad community shifts (clearly, an ecological process) and de novo mutations (clearly, an evolutionary process) are responses at intermediate levels of genetic organization. For example, many closely related bacterial and fungal strains coexist in microbial communities. When fine-scale genetic clusters of microbes are associated with ecologically relevant traits, the lineages are often called ecotypes (Cohan, 2006). In the surface ocean, ecotypes of the cyanobacterium *Prochlorococcus* are differentially adapted to temperature, nutrient and light levels, and their relative abundances correspondingly shift across these abiotic gradients. Ecotypes will also encompass additional standing genetic variation, or 'microdiversity' (Larkin & Martiny, 2017) that can further be grouped into co-occurring local populations, or what might be considered an evolutionary unit (Arevalo et al., 2019; Chase et al., 2019; Kent et al., 2019). In soils, this microdiversity also responds to environmental changes like drought (Scales et al., 2022). Changes at this level of genetic resolution result in shifts in allele frequencies within populations, a phenomenon that, among larger organisms, would be thought of as an evolutionary process.

At the same time, physiological acclimation and dispersal may also occur, potentially influencing the degree of demographic and evolutionary responses across these levels of genetic organization. These processes occur at an individual level, thus permeating the responses at all levels of genetic organization. For instance, physiological acclimation to the new conditions might allow an individual (and therefore the population and species that it is part of) to maintain its abundance and thereby, buffer demographic shifts. Similarly, dispersal of individual propagules (e.g. cells, colonies or spores) contributes simultaneously to ecological drift and mass effects at the community level (Leibold et al., 2004) and to evolutionary drift and rescue effects at the species/population levels (Garant et al., 2007) (Figure 2).

CONNECTING ECO-EVOLUTIONARY PROCESSES TO MICROBIOME PERFORMANCE

To sum up thus far, microbiomes respond simultaneously to environmental change via broadscale community shifts, rapid evolution and everything in between
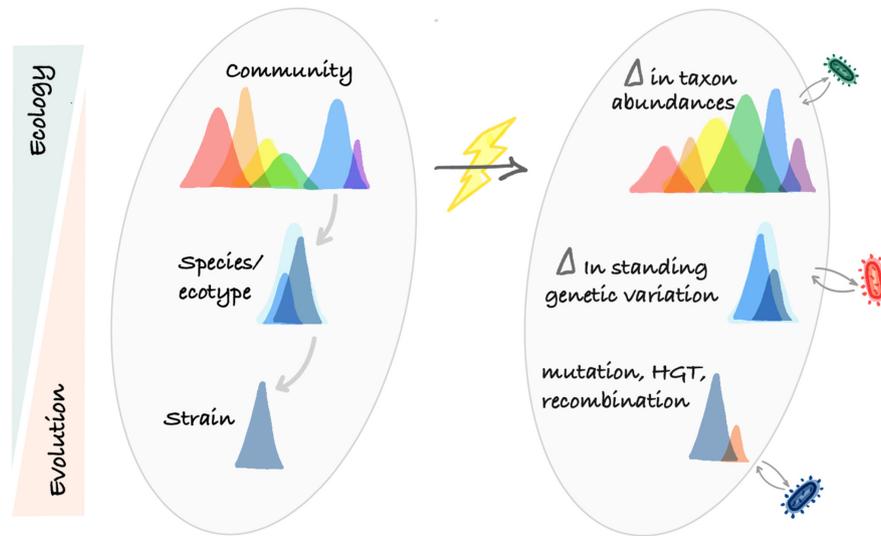
FIGURE 2 Current evidence indicates that environmental changes (indicated by the lightning bolt) cause changes in microbiome diversity at multiple genetic scales, from the community to the strain level, over the same time frame. These responses span from those that are clearly ecological responses—shifts (or lack of them in the case of physiological acclimation) in the relative abundance of microbial taxa—to those that are clearly evolutionary responses (de novo mutations, homologous recombination and horizontal gene transfer, HGT). At intermediate genetic scales, it is more unclear whether shifts in standing genetic variation of species or ecotypes should be considered ecological or evolutionary responses. An individual dispersing into (or out of) a microbiome potentially affects the response of a strain and the community of which it is a part.

(Figure 2). It will therefore be nearly impossible to neatly classify these responses into ecological or evolutionary dynamics (Hawkes & Keitt, 2015). Moving forward, we propose to focus on the importance of the four processes outlined in the Introduction to a microbiome's response over time, without regard to whether they contribute to ecology or evolution.

