A framework for integrating microbial dispersal modes into soil ecosystem ecology

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Abstract

Dispersal is a fundamental community assembly process that maintains soil microbial biodiversity across spatial and temporal scales, yet the impact of dispersal on ecosystem function is largely unpredictable. Dispersal is unique in that it contributes to both ecological and evolutionary processes and is shaped by both deterministic and stochastic forces. The ecosystem-level ramifications of dispersal outcomes are further compounded by microbial dormancy dynamics and environmental selection. Here we review the knowledge gaps and challenges that remain in defining how dispersal, environmental filtering, and microbial dormancy interact to influence the relationship between microbial community structure and function in soils. We propose the classification of microbial dispersal into three categories, through vegetative or active cells, through dormant cells, and through acelluar dispersal, each with unique spatiotemporal dynamics and microbial trait associations. This conceptual framework should improve the integration of dispersal in defining soil microbial community structure-function relationships.

Keywords: soil microbiology, dispersal, environmental filtering, dormancy, community assembly

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1. Introduction

The interplay between microbial dispersal, environmental filtering, and microbial dormancy introduces ecoevolutionary dynamics to soil ecosystems

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that limit our ability to decipher, much less predict, community structure-function relationships. Despite rapid development of high throughput molecular methods, decreasing sequencing costs, and accelerating generation of large ecological data, soils remain messy. This is because soils are massively complex superorganisms with emergent functions that are not yet easily predicted. To inform our predictions of amassed scale effects that determine soil behavior, we need a better understanding of how microbial processes, such as dormancy and environmental filtering, compound dispersal outcomes that transpire to whole ecosystems.

We suggest an adaptable framework for thinking about how microbial dispersal across space and time influences soil biodiversity, and ultimately, ecosystem function. Modes of microbial dispersal are categorized as cellular (*i.e.* vegetative or dormant cells) and acelluar (*i.e.* genetic material associated with viruses and/or gene flow independent of cellular life), where dispersal outcomes for organisms and/or their genes happen across different spatiotemporal scales (Figure 1). Here we discuss the mechanistic constraints of microbial dispersal modes and the interplay between dispersal, environmental filtering, and dormancy. Finally, we propose a traits-based approach for quantifying dispersal outcomes, and suggest how this framework can be used to evaluate soil microbial structure-function relationships.

1.1. Microbial community assembly

To predict ecosystem function from community composition, we first need to understand the community assembly processes that create and maintain patterns of microbial diversity. In both microbial ecology and the broader field of ecology, niche theory and selection-based models have classically explained patterns of community assembly, looking to environmental selection and biotic interactions to define niche space and determine what conditions a species will persist (Chase and Leibold, 2003, Holt, 2009). Alternatively, neutral theory relies on stochastic processes to explain community ecology patterns (Hubbell, 2001, Chave, 2004). Few elements of ecology are an absolute either-or, and mathematical frameworks unify both niche and neutral theory (Harshey, 2003, Mutshinda and O'Hara, 2011). In reality, comprehensive theory explains that variations in community assembly arise through both deterministic and stochastic processes, and that individual processes exist somewhere along a continuum between selection and neutrality (Chase and Myers, 2011).

