Biogeochemistry (2023) 162:285–307
https://doi.org/10.1007/s10533-023-01015-0

SYNTHESIS & EMERGING IDEAS

# Will free-living microbial community composition drive biogeochemical responses to global change?

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Received: 16 August 2022 / Accepted: 10 January 2023 / Published online: 8 February 2023

**Abstract** Microbes carry out many critical biogeochemical transformations in the biosphere such as greenhouse gas production and consumption. Characterizing how microbial communities vary through space and time may hold insights into understanding ecosystem function, particularly as it responds to ongoing climate change. However, it remains unclear to what extent variability in the composition of microbial communities exerts long-term control over biogeochemistry independently of the physiochemical and macroorganismal context in which microbes reside. In this synthesis, we reviewed literature about the versatility and adaptability of microbial communities, and analogous research in medicine, agriculture, and bioremediation. We synthesized data from microbial diversity experiments to determine thresholds at which loss of microbial richness impairs function and compared it to actual microbial richness in nature. The evidence suggests that, in environments such as surface soils, sediments, rivers, lakes, oceans, and the atmosphere, which are open to microbial inoculum and which dominate biogeochemical processes in the biosphere, microbial function equilibrates to environmental conditions over a much shorter interval (days to years) than the time scale on which anthropogenic climate change influences ecosystems (decades to centuries). We conclude that the degree of microbial control over ecosystem processes has been overstated because the correlation of taxonomic information with ecosystem function has obscured the understanding of causality in natural ecosystems. We recommend experiments in which microbial communities are manipulated in ways that allow us to disentangle the influence of microbial community structure from confounding environmental covariates.

**Keywords** Determinism · Historical contingency · Functional redundancy · Microbial biogeography

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## Introduction

Environmental change is altering the structure and function of ecosystems. How ecosystems respond is important because ecosystems can feed back to either exacerbate or moderate environmental change (Bardgett et al. 2008). For instance, climatic warming can alter accelerate soil respiration, which may result in further warming (Zhou et al. 2012). Microbes play a key role in these feedbacks because microbial enzymes catalyze the reactions that underlie many major biogeochemical fluxes, such as the breakdown of organic matter into carbon dioxide and methane (Schimel and Schaeffer 2012). How microbial community structure will play a role in determining future function remains in question. Fundamentally, it is a question as old as microbial ecology (O'Malley 2007).

Encapsulating the prevailing view of functional biogeography of microbes, Baas-Becking (1934) stated that, "everything is everywhere, but the environment selects". In other words, microbes are so ubiquitous and readily dispersed that the potential for the growth of any microbial group is geographically widespread, though the intended meaning has been commonly misinterpreted (Wit and Bouvier 2006). Because identification of microbial phylogeny was rudimentary at the time, "everything" referred not to species or taxonomic units necessarily, but certain microbial traits or functions, e.g. microbes that photosynthesize at high salt concentrations or fix nitrogen in soils (O'Malley 2007).

For decades, Baas-Becking's notion of **environmental determinism**, that local ecosystem-wide microbial function is controlled by the environment, remained largely unchallenged by observation (O'Malley 2007). Relying mostly on culturing techniques to characterize microbial communities, as was done at the time, one finds many of the same functional groups of microbes across a wide array of environments (Van Niel 1949). In the case of cultivation in the lab, the chemical environment of the media determines which microbes grow, but a small amount of soil or water from nearly anywhere has vast functional potential, which overlaps greatly among samples of distinct origin (e.g. Langenheder et al. 2005). For instance, growing inocula in media with hydrocarbons as the sole carbon source yields growth from a vast majority of samples regardless of origin (Buckley et al. 1976), though the abundance of hydrocarbon-degraders varies depending on exposure (Atlas 1991). The lack of clear patterns in microbial biogeography starkly contrasted the biogeography of macroorganisms, which is replete with **historical contingencies**, chance events of colonization or extinction that have lasting impacts on ecosystem structure and function.

The field of ecosystem ecology also grappled with this issue. How do historical contingencies interact with environmental factors to control soil processes? Hans Jenny articulated the "state factors", the fundamental drivers of soil formation as climate, organisms, relief, parent material and time, enshrined in the mnemonic "Cl.O.R.P.T." (Jenny 1941). Since then, ecologists have generally accepted that these forces set into motion the processes that generate soils, but also many other ecosystem properties and functions (Torn et al. 2009; Osland et al. 2018). Jenny (1941) noted that the microbiological component of "organisms" is "nearly identical for all soils" such that it could be ignored as an independent variable among soil forming factors. His view was nuanced in that he accepted that microbial communities may vary from place to place but stated, "the individual microbial populations of each soil within the region are merely the consequence of the great variety of constellations of the remaining soil-forming factors" (Jenny 1941). This appraisal stands in stark contrast to his view on vegetation as a soil-forming factor that must be considered independently from other environmental factors. Jenny also emphasized that, though he did not consider microbes to qualify as soil forming "factors", they were nonetheless fundamental in the study of soil-forming processes. That microbes can be absolutely critical to every process in biogeochemistry and yet unimportant as predictors of function is a key nuance that commonly is overlooked in this debate.

Beginning the 1970s, the molecular revolution allowed characterization of soil microbial community composition independently from the constraints of culturing (Tringe and Rubin 2005). In the subsequent decades, microbiologists described more taxa, by several orders of magnitude, and found variation in the microbial community composition across soil microaggregates (Fröhlich and König 2000; Wilpiszeski et al. 2019), across the globe (Martiny et al. 2006; Fierer et al. 2009), and every scale in between (Myers et al. 2001) as well as through time (Cleveland et al.

2007). The ability to characterize microbial community composition with molecular techniques led microbial ecologists to declare that "everything is *not* everywhere." A google scholar search of "everything is not everywhere" yields 362 papers published between 2000 and 2022 (scholar.google.com, search June 1, 2022). However, in most cases, "everything" refers to phylogenetic units, not to microbial functions (e.g. Ribeiro et al. 2018). Accumulating evidence of microbial biogeographic variation spawned new assertions that, because microbially produced enzymes catalyze many important biogeochemical reactions, biogeographical patterns in microbes should have functional consequences (Rondon et al. 2000; Delgado-Baquerizo et al. 2017).

Recent studies have found evidence that microbial inocula sampled from different places or at different times, not only differ in microbial taxonomic composition but also function differently in sterilized media (e.g. Strickland et al. 2009; Glassman et al. 2018), and suggestions have followed that contingencies influencing microbial composition could have lasting effects as ecosystems respond to climate change (Hawkes and Keitt 2017). Accordingly, the language used to describe microbial interactions has shifted so that microbial communities are commonly said to *drive*, *govern,* or *control* ecosystem function (Carrillo et al. 2017; Delgado-Baquerizo et al. 2017; Singh and Gupta 2018; Glassman et al. 2018; Li et al. 2019; Crowther et al. 2019; Chu et al. 2020; Domeignoz-Horta et al. 2020; Kroeger et al. 2021; Bertolet et al. 2022; García-Palacios and Chen 2022; Averill et al. 2022). It has been argued that changes in microbial communities may have functional consequences that are of similar magnitude and importance as changes in macro-organismal community composition, such as the shift from a forest to a grassland (Crowther et al. 2019). This elevation of status is more than semantic. By logical extension, if microbial communities "control" ecosystem function, then we can use microbial inocula to alter ecosystem function, perhaps as a strategy to mitigate climate change (Hutchins et al. 2019; Jansson and Hofmockel 2020; Averill et al. 2022; Tiedje et al. 2022).