Taken individually, all four processes have the potential to affect overall microbiome performance, or the collective metabolic activity of a community. Microbiome performance can be measured directly by metrics of the community's ability to acquire resources and build biomass (e.g. microbial growth rate or productivity), or indirectly through its imprint on ecosystem functioning like organic carbon/nitrogen accumulation or removal (e.g. litter mass loss or soil gas fluxes). Below, we discuss examples of both direct and indirect measures of microbiome performance. We acknowledge, however, that while likely generally positively correlated, they are not the same. In particular, trade-offs between microbial resource acquisition, survival and yield mean that microbiome performance will be more tightly linked to ecosystem functioning in some circumstances than others (Krause et al., 2014; Malik et al., 2020; Wood et al., 2018).

In terms of microbial physiology, changes in microbial metabolic rates, resource allocation and survival will, in turn, alter carbon and nutrient cycling (Hutchins & Fu, 2017; Malik et al., 2020). Somewhat more controversial is the importance of demography for a microbiome's performance. Indeed, the compositional variation of microbial communities was long presumed to be functionally redundant, such that variation in microbiome composition would not affect their overall activity and thereby, their influence on ecosystem functioning (Allison & Martiny, 2008). More recently, however, laboratory and field experiments demonstrate that variation in microbiome composition can result in differences in ecosystem functioning in soil, sediments and the surface ocean, even when holding abiotic conditions constant (e.g. Domeignoz-Horta et al., 2021; Martiny et al., 2020; Reed & Martiny, 2013; Strickland et al., 2009; Waldrop & Firestone, 2006), but not always (Bier et al., 2015; Nunan et al., 2017).

Dispersal has the potential to alter microbiome performance by introducing novel genetic diversity (alleles and genes) including entirely new strains and taxa. Despite an earlier paradigm that microorganisms are everywhere (Baas Becking, 1934; Finlay & Fenchel, 2004), microbial ecologists are increasingly aware that microbial dispersal is limited, alters microbial composition in natural communities (Albright and Martiny 2017; Cline and Zak 2013; Adams et al., 2013) and thereby, can affects functioning (Zha et al., 2016). Finally, in laboratory experiments, rapid microbial evolution of just a few nucleotide differences between bacterial strains has been shown to have ecological consequences for carbon use, species interactions, stoichiometric allocation of nutrients and overall community productivity (Fiegna, Moreno-Letelier, et al., 2015; Goyal et al., 2022; Lennon & Martiny, 2008). Furthermore, theoretical models suggest that the evolution of microbial physiological traits under a changing climate could have large effects in soils, including global carbon stocks (Abs et al., 2020).

Given the potential influence of these processes on microbiome performance, how do we quantify and compare these impacts? Ecosystem models typically use a static mathematical function to predict the rate of an ecosystem function (e.g. heterotrophic respiration or decomposition) across an abiotic gradient such as temperature or moisture (Figure 3a). When the function of interest is largely driven by microorganisms, the curve is an indirect measure of microbiome performance. This performance curve captures the idea of a community's plasticity to new environmental conditions and is thus analogous to a reaction norm of a genotype within a species (Kingsolver et al., 2014). However, instead of one genotype, the function captures the plasticity of the emergent, collective phenotype. Notably, we expect that community performance curves will generally be flatter than individual reaction norms, as individual genotypes will be better adapted to different conditions (Martiny et al., 2022). For example, the growth rate of individual *Prochloroccocus* ecotypes is lower and more restricted by temperature than the growth of all *Prochlorococcus* and the entire phytoplankton community across ocean temperature gradients (Figure 3b).

The assumption that a microbiome's performance curve is temporally and spatially invariant would be adequate if microbiomes that differed in composition were functionally redundant, such that their performance curves did not differ over time or space. To quantify such a curve in the field, surface soil microbiomes from five ecosystems were reciprocally transplanted, and their performance was assayed by measuring decomposition rates of leaf litter. The results captured the performance curves of the different communities across a climate gradient over a year. While three communities shared very similar curves, two other communities varied in their rates by as much as 40% depending on the environment (Glassman et al., 2018) (Figure 3c).