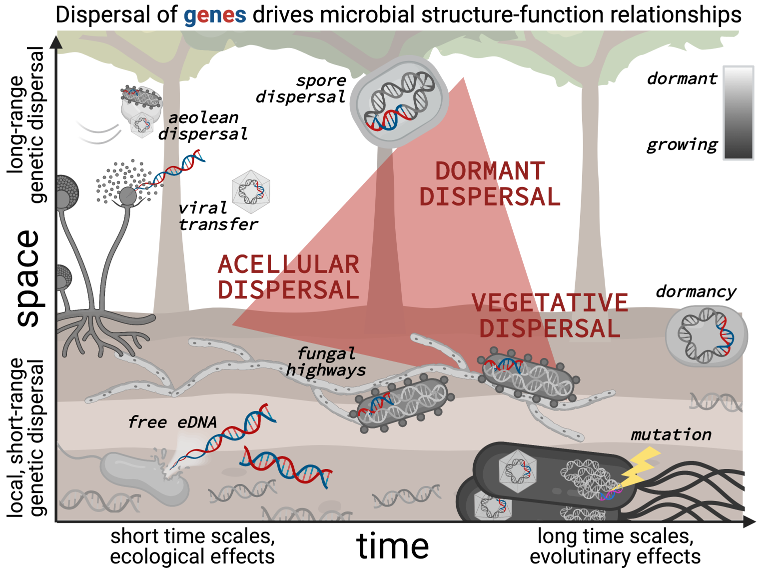

Figure 1: Microbial dispersal modes. Dispersal affects microbial structure-function relationships in soils by distributing genes (*i.e.* potential ecological functions, which are represented here by blue/red DNA fragments) in three primary ways: through active or vegetative cell dispersal, through dormant cell dispersal, and through acellular dispersal. Dispersal can occur at different scales over space and time, and can be independent of environmental filtering and ecological constraints that structure organism-level rules of microbial community assembly. Long-range spatial migration is likely dominated by dormant (*i.e.* spore) dispersal through aeolian deposition, though active cells and viruses also constitute the air microbiome. Local dispersal over short time scales includes viral-mediated genetic transfer as well as uptake of free environmental DNA (eDNA) from soil necromass pools. Cellular dispersal over intermediate spatial scales can occur via fungal highways or vectors including soil arthropods. Over longer time scales, dormancy shapes population genetics by effecting evolutionary diversification processes.

A useful synthesis describes community assembly as a function of the four fundamental ecoevolutionary processes of dispersal, selection or environmental filtering, ecological drift, and diversification (Vellend, 2010). How these same mechanisms extend to microbial biogeography has been eloquently summarized previously (Nemergut et al., 2013, Hanson et al., 2012, Martiny et al., 2006). Much research in the last few decades has quantified the relative contributions of these community assembly processes in microbial systems, see (Stegen et al., 2013, 2015, Caruso et al., 2011, Ofiţeru et al., 2010, Liao et al., 2016). Of Vellend's four fundamental processes, dispersal is the least understood in terrestrial microbial systems and often assumed to be negligible. Due to small cell size, large populations, high potential for dispersal, and a bias for niche-based approaches, the influence of stochastic processes, including dispersal, is historically under-explored in microbial ecology (Zhou and Ning, 2017). We believe that a renewed focus of research efforts on understanding microbial dispersal will advance our understanding of microbial structure-function relationships considerably.

2. What is microbial dispersal?

Dispersal is predominately defined as ”the movement of individuals or propagules with potential consequences for gene flow across space” (Ronce, 2007). Consequently, dispersal entails both dissemination and establishment or colonization, each with unique constraints. But dispersal remains poorly conceptualized for microbes. This is because theoretical frameworks in ecology were historically built on observations of plants and animals, yet it is crucial to apply, adapt, or develop theory that includes the microbial perspective (Prosser et al., 2007). While unification of micro- and macroecology theory seems conceptually attainable, there remain unique aspects of microbial systems, including scaling, microbial species concepts, and gene flow dynamics that continue to impose challenges to reconciliation (Shade et al., 2018, Barberán, Casamayor and Fierer, 2014).

Current sampling methods limit our ability to accurately enumerate soil microbes and their dispersal, though sampling challenges are certainly not unique to microbes (Shade et al., 2018, Elphick, 2008). Perhaps the largest hurdle to quantifying microbial dispersal is counting individuals and species and identifying their presence-absence across sites. For census numbers, direct counts using microscopy has both low feasibility and little resolutions beyond basic cell morphology. Alternatively, quantification using molecular approaches like quantitative PCR of 16S ribosomal RNA (rRNA) genes (or other marker genes) is preferred, although imperfect given biases in nucleic acid extraction, amplification, and uneven distribution rRNA operon copy numbers. More importantly, marker genes lack sufficient resolution to address dispersal patterns of individual species (Choudoir et al., 2012).

Microbial species concepts are well supported with theoretical and empirical data (Achtman and Wagner, 2008, Rosselló-Móra and Amann, 2015, Ward et al., 2008), but practical demarcations of microbial species remain challenging. Gene flow across space and time further obscures microbial population boundaries. Gene exchange dynamics vary greatly between macro and microorganisms, making it difficult to apply macroecology dispersal theory to microbial systems. Furthermore, recombination patterns differ between microbial taxa, with microbes ranging form strictly clonal to wildly promiscuous (Gogarten et al., 2002, Didelot and Maiden, 2010, Jain et al., 2002). This is not to say that quantifying microbial dispersal is unattainable, but it does require careful experimental design and appropriate cultivation-based and/or molecular methods.