We make the case in this synthesis that microbial communities, owing to their supreme versatility, adaptability and dispersibility, do not vary meaningfully in functional potential within most ecosystems on time scales relevant to climate change. We propose a conceptual model of the hierarchy among state factors, which vary along an axis representing an inverse relationship between adaptability and primacy (Fig. 1). In our view, free-living microbial communities are subordinate to other state factors such as plants, climate and geology that are less flexible and exert more long-term control over ecosystem function. To probe the validity of this model, we:

(I) surveyed literature on how the adaptability of microbial communities allows microbial function to adjust much more rapidly than macroorganisms, organisms that are visible with the naked eye, particularly under changing environmental conditions,
(II) reviewed recent evidence for redundancy of microbial function across taxa
(III) compared results from similar lines of inquiry about the functional importance of microbial biogeography in agriculture, bioremediation, and microbiome research
(IV) provide examples of exceptional cases in which microbial biogeography can exert control over ecosystem function,
(V) discuss how some experiments, when designed with restricted microbial adaptability, can lead to overestimations of the ultimate control of microbial community composition over ecosystem function, and
(VI) suggest experimental approaches to evaluate microbial functional potential.

## I. Microbial adaptability

High functional versatility of microbial taxa compared to that typical of macroorganisms underlies the proliferation of microbes in nearly every niche on Earth where liquid water is available. We submit that this extreme flexibility diminishes the importance of biogeographical patterns in microbial community composition for explaining variability in ecosystem function. In response to a perturbation or colonization of a new environment, individual microbes can respond physiologically, populations can evolve, genes may be exchanged among populations, species may reorder in rank abundance, or communities can exchange taxa with the larger metacommunity. Here, to establish the potential for microbial communities to respond to climate change, we briefly survey the limits of microbial

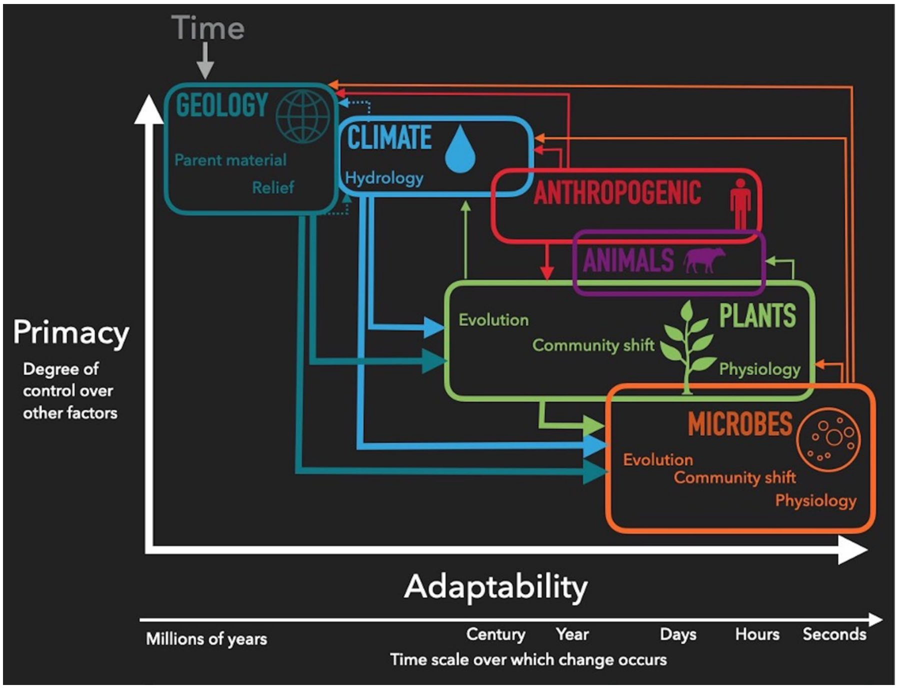

**Fig. 1** Hypothesized hierarchy of how state factors interact to affect current ecosystem function. Factors are oriented along two axes, primacy and adaptability. Arrows represent the unique influence one factor may have that cannot be explained by other factors. For instance, climate change drives changes in plant community composition, such that plants mediate the influence of climate change. Plant responses can also exert a unique influence on ecosystem processes, when communities are in disequilibrium with climate and geology, but plant response is subordinate to climate (lower on the y-axis). Even though microbes carry out many biogeochemical functions, the majority of variability in microbial functioning is attributable to variability in other factors rather than intrinsic properties of microbial communities such as historical contingencies

adaptability across levels of organization from phenotypic plasticity of individual cells to metacommunity dynamics, reasoning that the most adaptable microbes will have the largest impact on the functioning of future communities.

## Individual plasticity

The adaptability of function within the lifespan of individual prokaryotes can be staggering. A single bacterial cell can exhibit greater metabolic versatility than the entire Eukaryotic domain (Narancic et al. 2012; Castelle et al. 2013; Koch et al. 2015). *Rhodospirillum rubrum*, for example, can respire in the presence of oxygen but can also use anaerobic respiration or fermentation in anoxic conditions (Willey et al. 2017). In addition, *R. rubrum* can photosynthesize as a photoautotroph or photoheterotroph if light is present, or it can fix nitrogen if needed, using the unusual catabolic pathway of oxidizing carbon monoxide with water to yield hydrogen. A monocultural soil mesocosm containing only *R. rubrum* could theoretically perform enough components of the carbon cycle to mimic the major aerobic and anaerobic $CO_2$ fluxes on earth. While not all prokaryotes are capable of such dynamism, this level of individual versatility is commonly found in soil microbiomes. Eleven of the 500 most common prokaryotic phylotypes in soils globally belong to the Rhodospirallaceae (Delgado-Baquerizo et al. 2018). The species *R. rubrum* is just one of many taxa known to exhibit extreme versatility (e.g. Shapleigh 2006).

Within the organoheterotrophic strategy, and even within a species, bacteria can exhibit extreme flexibility. Owing to its clinical importance, *Pseudomonas aeruginosa* is one of the most well-studied generalist organoheterotrophs. *P. aeruginosa* alone can degrade materials as varied as leaf litter, plastic, phenol, crude oil, and human flesh (Zhang et al. 2012). This is an additional example of one species of many hundreds or thousands that exhibit extreme generality in function. As discussed below, mixed microbial communities, even in ecosystems with relatively low microbial richness, contain many of these highly versatile organisms that have expansive capacity of microbial function (Ryan et al. 2009; Arai 2011).

### Population adaptability

Prolonged exposure to an environmental stressor that does not kill a population will select for the genotypes suited to tolerate, or even to thrive in the presence of, that stressor. Selection can occur rapidly in prokaryotic populations because of their genotypic variability, potentially fast generation times, and vast numbers (Sauterey et al. 2015; Chase et al. 2021). Mutations provide the variability on which selection can act. Mutation rate in prokaryotes ranges from $10^{-8}$ to $10^{-10}$ mutations per nucleotide site per generation, a rate that relates negatively with effective population size across the domains of life (Lynch et al. 2016). However, there is evidence that the mutation rate itself is subject to rapid selection and may increase in stressful or changing environments (Wielgoss et al. 2013). Box 1 displays a conservative estimate of the mutation rate in one gram of soil.