Even if composition is not functionally redundant, a static performance function would also be adequate if it captures not only the physiological acclimation of the microbiome to the environment (e.g. changes in cellular metabolic rates), but also the other three
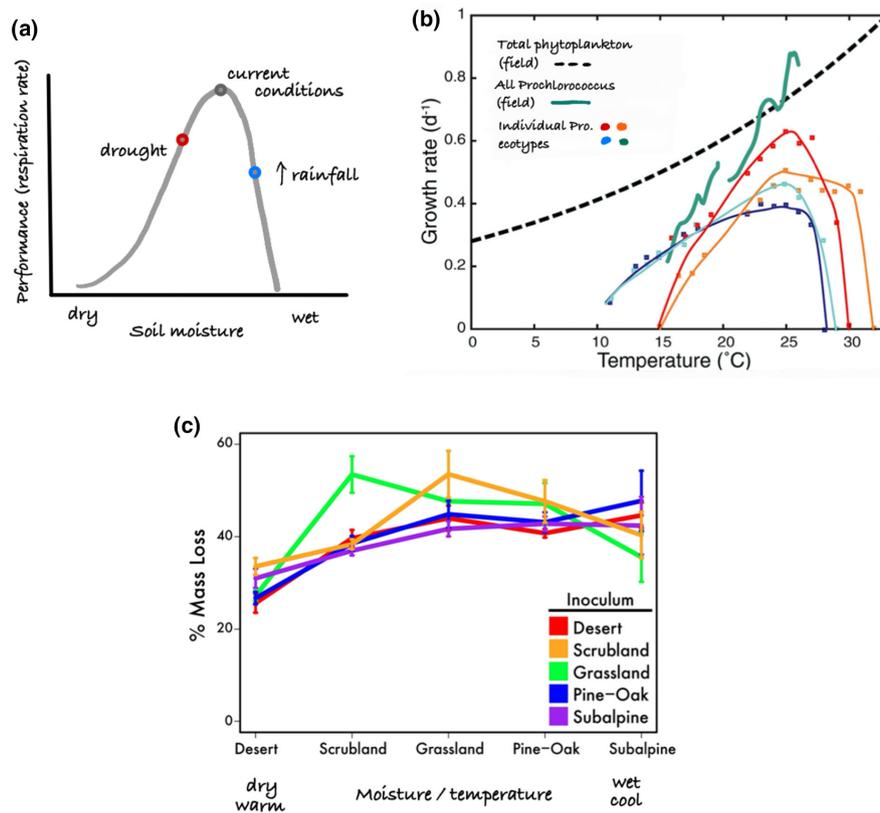
FIGURE 3 (a) Ecosystem models typically assume a static response of microbial performance in response to environmental drivers such as soil moisture (grey line). Respiration is highest under current moisture conditions (grey point) and is predicted to decline under both increased (blue point) and decreased (red point) rainfall. (b) Community performance curves are likely to be flatter than typical reaction norms of one genotype. An example comparing the performance of individual ecotypes of marine *Prochlorococcus* across temperature to that of all *Prochlorococcus* and all phytoplankton across ocean temperature gradients (reproduced from Martiny et al., 2022). Globally averaged growth of phytoplankton communities (dashed black line) appears to follow the so-called Eppley curve, a proposed boundary of maximum growth rate depending on temperature (Eppley, 1972), and the solid green line represents in situ growth rates of *Prochlorococcus* populations along a field transect. (c) An example of how microbiome performance curves can differ spatially. Leaf litter communities collected from five locations display differential decomposition rates (measured by % mass loss) across a gradient of warmer, drier conditions to cooler, wetter ones (redrawn from Glassman et al., 2018).

processes—demography, evolution and dispersal. This would be the case if they occur on the same timescale that the function was empirically assessed. Indeed, if evolution and dispersal happened so fast such that their gains are nearly immediate, then they would be captured by this function. The problem arises if the impacts of these processes have longer-lasting impacts that are not captured by a temporally invariant function (Hawkes et al., 2017; Schimel & Gulledge, 1998).

INTEGRATING ECO-EVOLUTIONARY RATES AND TIMESCALES

The discussion above illuminates two points. First, the processes of physiological acclimation, demography, dispersal and evolution all likely contribute to microbiome functioning. Eco-evolutionary dynamics will thus be central to any response to environmental change. Second, and somewhat paradoxically, if the major contributions of these processes occur simultaneously, then their individual effects could be collapsed into a static function and essentially, ignored. In other words, the fact that microbial evolution (or dispersal or demography) is so fast could mean that we do not have to worry about it.