2.1. Modes of microbial dispersal

We propose classifying microbial dispersal into three categories, each with unique microbial trait associations and spatiotemporal dynamics: vegetative or active cells, dormant cells, and acelluar or genetic dispersal (Figure 1). This conceptual framework is intended to better integrate microbial dispersal outcomes into community structure-function relationships. We note that molecular ecology methods (*e.g.* 16S rRNA gene amplicon surveys, shotgun metagenomics, whole genome sequencing of isolates) are often exclusively used to infer patterns of cellular dispersal. Thus, we encourage moving away from a strictly cellular framework and towards thinking about dispersal and its consequences for ecosystem function in terms of genetic dispersal, since ultimately, genes underlie functional potential. Finally, we acknowledge that these categories are not mutually exclusive, sometimes overlap, and exist on a multi-dimensional continuum.

2.1.1. Vegetative dispersal

Vegetative dispersal is the movement of growing, physiologically-active microbial cells across space. Vegetative dispersal in soils can be passive or active and occurs at cellular, micro-habitat, and local spatial scales. Sporadic wetting events that saturate soils can induce passive cell dispersal via Brownian motion (Mitchell and Kogure, 2006), but most of the time the soil is an unsaturated and irregular matrix of solid particles and liquids connected by gaseous pores (Or et al., 2007). From the perspective of a single microbial cell the soil is cavernous, and movement across this habitat requires some evolutionary ingenuity. Bacteria and archaea have evolved diverse methods of motility and active dispersal across surfaces including flagellar and non-flagellar swimming, twitching, or gliding mechanisms (Jarrell and McBride, 2008). Social microbes have evolved multi-cellular modes of dispersal like biofilm or fruiting body formation (Harshey, 2003). Hyphal growth in filamentous microorganisms, including some fungi and bacterial actinomycetes, is another form of dispersal that creates mycelial networks (Prosser and Tough, 1991). In additional to a filamentous developmental stage, some *Streptomyces* bacteria assume a newly discovered life stage termed "exploratory growth" which allows cells to rapidly transverse surfaces in response to environmental or biotic signals (Jones and Elliot, 2017, Jones et al., 2017). Although similar in structure to filamentous bacterial hyphae, fungal hyphae are much larger, and in fact bacteria can migrate along these fungal highways (Kohlmeier et al., 2005, Warmink et al., 2011).

2.1.2. Dormant dispersal

Dormant dispersal is the movement of dormant microbial cells across space. Dormancy is an organism's ability to reduce cell function to the minimum allowable energy expenditure, defined as maintenance energy (Pirt, 1987). Therefore, conduits of dormant dispersal are, by definition, passive. Dormancy is reversible, which permits survival during periods of unfavorable environmental conditions. In macroecology, the "temporal storage effect" refers to a mechanism that contributes to species coexistence and depends on varying environmental conditions, competition, and a persistent long-lived state (Chesson and Warner, 1981, Warner and Chesson, 1985). In this sense, we can also conceptualize microbial dormancy as the dispersal of cells through time as well as space. Dormancy has recurrently evolved among microorganisms, manifesting in diverse physiologies which may include morphological differentiation and formation of spores, endospores, conidia, cysts, or akinetes (Lennon and Jones, 2011). Dormancy is also surmised to include "resting states" in which minimal energy is invested only in stopping cell damage or decay, and is usually accompanied by a reduction in size, sometimes called viable-but-not-cultivable (Roszak and Cowell, 1987, Lennon and Jones, 2011). For fungi engaging in sexual reproduction, dispersal of both sexual and asexual spores may be crucial for successful establishment and range expansion.

Soil microbes continuously fluctuate between active and dormant physiological states (Stenström et al., 2001), and these varying stages of resting states is exemplified by the wide diversity of soil microbes that respond within minutes to the first season's rain in a Mediterranean grassland (Placella et al., 2012). This is a demonstration of the taphonomic gradient (Lynch and Neufeld, 2015), an idea which suggests that cellular metabolic state is not a dichotomy of "active" or "dormant", but that microbial activity falls along a gradient from active to dormant to fossilized. Measurements of soil microbes being dormant at any one time range from most (Lennon and Jones, 2011) to almost none (Papp et al., 2018). Modern estimates of dormancy in soils are largely based on the detection of rRNA, and in fact, many papers use the absence of rRNA as an indication of dormancy (Aanderud et al., 2016, Loeppmann et al., 2018, Kearns et al., 2016). The use of rRNA as a proxy for active populations is problematic, as not all taxa degrade their rRNA as they move into dormancy (Blazewicz et al., 2013). This means that certain taxa will retain rRNA even when dormant, which can create a stochastic, or worse, phylogenetically-conserved bias in discriminating between dormant and active microbes. In other words, since dormant cells can include rRNA, the use of rRNA as an indicator of an active state will under-estimate the dormant population in natural systems.