Long-term microbial evolution experiments have probed the evolutionary potential of pure cultures growing in isolation (Elena and Lenski 2003). Since 1988, 12 initially identical populations of asexual *Escherichia coli* bacteria have been followed for phenotypic and genotypic changes in the evolving populations of 75,000 generations. Generally, the experiments reveal evolutionary convergence. For instance, all 12 lineages increased in cell size in one prominent long-term evolution experiment (Lenski and Travisano 1994). Deterministic evolution suggests that populations will tend to converge functionally under the same conditions. Interestingly, though, one population in the Lenski experiment tended to diverge into variants that filled two separate niches. One variant attuned to efficiently consuming the media, and the other attuned to digesting dead cells (Blount et al. 2018), providing further evidence that populations can rapidly adapt to exploit niches, even if that entails evolutionary divergence within a pure culture.

While the abundance of mutations can fuel substantial adaptation, in many situations, horizontal gene transfer (HGT) may supply the primary source of genetic variability within a population (Larkin and Martiny 2017). Horizontal gene transfer may have been the dominant driver of genetic change for the early era of evolution of life on Earth (Falkowski et al. 2008) and continues to contribute to microbial evolution (Boto 2010). For instance, HGT allows for rapid acquisition of antibiotic resistance among populations in clinical environments (McInnes et al. 2020). While the extent to which microbial populations adapt through HGT in soil environments remains poorly quantified (Nielsen and Elsas 2019), it depends strongly on environmental conditions (Koonin et al. 2001; Aminov 2011). Individual microbial lineages evolve by steady mutation and selection punctuated with leaps afforded by HGT events.

Box 1 How much mutation occurs in soil prokaryotes?

To constrain the potential for mutations to generate variability in actual soils, we estimate the number of mutations occurring in a gram of dry soil per day.

- Bacterial abundance = 1–3 × $10^9$ cells $g^{-1}$ soil (Clark and Kemper 1967)
- Mutation rate $10^{-10}$ to $10^{-8}$ (Wielgoss et al. 2013)
- Generation time in soil from 0.5 to 100 days (Rousk & Bååth 2011)
- Average genome size ~ 6.8 million base pairs (NCBI)

Hence, $10^9$ cells $g^{-1}$ soil × 0.2 divisions $day^{-1}$ x ( $10^{-9}$ mutations / base pairs / division) x (6.8 × $10^6$ base pairs/genome) = 1,360,000 mutations $day^{-1}$ $g^{-1}$ soil.

In contrast, mammalian mutation rate in average germ line cell = 2.2 × $10^{-9}$ mutations base $pair^{-1}$ $year^{-1}$ (Kumar & Subramanian 2002).

Human genome = 3 × $10^9$ base pairs * 1 × $10^{-8}$ mutations per base pair per generation = 30 mutations per generation.

So, everyday there are likely more mutations in a gram of soil than there have occurred in a human's lineage over the past 1 million years.

### Community shifts

Physiological adjustments and evolutionary changes of populations are certainly important for responses to environmental change in pure cultures and for long-term evolution. However, for natural communities, the most important responses to perturbation are often community shifts among taxa because these shifts harness the full diversity present within microbial communities. Immediately upon an environmental change, some taxa will go locally extinct or go dormant while others will be triggered out of dormancy and proliferate (Cleveland et al. 2007; Mackelprang et al. 2011). The extent to which a community can adjust to new conditions, therefore, depends largely on the viable microbial diversity present in that environment or that may be introduced to that environment, both of which are discussed below.

### Metacommunity dynamics

While individual microbes and entire microbial communities can adapt in place through the mechanisms described above, dispersal allows for exchange of microbes among communities. The pool of taxa that could potentially disperse into a given ecosystem is known as the 'metacommunity' (Wilson 1992; Gilpin 2012). Though the dividing line between community and metacommunity is as nebulous as the bounds of an ecosystem, the concept of metacommunity is critical for characterizing mechanisms of microbial response to environmental change. The functional diversity of the metacommunity, by definition, must equal or exceed community and functional diversity of a given ecosystem and can therefore promote rapid adaptation, particularly following a disturbance or environmental change (Sörenson 2020), and especially for closed ecosystems with low endogenous functional potential. So, how many microbial taxa may be delivered to an ecosystem?

Microbes disperse in great numbers over a wide geographic range due to their abundance and small size (Finlay 2002; Choudoir et al. 2018). Dust particles, which may be covered with bacteria, can pass over the Atlantic Ocean in 3 days (Chakraborty et al. 2021). Estimates of global dust emissions range from 1 to 3 Pg $yr^{-1}$ with a mean residence time of particles of about 5 days (Tegen et al. 2004). Hitching a ride with actively dispersing organisms like a migrating bird or human can further accelerate long-distance dispersal of microbes (Table 1, Louca 2022). These forces can deliver large and diverse communities of microbes to distant ecosystems where they can inoculate soils and sediments with the potential to alter community composition and increase microbial functional potential, the sum of all microbial capabilities present (Kellogg et al. 2006).

## II. Diversity and function

Quantifying microbial diversity remains difficult and controversial. Microbes elude conventional species classification systems due to rapid adaptation and modular genomes. Several studies have focused on global microbial richness but with conflicting results; estimates range anywhere from hundreds of thousands to trillions of species (Locey and Lennon 2016; Thaler 2021). Recently, the Global Prokaryotic Census (Louca et al. 2019) integrated hundreds of studies worldwide to estimate 2.2–4.3 million species. However, this extremely high diversity of microbes only has functional consequences if individual lineages perform unique functions, yet there is evidence of great overlap in function among lineages (Louca et al. 2018). Results of metagenomic surveys have revealed great functional redundancy even when taxonomy varies across ecosystems globally (Chen et al. 2022). How many microbial taxa does it take to make an ecosystem operate?

**Table 1** The average bacterial count in different dispersal agents from primary literature sources. Bacteria-like particles (BLPs) range from 0.5 to 5 μm

| Passive dispersal forces | Bacterial count | Study |
|---|---|---|
| Indoor air | $5.4 \times 10^5$ BLPs $m^{-3}$ | (Prussin et al. 2015) |
| Outdoor air | $8.4 \times 10^5$ BLPs $m^{-3}$ | |
| Rain drops | $1.2 \times 10^{22}$–$8.5 \times 10^{23}$ bacterial cells per year | (Joung et al. 2017) |
| Melted snow | $8.4 \times 10^4$ cells $mL^{-1}$ | (Segawa et al. 2005) |
| Aeolian dust particles | $10^4$ to $10^5$ cells $m^{-3}$ air | (Yamaguchi et al. 2012) |
| Reference man: 70 kg and 170 cm in height | $3.8 \times 10^{13}$ cells on the surface of skin | (Sender et al. 2016) |

The biodiversity-ecosystem function (BEF) relationship for macroorganisms has been relatively well-studied, and the consensus is that a certain level of biodiversity is required to sustain ecosystem functions particularly in the face of environmental change (Cardinale et al. 2012). However, we do not know how many microbial types are required to maintain ecosystem functions (O'Connor et al. 2017; van der Plas et al. 2016). Microbes possess a much greater range of enzymatic capabilities than macroorganisms, so we may consider their functional diversity to be higher than macroorganisms, but we also know that microbes exhibit extensive overlap in potential function across taxa, such that there exists a high functional redundancy (Daam et al. 2019). Though microbes execute ecosystem functions such as decomposition and biogeochemical cycling, as well as ecosystem services like bioremediation (Falkowski et al. 2008; de Graaff et al. 2015; Crowther et al. 2019), the diversity-function relationship has not been well characterized for microbes (Zak et al. 2003; Heintz-Buschart et al. 2020).