Future research must therefore address the timescales on which evolution, relative to the other three processes, alters a microbiome's performance. We hypothesize that as a community is exposed to a new environment, its performance curve will change over time, leading to a higher performance than expected relative to the initial, physiological response of a community. For instance, increased drought generally decreases decomposition rates in soil; however, the rate of decomposition will be higher than predicted based on an initial (primarily physiological) response, because of the demographic shift in community composition (Figure 4a). Moreover, we expect that dispersal and evolution will also result in additional performance gains above and beyond that provided by short-term demographic shifts (Figure 4b). If our hypothesis holds, then the dynamics of a microbiome's performance curve will depend on the rates and magnitudes of performance gains driven by demography, dispersal and evolution.

We do have some idea about the rates of demographic change at the broad community level. Although microbial composition shifts quickly in response to environmental change, it is not instantaneous. In aquatic and marine ecosystems, demographic shifts of water column communities in response to changes in water temperature and nutrients seem to occur within weeks to a month (Fuhrman et al., 2006; Shade et al., 2007). In contrast, in soil, legacies of historical climate via the microbial community alter soil respiration and decomposition rates and last months to several years (Evans & Wallenstein, 2012; Hannula et al., 2021; Hawkes et al., 2017; Martiny et al., 2017) and even up to 17 years
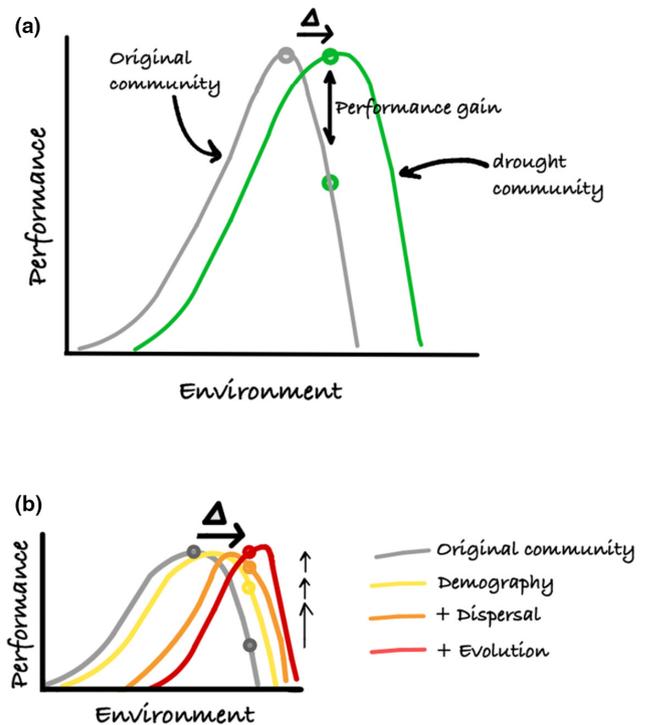
FIGURE 4 (a) Performance gain is defined as an increase along the y-axis when comparing the original and drought-shifted communities under dry conditions. (b) In addition to demographic shifts, dispersal and evolution could further allow the community to optimize its performance to the new environment by contributing to new genetic diversity.

(Bond-Lamberty et al., 2016). Thus, we expect that the demographic response and marginal effects on a microbiome's performance curve in the face of a press disturbance (such a gradual change in climate) will occur relatively quickly but will be faster in marine (weeks) than terrestrial (years) ecosystems (Figure 5, green line).

Compared to demography, we know much less about the rates of dispersal and microbial evolution in natural communities (Barbour et al., 2023). Generally, the dispersal of new strains and taxa into the community will accumulate over time and level off once all diversity has arrived. New colonists might contribute to performance gains under the new conditions if their original environment shares similar conditions. However, the timescale on which microbial dispersal affects biogeochemical processes in the field remains largely unstudied. One study found that blocking microbial dispersal reduced the decomposition of newly fallen leaves for at least a month (Walters et al., 2022).