2.1.3. Acellular dispersal

Genetic dispersal is the movement of genes across space that can be independent of cellular dispersal. Acellular dispersal can facilitate the expansion of functional capabilities with ecosystem-level ramifications. For example, genetic dispersal has long been observed for antibiotic resistance genes (Zhu et al., 2019) and microbial virulence factors (Wagner and Waldor, 2002). Viruses are ubiquitous with microbes and are a major source of genetic diversity in natural systems (Correa et al., 2021). Viral-mediated horizontal gene exchange creates a model of dispersal that, while dependent on cellular machinery for replication and transmission, possesses unique spatial and temporal dynamics. New research has demonstrated that viruses are agents of genetic diversity that shape biogeochemical cycling (Starr et al., 2019, Trubl et al., 2018). Viruses direct carbon flows in ecosystems through a top-down manner, in which viral cell lysis increases organic matter concentrations. The 'viral shunt' as a source of fresh organic matter from viral predation has long been appreciated in marine systems, but is also important in terrestrial systems (Hungate et al., 2021). In a study of viral sequences from across a permafrost thaw gradient, authors found that many viruses encoded glycoside hydrolases, some with confirmed activity, targeted at degradation of pectin, hemicellulose and starch. Further, modeling revealed that in almost every case viral abundance predicted pore water dissolved organic carbon, sometimes better than the host abundance (Emerson et al., 2018). Though evidence for viral-mediated genetic dispersal in soils remains somewhat limiting, there is clear precedent for viruses to act as agents of dispersal of genes that can shape the functional capacity of soil microbial communities.

Extracellular relic DNA is abundant and stable in soils (Carini et al., 2016, Lennon et al., 2018), representing a large reservoir of genetic diversity uncoupled from cellular identity. Furthermore, transformation of free environmental DNA (eDNA) by naturally competent soil bacteria (Paget and Simonet, 1994) may represent an under appreciated mechanism of gene flow and introduction of new heritable traits in soil populations. While acellular dispersal is not unique to microbes, it likely plays a much larger role in microbial ecology than it does in plant or animal ecology.

2.2. Long-distance dispersal

Aeolean deposition, or dispersal promoted by the action of wind, can cause dramatic changes in immigration rates of microbes in natural environments. Microbes from terrestrial, marine, and glacial origins were found in the Arctic air microbiome (Šantl-Temkiv et al., 2018), indicating that the atmosphere represents a potentially important channel connecting Earth's bioshperes. Aerial dispersal shapes fungal community structure at local scales (500 m) with strong seasonal trends (Adams et al., 2013). At continental scales, regional climactic and environmental variables shape the distribution of bacterial and fungal taxa associated with settled dust (Barberán et al., 2015). Wind and weather patterns have been connected to microbial migration at global scales (Kellogg and Griffin, 2006, Smith et al., 2013), and in particular, microbes on dust particles originating from seasonal desert storms are associated with transoceanic and intercontinental airborne dispersal routes (Kellogg and Griffin, 2006, Barberán, Henley, Fierer and Casamayor, 2014). Functional attributes related to dormancy are enriched in desert microbes (Fierer et al., 2012), supporting the hypothesis that airborne dispersal is dominated by dormant cells.

Atmospheric viral transmission of genetic material is possible considering estimates of viral particles in the air microbiome. By one account, viral-like particles and bacterial-like particles exist at concentrations of about 10e5 per cubic meter of air, with similar concentrations inside and outside, and a viral to bacterial ratio of about 1.4–1 (Prussin et al., 2015). The enumeration of bacterial and viral particles based on size may have resulted in over-estimating their abundances, but reliably quantifying airborne biotic particles is notoriously difficult (Judith et al., 2020). Further, it is unclear whether the viral constituents of the air microbiome are mostly human-derived, or whether the focus on human health has biased this estimation

(Prussin and Marr, 2015). Most of the work on the viral component of air microbiomes is focused on the built (*i.e.*indoor) environment with an effort to quantify pathogens, so the natural ecology of outdoor particles and their dispersal constraints remain under-explored.