Here, we synthesized 27 studies that have manipulated or assessed microbial biodiversity in aquatic or terrestrial environments and quantified resulting functional responses (Table 2). We define aquatic hereafter to encompass both freshwater and marine environments. We searched Web of Science for "microbial diversity AND "function" OR "functioning" OR "ecosystem function" OR "functional redundancy". The search yielded about 25,000 ecological studies. From the search results, we ranked studies using the relevance ordering which was based on usage in title, abstract and keywords. We scanned the first 200 results to identify suitable papers, spot checked others beyond 200 for other studies to ensure the relevance filter worked as expected, and added nine studies of which we were already aware. Many microbial BEF studies suggested a direct relationship between diversity and ecological functions, in line with macroorganismal BEF theory where biodiversity loss reduces ecosystem functionality (Balvanera et al. 2006; Delgado-Baquerizo et al. 2016), ecosystem services (Bakker et al. 2019), and carbon cycling capacity (Nielsen et al. 2011). However, many studies indicated the relationship between microbial diversity and function is not as simple as assigning a positive, negative, asymptotic, or neutral relationship and must be understood in context of the local environment (Jung et al. 2016; Zhang et al. 2016; van der Plas 2019; Orland et al. 2019).

We further explored these data seeking the threshold of richness below which function may become impaired. Three of the studies in which microbial richness was manipulated also reported richness in operational taxonomic units (OTUs, Philippot et al. 2013; Maron et al. 2018; Wagg et al. 2019), which

**Table 2** Collection of recent manipulative and observational experiments exploring Microbial Biodiversity Ecosystem-Function (BEF) in soil and marine ecosystems. Studies in bold manipulated diversity

| BEF Relationship | Soil | Aquatic |
|---|---|---|
| Biodiversity related to ecosystem function | **Philippot et al.** (2013)<br>**Wagg et al.** (2014)<br>**De Graaff et al.** (2015)<br>**Maron et al.** (2018)<br>**Schnyder et al.** (2018)<br>**Trivedi et al.** (2019)<br>**Wagg et al.** (2019)<br>**Xun et al.** (2019) | Danovaro & Pusceddu (2007)<br>Leflaive et al. (2008)<br>Galand et al (2015)<br>**Hunting et al.** (2015)<br>Delgado-Baquerizo et al. (2016)<br>**Saleem et al.** (2016)<br>**Santschi et al.** (2018)<br>Schmidt et al. (2017)<br>Galand et al. (2018)<br>Orland et al. (2019)<br>Virta et al. (2019) |
| No relationship or hard to determine | **Griffiths et al.** (2000)<br>**Griffiths et al.** (2001)<br>**Wertz et al.** (2006)<br>**Wertz et al.** (2007)<br>**Jung et al.** (2016)<br>Zhang et al. (2016)<br>Samaritani et al. (2017)<br>Cotta et al. (2019) | **Peter et al.** (2011)<br>**Andersson** (2017) |

we compared to OTU richness for soil environments from the Earth Microbiome Project (Thompson et al. 2017). Ecosystem processes in these studies were not strongly impacted until microbial richness fell below ~ 200 OTUs (Fig. 2). According to global soil richness data from the Earth Microbiome Project, only 16% of soil environments (Fig. 2) have richness below this threshold (Thompson et al. 2017). Importantly, in these studies, richness was determined from one small sample and does not account for potential immigration from the wider metacommunity. Sample processing, sequencing, and core amplicon data analysis were performed by the Earth Microbiome Project (www.earthmicrobiome.org), and all amplicon sequence data and metadata have been made public through the EMP data portal (qiita.microbio.me/emp). The results of our synthesis of recent studies are consistent with previous results showing great resilience of microbial function even with 99% reductions of microbial diversity in some cases (Wertz et al. 2006, 2007).

**Table 3** Examples of closed microbial systems with some combination of restricted dispersal and highly specialized functions

| Studies – environment | Citation |
|---|---|
| Chernobyl bird feather microbiome | Czirják et al. (2010) |
| Volcanic sulfur dioxide | Fujimura et al. (2016) |
| Ultra-acidic lake | Hynek et al. (2018) |
| Antarctic hypolithons- community | Lebre et al. (2021) |
| Icelandic subglacial lakes | Marteinsson et al. (2013) |
| Antarctic hyperarid polar desert soil and hypoliths | Pointing et al. (2009) |
| Microbial evolution in hydrothermal systems | Raymond and Alsop (2015) |

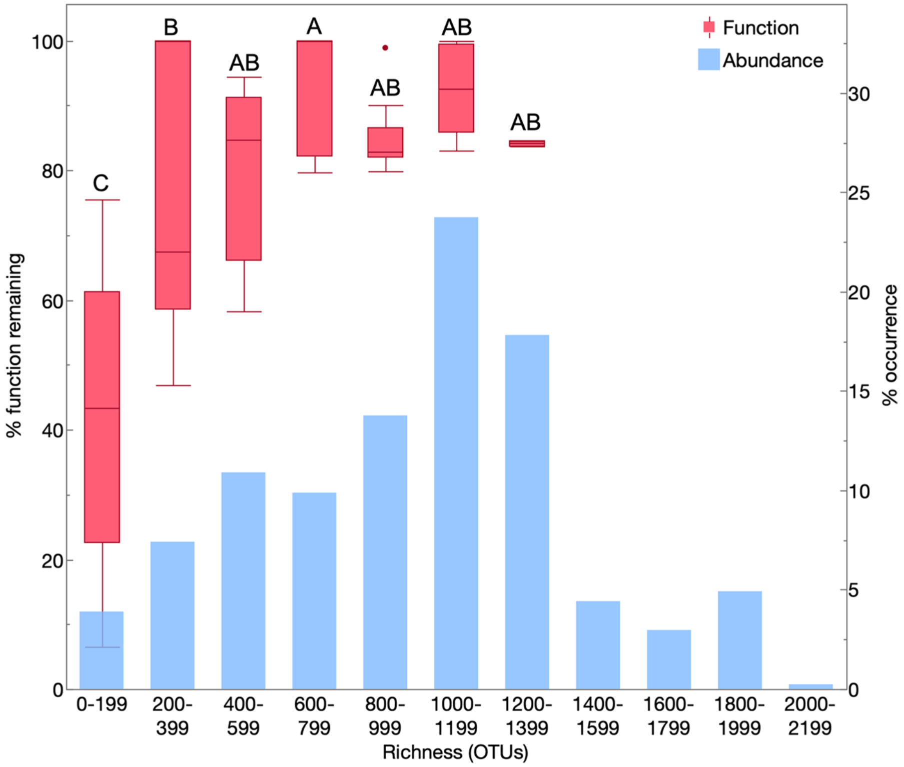

**Fig. 2** The relationship of microbial diversity (expressed in OTUs) and ecosystem function in studies where microbial soil diversity was experimentally manipulated (box plots) and the distribution of microbial richness across soil samples (bars). Microbial % change in function by microbial richness were combined from three studies (Philippot et al. 2013; Maron et al. 2018; Wagg et al. 2019). The distribution of richness (OTUs) in soil and sediment samples were taken from the Earth Microbiome Project (Thompson et al. 2017). Different letters denote significant differences across % function remaining as richness decreases (ANOVA, $p < 0.05$)