A key question, though, is how fast dispersal occurs compared to demographic changes. Microbial dispersal is limited in both terrestrial and marine ecosystems, albeit to different extents (Andam et al., 2016). While likely much faster than in terrestrial ecosystems, microbial dispersal in the oceans is not instantaneous (Hellweger et al., 2014; Sommeria-Klein et al., 2021); full mixing of the ocean basins occurs over a thousand years. Based
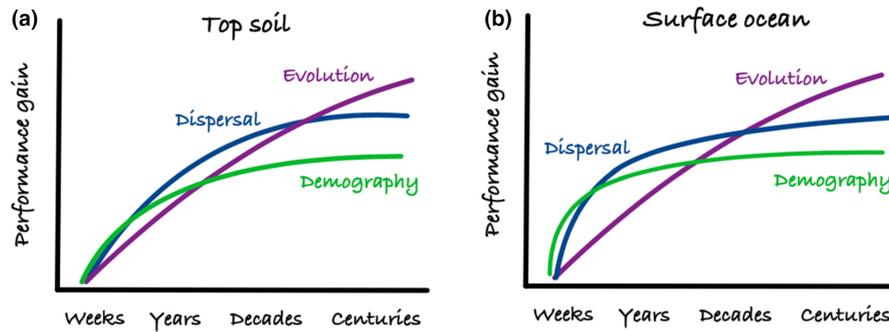
FIGURE 5 Hypothetical performance gains of a microbiome over time in the face of a long-term press disturbance. (a) In soil, demographic gains (green line) will be rapid but saturate at annual timescales. The effects of dispersal (blue line) will contribute higher performance gains as colonists well-suited to the new conditions eventually arrive over many years. Finally, gains from the evolution of new diversity (purple) will initially be small but increase steadily, especially if the new environment does not have a contemporary analogue from which microbes will colonize. (b) In the ocean, dispersal will contribute to performance gains on weekly timescales, reducing the importance of demography relative to the soil.

on recent estimates (Louca, 2022; Walters et al., 2022), we hypothesize that the contribution of dispersal to terrestrial ecosystems will peak much later than for marine ecosystems, perhaps on the order of decades versus months (Figure 5, blue line).

Finally, we are only beginning to document microbial evolution under field conditions, let alone understand the rates of evolution within complex communities. We hypothesize that such changes will initially have a negligible impact on the performance curve relative to the broader taxonomic changes in the community. However, the potential for evolutionary adaptation within the community to the new environment will increase over time as advantageous mutations accumulate (Figure 5, purple line). Evolution may also be particularly important if the changed environment has no modern analogue such that dispersal of a pre-adapted taxon is not possible. Such non-analogous conditions may become increasing common as global change affects many abiotic parameters at once (Williams & Jackson, 2007).

CONCLUSIONS AND OUTLOOK

Eco-evolutionary dynamics are likely occurring in nearly all microbial communities. The processes of physiological acclimation, demography, dispersal and evolution will all contribute to changes in microbiome performance in response to environmental change. Rather than focusing on classifying these responses into ecological or evolutionary categories, we propose that considering how the four processes' impacts on functioning vary at different timescales will be more fruitful. For instance, it seems likely that evolution will contribute most to ecosystem responses on longer timescales, but we will need clever experiments and models to quantify its effects.

The conceptual framework presented here glosses over many complications including interactions and feedbacks between the four processes. For example,

dispersal limitation can contribute to both demography and evolution through ecological and evolutionary drift. Similarly, new genetic diversity through dispersal and/or evolution can modify species interactions/demography (e.g. Fiegna, Scheuerl, et al., 2015; Hansen et al., 2007) and ultimately, influence functioning (e.g. Lawrence et al., 2012; Rodríguez-Verdugo & Ackermann, 2021). Moreover, we only consider one functional outcome at a time, but as has been shown for plant communities (Giling et al., 2019), shifts in microbial diversity may lead to unpredictable responses if there are trade-offs between ecosystem functions (although see, Delgado-Baquerizo et al., 2016). Finally, as mentioned above, the impact of a microbiome on ecosystem functioning is not a direct translation from its overall performance and will be mediated by biological trade-offs of the community's members (Malik et al., 2020; Wallenstein & Hall, 2012).

Although microorganisms are distinctive in their nature, such as their increased ability for HGT, we can think of no reason why a similar framework would not also apply to communities of larger organisms. Certainly, the intricate role of microorganisms in biogeochemical cycling provides ample reason to consider them more explicitly in biodiversity–functioning relationships. All biodiversity, including microorganisms, will increasingly experience more climate variability and extremes. The response of microbial communities and the biogeochemical transformations that they drive will require an integrated understanding of their ecology and evolution.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14209.

DATA AVAILABILITY STATEMENT

No new data were used in the manuscript.

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