Box 2 Case study of soil microbial function in warming soils

In the past few decades, thousands of experiments have addressed microbial responses to soil warming to determine how individuals, populations, and communities will function in elevated temperatures. We explore microbial responses to experimental warming as a case study to compare how microbes respond on multiple levels of organization. Microbial communities adapt to thermal regimes by producing warm-adapted isoenzymes and membrane structures (German et al. 2012; Bradford 2013), but it is not clear how much of this adaptation can be attributed to within-taxon phenotypic plasticity versus evolutionary selection or shifts in microbial community composition. We know that considerable evolutionarily stable adaptation to high temperatures is possible in a pure culture of bacteria within 200 generations or about 1 month in the lab (Bennett et al. 1992). Such results imply that it is feasible for bacteria in natural settings to adopt to climate change.

On the community level, a long-term warming field study showed significant changes in soil microbial community structure, which correlated with population-level shifts such as decreased abundance in dominant taxa (DeAngelis et al. 2015). Such a modification may not be observed with shorter-term experimental warming (Melillo et al. 2002). With reduced abundance of some dominant taxa, less abundant taxa had the ability to fill in niche space. A study of a three-year experimental warming also showed a shift in the bacterial community to favor microbes optimized for the environment under chronic soil warming where the communities increased their minimum temperature for growth (Rousk et al. 2012)

If individual lineages and entire soil communities can respond to elevated temperatures, then *functional* capacity could be shaped by those changes. Ephemeral increases in soil respiration under long-term experimental warming has been observed in field studies (Melillo et al. 2002; Eliasson et al. 2005, DeAngelis et al. 2015). While there is an initial surge in the rate of carbon dioxide release, after several years, the rate declines to control levels, a decline that is attributed to substrate depletion (Kruse

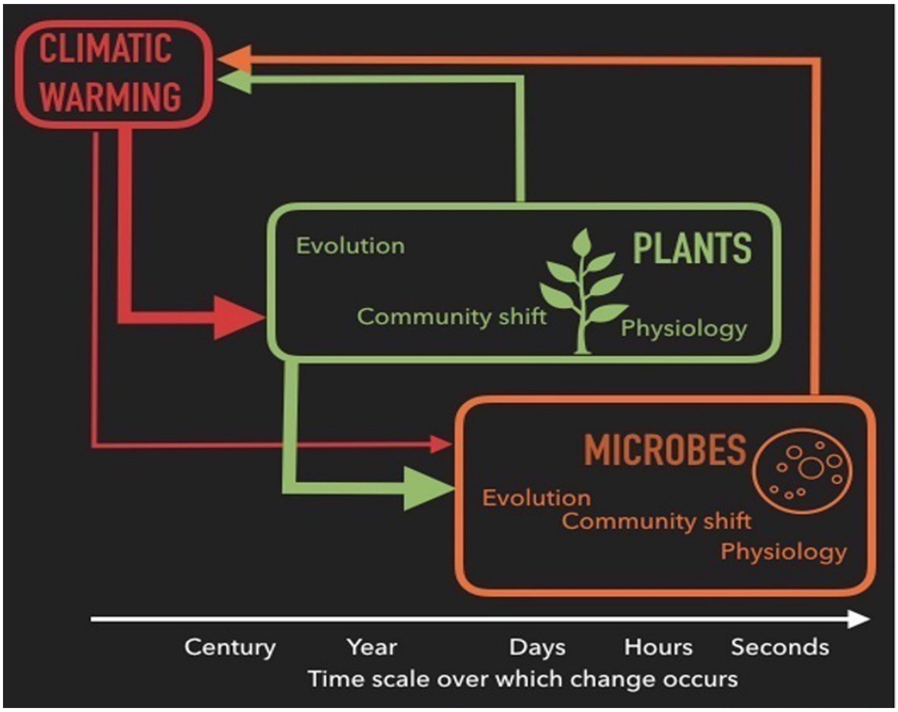

**Fig. 3** Climatic warming will drive direct shifts on microbial communities (thin red arrow). Warming also has an indirect influence on microbes, mediated by its influence on plants (thick red and green arrow). Activities of both plants and microbes can feed back to influence warming over longer time scales (thin green and orange lines). We suggest that over the scale of decades to centuries, the indirect, plant-mediated influence of warming will outweigh the direct influence on microbes

et al. 2013). However, thermal adaptation may coincide with substrate depletion (Allison et al. 2010). Thermal adaptation, likely occurring on multiple levels of organization, allows microbial function to adjust to the new temperature regime. With clear evidence for rapid population-level adaptation and community level adjustment, it is difficult to imagine that microbial function will lag behind thermal regimes that shift over decades. Moreover, the changes in the plant physiology and composition over those decades are likely to exert much stronger effects on carbon cycling, overwhelming direct microbial responses (Fig. 3; DeAngelis et al. 2015; Hautier et al. 2015; Wilson et al. 2021).

## III. Contingent vs. deterministic ecosystems

The composition and function of organisms in an ecosystem result from a combination of deterministic and contingent forces (Blount et al. 2018). The deterministic forces are those that are driven by environmental conditions (e.g. climate, geology, carbon and nutrient availability etc.). If an ecosystem was purely deterministic, we might expect to be able to project future functioning from knowledge of environmental conditions alone. However, stochastic events can modify these abilities. Contingent forces result from stochastic occurrences. An example is penguin distribution. There are northern habitats that, environmentally, could sustain penguins; however, because of unpredictable accidents of evolution, continental drift and poor dispersibility of penguins, they do not. To test this idea, one could introduce penguins to the northern hemisphere. If they take hold, then their distribution is contingent. If they don't then there may be some deterministic environmental reason for their absence. This question frames the present debate succinctly: can we add microbes to ecosystems and change the way it functions?

Here we briefly explore what is known about determinism and contingency in other well researched fields: human microbiome, bioremediation, and agriculture that hinge on a similar question: can you alter the function of the system by introducing novel microbial inoculum? Though we wish to emphasize that each of these fields represents an enormous body of research, each with its own conflicting evidence and ongoing controversies, we argue that in most ecologically relevant cases the likely answer is no. Then, we highlight some exceptional cases from ecology where novel microbial inoculum *is* likely to alter function.

### Case studies about the effectiveness of microbial inoculation

The gut ecosystem shares many similarities with other ecosystems but with a stronger barrier to dispersal. In this case, the focal ecosystem function is healthy digestion including the breakdown of food and uptake of nutritionally required products into the body. Probiotics, microbial inocula marketed as promoting digestive health, represent a suitable test of the influence of contingency in gut ecosystems. Does adding probiotics alter function? Many of the linkages between microbiota and gut function remain correlative (de Vos and de Vos 2012). Environmental conditions such as diet, rather than inoculum potential, dictate function in healthy individuals (David et al. 2014; Zmora et al. 2019), though this relatively young field remains highly controversial. Probiotics have demonstrated some success in treating severe dysbioses, pathological perturbations of the gut microbial community (Goldenberg et al. 2017). For instance, fecal transplants have been effective in treating *Clostridium difficile* infection, a potentially lethal dysbiosis (Hirsch et al. 2015). However, the amount of probiotic inoculum required was immense, roughly one-tenth of the gut microbiome population size (Leahy et al. 2005; Hirsch et al. 2015) and may require multiple applications (Wrzosek et al. 2018). The weight of the evidence at this time suggests that addition of large quantities of inoculum can shape gut microbiome function especially under disturbed conditions. However, it is not clear that the clinical situations in which inoculation can be effective have analogs in open environments like surface ecosystems.

Bioremediation, the use of natural processes and biological agents to degrade environmental pollutants, relies on the notion that we can manipulate microbial activity to control ecosystem function. In small-scale laboratory studies and closed wastewater treatment reactors, biostimulation, the addition of limiting nutrients and bioaugmentation, the addition of microbial inocula, have both proven effective for degrading or neutralizing a range of environmental pollutants, including agricultural pesticides, acid mine drainage, industrial toxins, and crude oil (Johnson and Hallberg 2005; Singh et al. 2008; Mrozik and Piotrowska-Seget 2010; Singh and Borthakur 2018; Bosco et al. 2020). However, the success of bioaugmentation has not translated to open field experiments due to strain death, competition of indigenous microorganisms, and incompatible environmental conditions such as anoxia (Mrozik and Piotrowska-Seget 2010; Nzila et al. 2016; Singh and Borthakur 2018). The vast metabolic potential and flexibility of microbes renders the addition of exogenous microbes redundant because the degradative ability of the target compound is likely already present and maximized by the indigenous community (Mrozik and Piotrowska-Seget 2010; Prince and Atlas 2018). We submit that the same principle holds for free-living microbes and ecosystem function—the initial identity of microbes does not control long-term function nearly as strongly as variability in environmental conditions.

In the context of biofertilizer, the ecosystem function of interest is plant growth and ultimately crop yield. Can we add certain free-living microbes to agricultural soils to liberate nutrients and decrease our dependence on chemical fertilizers (Fasusi et al. 2021)? Biofertilizer has received extensive field attention in the last two decades because of the enormous benefits at stake if farmers can maintain productivity and offset conventional fertilizer application. The conclusions from biofertilizer experiments parallel bioaugmentation studies, though this is a new field of study (Chakraborty et al. 2019). Here again, the effects of added inoculum can be large in artificially closed environments but have not been demonstrated as consistently in the field (Schmidt and Amelie 2018). For instance, agricultural studies of plant-growth promoting bacteria mostly occur in the greenhouse where they show sizable effects on reducing plant sensitivity to drought, but those effects have not translated as clearly to field experiments which hold the greatest relevance for most of agriculture (Rubin et al. 2017). Free-living microbial biofertilizers have limited to no significant impact on crop yield in the field, and overall performance seems to strongly depend on soil conditions, such as pH and innate nutrient availability (Singh et al. 2016; Schütz et al. 2017). The greatest potential for biofertilizers to impact crop performance appears to be through addition of symbiotic microbes, rather than free-living ones, that can produce chemicals to defend against plant pests (Adetunji and Anani 2020; Nayak et al. 2020; Fasusi et al. 2021).

## IV. When and where microbial contingency may matter most in ecology

Soils, sediments, lakes, rivers, oceans and atmosphere account for most biogeochemical cycling on Earth. The ecosystems are also open to free exchange of microbial inoculum. We assert that most of these ecosystems lack consequential variation in long-term functional potential of free-living microbial communities, yet, there remain important exceptions. These exceptional cases are most likely to occur (1) where microbial dispersal is highly restricted, (2) where immigration of inocula requires passage through environmental filters that select only a small subset of microbial taxa, or (3) in the case that the function of interest is highly specialized such that there is low redundancy among taxa (Schimel and Schaeffer 2012).

Where do dispersal-limited systems occur in nature? Interest has been growing in exploring relatively deep soils (Stegen et al. 2013). Owing to restricted dispersal, deep soil microbial communities hold greater potential to vary by contingency (Luan et al. 2020). Particularly, in saturated soils, or permanently frozen soils where advective flow of microbe-carrying fluids is greatly restricted, we expect that rates of microbial immigration to be especially low.

The ecosystems where microbial function is most influenced by contingency are those that exhibit one or more of these characteristics: strong environmental filtering, isolation, and unique biogeochemical functions (Table 3). For example, hot springs or deep-sea thermal vent communities, may be spatially isolated and the conditions therein may exclude most microbes. The types of metabolisms that occur are relatively rare in the immediately surrounding environment. Indeed, an examination of *Sulfolobus* in surface hot springs found that geography explained more variation than the environment in microbial community among springs (Whitaker et al. 2003), though function was not assessed. However, Raymond and Alsop (2015) found phototrophic communities in Yellowstone National Park with strong genomic similarities to communities in Great Boiling Springs, Nevada. Nishiyama et al.

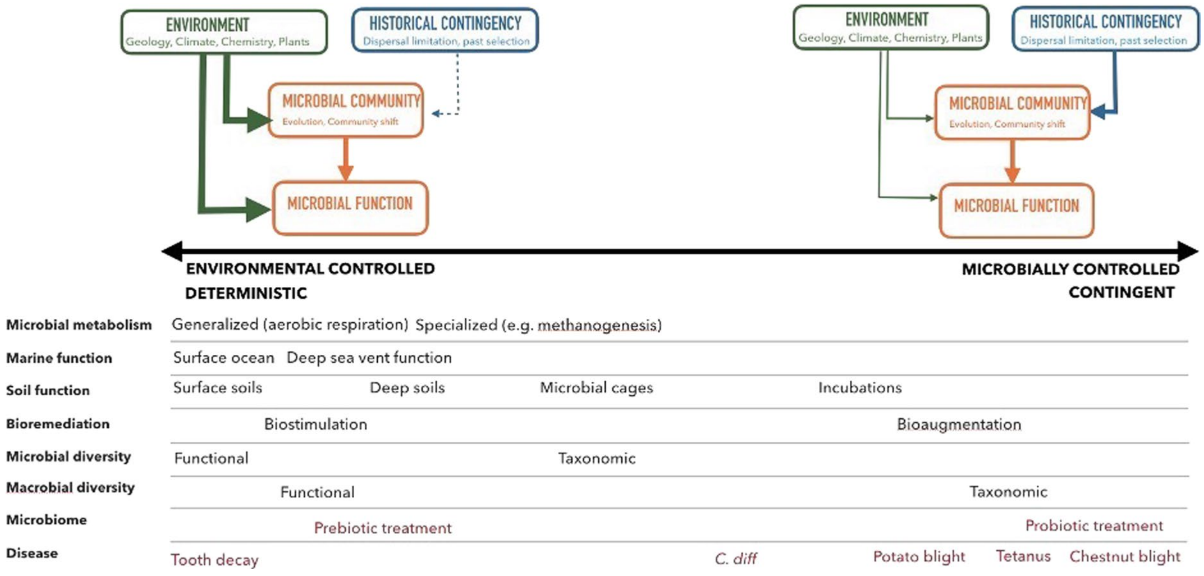

**Fig. 4** The hypothesized relative importance of environmental conditions in explaining variability across several example systems. On the left are deterministic systems, driven by environmental factors. On the right are processes that are influenced by historical contingencies, i.e., the process depends on variability in inoculum potential. Items in red involve mostly symbiotic, not free-living, microbes

(2018) found that hot spring chemistry explained variability in microbial function across nine hot springs in Japan. Therefore, even in specialized hot spring bacteria, which may not be widespread and for which dispersal may be much slower than other microbes (Louca 2022), environmental variability, rather than historical contingencies in microbial biogeography, often still drives microbial function.

Another tangible example that may hold relevance for surface ecology is recovery from catastrophic disturbance. Extreme events such as high-intensity fires or volcanic eruptions can sterilize at least the upper layers of soil (Cutler et al. 2017). The incipient soil communities will be dispersal limited at least for a short time. Recovery of microbial communities from fire is a decadal response, though comparing the importance of confounding environmental drivers (e.g. pH, resource supply) to dispersal limitation is difficult (Xiang et al. 2014; Cutler et al. 2017).

## The analogy of plant and microbial communities

Aristotle inferred the existence of "prime movers", forces in the universe which could influence other entities but remain uninfluenced. Determining causation can get murky in ecology (Fig. 4). That is why early ecosystem scientists set out to define what "prime movers" ultimately drive ecosystem formation, work that culminated in definition of the state factors of Cl.O.R.P.T (Jenny 1941). One of these factors, organisms, begets circular logic (Jenny 1980). Unquestionably, organisms can influence soil formation and ecosystem function, but the composition of organisms also responds strongly to the other state factors. As Jenny (1980) articulated, "The accord fails to divulge what is direct action and what is feedback. Is soil pH the cause or effect of vegetation?" If the activity of organisms is entirely controlled by other factors, then the composition of organisms does not merit separate consideration as a state factor.

Macroorganisms, though, clearly impart an influence independently of the other state factors. Forest species composition can persist for centuries in disequilibrium with the environment owing to human planting or past climate change (Latham and Ricklefs 1993) and exert legacy effects on key soil properties such as soil pH for millennia (Blondeel et al. 2019). While plant communities strongly depend on geology and climate in the long-term, plant community composition and plant function commonly exist in a state that could not be predicted solely by current climate and geology. The analogy of microbial communities to plant-defined biomes (as in Crowther et al. 2019) is flawed because we lack evidence that enduring microbial legacies exist independently from their environmental context.

For a highly contingent example from plant ecology, consider that few plant species can tolerate the harsh conditions in salt marshes. Large areas of a salt marsh may be monospecific or even monoclonal– one genotype may dominate hundreds of $m^2$ (Silander 1979). These clones may exhibit unique traits such as pest susceptibility or tolerance for abiotic stress. Interestingly, the clones may also die all at once, creating large zones of plant die-off (Altieri et al. 2012). That area may remain uncolonized for years and even convert to tidal flats or open ocean (Schepers et al. 2017). So, one could reason that an accident of history, such as a chance dispersal event, can lead to spatial differences in plant composition and function that may control the existence of the ecosystem for millennia. We remain unaware of analogous, highly contingent phenomena in free-living microbial communities. The examples in which historical contingencies in microbial inoculum potential clearly do matter, such as nitrogen fixation in Hawaii (Vitousek and Walker 1989), dispersal-limited mycorrhizal inoculum (Peay et al. 2010), or Chestnut blight (Anagnostakis 1987) all are cases of symbiotic and/or pathogenic microbes. Variation in free-living microbial community composition appears to matter only over the short term, and its importance diminishes through time such that it may be insignificant on the time scale of climate change (Koyama et al. 2018; Finks et al. 2021).

## V. Experimentation

Novel approaches in microbial ecology have greatly advanced the field in the last decade, but some experimental designs may be biased in ways that overestimate the importance of free-living microbial communities in driving ecosystem function. Separating causation from correlation is a persistent difficulty in microbial ecology. Microbial ecologists have examined the role of microbial communities in driving ecosystem processes by incorporating microbial molecular or taxonomic information into models along with conventional physiochemical parameters and comparing their ability to predict function to models that lack microbial information (Allison 2012; Graham et al. 2016). It should be noted that this approach is distinct from incorporating microbial processes or properties, such as biomass, into models (Wieder et al. 2013). In some of these correlative studies, microbial structural information proves valuable and in some it does not.

Typically, environmental parameters are better predictors than taxonomic ones (Liu et al. 2019). For instance, microbial community structure improved models for only 29% of 89 datasets (Graham et al. 2016). Even when microbial community structure does relate to function in models, causality oftentimes remains unknown. Did the microbial community cause the function, or do both simply relate to environmental factors? As the physiochemical data inputs are incomplete and imperfect, microbial genomic data may reflect unmeasured, microscale environmental variability in parameters such as pH, redox, resource quality and resource availability. In fact, microbial community assessment may be the most sensitive and integrative way to characterize the abiotic environment (Kaur et al. 2005, Astudillo-Garcia et al. 2019). Microbial community structure and functions undoubtedly covary through time (e.g. Cleveland et al. 2007) and over environmental gradients (Fierer et al. 2012), but these analyses cannot tell us to what extent differences of changes in microbial community structure *drive* changes in function. To determine causality requires an experimental manipulation of microbial communities.

Soil transplant studies, wherein soil cores or monoliths are moved to new climates, have exhibited stability of microbial communities and in some cases microbial function (Balser and Firestone 2005; Bond-Lamberty et al. 2016) and have been considered evidence that microbial communities can exist in enduring disequilibrium with environmental conditions (Debray et al. 2022). However, in transplanting soil with microbes, these studies conflate the influence of soil microbial communities with the many other environmental factors that may be transplanted in soil such as carbon quality, soil particle size and parent material. We assert that to make conclusions about the influence of microbial communities, one must isolate the microbial community from the slew of confounding side effects that may persist in soil.

A recent wave of experimental studies have manipulated microbial communities to demonstrate the importance of variation in microbial community structure for ecosystem function. While these studies have made tremendous contributions, we argue that they are biased by lacking realism or by lacking the independence of microbial community composition as a factor. Microbial ecologists have performed "common garden" experiments to examine how different inoculum sources function differently (Delgado-Baquerizo et al. 2016; Fukami et al. 2010; Matulich and Martiny 2015; Strickland et al. 2009, 2015; Polussa et al. 2021). For example, Strickland et al. (2009) recovered inocula from three plant species to inoculate litter in sealed vials. While these studies demonstrate that inoculum may differ in functional potential in the lab, vessels that are biologically closed have limitations for extrapolating to the field, where communities would likely be bombarded with new inocula that would tend to equalize functioning among treatments. Moreover, the composition of microbial communities changes dramatically when soil is taken from the field (Drenovsky et al. 2004; Glassman et al. 2018; Bertolet et al. 2022), likely owing to a combination of abiotic and biotic factors. To maximize in situ realism, experimenters have developed techniques to perform similar studies in the field (Wagner et al. 2006).

To examine the differences in functional potential among inocula in realistic contexts, researchers have performed *in-situ* inoculum manipulations using "microbial cages" (Balser and Firestone 2005; Reed and Martiny 2007; Allison et al. 2012; Bond-Lamberty et al. 2016). Microbial cages restrict the passage of cellular microbes but allow passage of water and solutes so that the physiochemical environment may be similar inside and out. Here, too, differences in microbial inoculum have yielded differences in function. For instance, differences in litter inoculum explained 10% of variation in decomposition, while site explained 63% in a litter experiment across a gradient (Glassman et al. 2018). However, sub-micron openings prevent the entry of microbial cells, thereby restricting the introduction of microbial cells far below what would occur in nature (Albright and Martiny 2018). If microbial immigration were allowed to proceed at natural levels, it could overwhelm the initial differences among the inoculum treatments. In restricting the immigration of novel microbes, which is a ubiquitous and important mode of microbial adaptation in nature, microbial cages suffer from the same artifacts as laboratory incubations. Would an inoculum source treatment (as in Strickland et al. 2009) have the same effect on unbottled or uncaged soil? While much has been learned from these innovative inoculum-manipulation experiments, they are likely to lead to overestimations of the importance of functional differences among inoculum sources as the communities are not allowed to adapt by exchanging taxa with the metacommunity.

Another experimental artifact that may lead to the overestimation of the importance of microbial community structure in determining ecosystem response to global change is that nearly all global change experiments impose a step change in treatments while many global change drivers actually change gradually. For instance, elevated $CO_2$ experiments typically increase atmospheric $CO_2$ from ambient to future concentrations immediately in order to simulate conditions in the distant future (e.g. Langley and Megonigal 2010). Few experimenters elevate $CO_2$ gradually to allow for more realistic community responses (as in Klironomos et al. 2005). These step changes may result in overestimation of many ecosystem effects, (Leuzinger et al. 2011) including microbial responses (Klironomos et al. 2005).

## VI. Future directions

Here, we make recommendations for research to help us understand where and when variability in microbial functional potential may influence ecosystem function. Above, we have suggested that future research into the link between microbial community variation may play in determining ecosystem function should be focused on ecosystems, like deep wetland soils, where historical contingency of microbes is most likely to engender enduring disequilibria between environmental conditions and microbial function. Additionally, we argue that new molecular approaches may hold utility not for characterizing microbial functional potential of ecosystems but for serving as bioindicators of microenvironmental variation. Future studies should innovate new approaches, likely involving 'omics techniques with controlled inoculum manipulation, to distinguish causation from correlation more conclusively (Hall et al. 2018).

We recommend that researchers employ experimental designs that explicitly isolate community composition from environmental effects. Typically, common garden experiments employ a "batch culture" approach.

Vials in the lab or microbial cages contain a substrate, often plant litter (e.g. Strickland 2009). As with microbial batch cultures, the initial differences in inoculum will leave a legacy by depleting or chemically altering the substrate. Even if the microbial community adjusts, the chemical differences in the substrate will persist, altering the trajectory of function (Strickland et al. 2009). In this experimental framework, one cannot distinguish inoculum effects from environmental effects. The same problem could affect field-based historical contingency studies (Balser and Firestone 2005; Dickie et al. 2012; Hawkes et al. 2017). As an alternative, serial passage experiments can take the resulting inoculum from one incubation and continuously introduce it to fresh media to eliminate the confounding legacy effects on substrate quality and the chemical environment. This approach could be applied in realistic settings such as soils, amounting to a serial passage experiment for soil incubations. Or, chemostatic approaches that continuously replenish substrates, mimicking more consistent substrate supply in many ecosystems such as rhizospheres can help eliminate confounding environmental variables.

New molecular techniques hold great promise regardless of the nature of the relationship between microbial community and ecosystem function (Vilchez-Vargas et al. 2010). If we could perfectly characterize the physiochemical environment, additional microbial information may not greatly enhance our predictions of future function. However, characterizing the physiochemical environment on a microbial scale remains difficult, particularly in heterogeneous and fluctuating systems such as soil. Microbial metagenomics or transcriptomics may represent the simplest and most effective ways to characterize the physiochemical environment, as has been suggested for soil health (Fierer et al. 2021).

## Conclusions

Microbial ecologists surmised a century ago that the potential for every microbial function is everywhere. In recent decades, a spate of literature has described microbes as “drivers” of ecosystem function, on par with other state factors. This shift in language has important consequences that transcend semantics. If microbial community composition controls ecosystem function, then we can directly manipulate microbial incoula to control ecosystem function, perhaps to mitigate the effects imparted by climate change or help ecosystems adapt to climate change. If instead, environmental variability controls microbial community structure and function, then we need to focus more squarely on proven strategies for global change mitigation and adaptation, which may involve manipulating the environmental controls on microbial functions. For instance, managers may focus on restoring flooding regime in coastal wetlands (Eagle et al. 2022) or reducing tillage (Conant et al. 2007) to boost carbon storage rather than trying to manipulate microbial inocula directly. With limited resources for conservation and restoration, focusing on microbial communities, fascinating as this frontier may be, may divert the attention of ecologists, land managers, and policy-makers. Instead, the attention should center on ecological fundamentals, such as maintaining plant biomass, biodiversity and minimizing soil disturbance, that, along with reducing emissions, we know will help counteract climate change and support biodiversity.

Recent molecular advances have illuminated the extreme diversity of microbial communities compared to macroscopic communities, extensive microbial dispersal abilities, ample functional redundancy, and rapid microbial adaptation to new conditions through physiological adjustment, evolution and community shifts. Extreme versatility is the strategy that has allowed microbes to survive, flourish, diversify and function through mass extinctions that have several times decimated the functional diversity of macro-organisms (Falkowski et al. 2008). This great plasticity allows microbial function to respond to changes in the physiochemical environment, and strong selective forces have necessitated that they do so rapidly. As a result, in surface environments that are open to exogenous inoculum, microbial functional potential varies little with regard to major biogeochemical fluxes. In these environments, the dynamism and malleability of microbial communities generally diminishes the importance of historical contingencies for microbial function compared to macro-organismal function, particularly for processes, like climate change, which occur over timeframes that exceed microbial lifespans.

**Acknowledgements** Thanks to S. Chapman, A. Classen, D. Wagner, K. Wieder and an anonymous reader for helpful contributions to earlier drafts. Thanks to three anonymous reviewers for helpful advice.

**Author contributions** All authors contributed to the study conception, literature searching and first draft. Biodiversity synthesis, analysis and significant revisions of the original draft was performed by PFY, NS and JAL. All authors read and approved the final manuscript.

**Funding** The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

**Data availability** The datasets generated and analyzed for the current study are available in the in the supplemental datasheet.

**Declarations**

**Competing Interests** The authors declare no relevant financial or non-financial interests.

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