2.3. Vector-mediated dispersal

Finally, microbes can disperse through animals vectors across varying spatial scales. Across intermediate to long-range distances, small mammals and birds are dispersers of arbuscular mycorrhizal (AM) spores (Correia et al., 2019, Mangan and Adler, 2000). At local scales, it's long been appreciated that soil arthropods assist fungal and bacterial dispersal (Ruddick and Williams, 1972, Lussenhop, 1992). A recent study demonstrates that geosmin, a volatile compound emitted by sporulating actinomycetes that smells like fresh soil after the rain, recruited arthropods and facilitated spore dispersal (Becher et al., 2020). Soil arthropods *Collembolans* accelerated the dispersal of antibiotic resistance genes in a controlled experiment, likely indirectly as a result of altered bacterial community structure in Collembolan-inhabited soils (Zhu et al., 2019).

2.4. Consequences of microbial dispersal

Dispersal is a key ingredient for spatial structuring of genetic diversity and population structure. Dispersal is also a unique mechanism as it impacts both ecological (Stegen et al., 2015) and evolutionary (Thompson and Fronhofer, 2019) processes. Dispersal connects local populations with regional pools, and thus dispersal is the important glue connecting metacommunities and facilitating metacommunity dynamics (*e.g.* patch dynamics, species-sorting, and mass effects) (Leibold et al., 2004). For instance, cellular dispersal can influence community ecology by altering local abundance and distribution patterns of community members. As an evolutionary force related to gene flow, dispersal and can increase local diversity through the introduction of novel genetic material or can homogenize genetic diversity at high dispersal rates due to mass effects.

The prevalence of non-random distributions of bacterial species supports the idea that dispersal limitation is an important factor shaping community assembly (Martiny et al., 2006). Dispersal limitation refers to geographic or ecological constraints of dispersal, and in some cases can create distance-decay relationships. Distance-decay relationships are observed in patterns of soil microbial community composition and structure across geographic distances ranging from micro to local to global scales (Albright and Martiny, 2018, Peay et al., 2007, Martiny et al., 2006). The taxa-area relationship is another illustration of dispersal limitation (Horner-Devine et al., 2004, Green and Bohannan, 2006). For instance, isolation by distance (IBD) describes a linear relationship between genetic variation and geographic distance (Wright, 1943), and this pattern is observed in the population structure of the soil microbe *Myxococcus xanthus* (Vos and Velicer, 2008). Biogeography studies in other microbial systems highlight the importance of dispersal limitation on spatial structuring of genetic and genomic diversity (Reno et al., 2009, Peay et al., 2010, Andam et al., 2016, Bottos et al., 2018).

3. Dispersal and its dependencies

The outcomes of dispersal on community function are interdependent on environmental filtering and dormancy dynamics acting at dispersal locations. Stronger environmental filtering reduces perceived rates of dispersal and shifts dispersal outcomes from more stochastic to more deterministic. Dormancy can mitigate environmental selection in heterogeneous or changing habitats, effectively increasing perceived rates of dispersal. In this way, environmental filtering and dormancy are opposing constraints related to dormancy in community assembly processes. However, the variables that dictate dispersal outcomes on soil community composition are still not mapped out to an extent that will facilitate prediction of structure-function relationships in soil.

3.1. Dispersal and environmental filtering

The Baas Becking hypothesis, "Everything is everywhere, but the environment selects" (Translated from the original Dutch: "Alles is overal: maar het milieu selecteert") (O'Malley, 2007) has persisted since its publication in the 1930s because of our continued and growing appreciation for microbial biodiversity and the rare biosphere, with modern high throughput methods still not plumbing the depths of the microbial species catalogue (Lynch and Neufeld, 2015). This hypothesis has been rejected (Papke et al., 2003, Telford et al., 2006) and accepted (Finlay, 2002, Finlay and Fenchel, 2004) for various ecosystems, scales, and populations. At its heart, the Baas Becking hypothesis is a direct test of the relative contributions of dispersal and environmental selection in determining patterns of biogeography. Spatial scale plays an important role, with niche selection functioning at smaller scales and dispersal at broader scales (Wisnoski et al., 2019). The hypothesis of cosmopolitan dispersal has been recently evaluated for genes, and authors found that gene pools show stronger evidence of environmental filtering and lower geographic constraints compared to whole organisms (Fodelianakis et al., 2019).

In a study modeling the interaction between dispersal rates and environmental filtering on microbial communities assembled on different litter qualities, dispersal limitation (defined as less than 25 percent turnover) resulted in high within-group and between-group distances, suggesting a prevalence of stochastic processes (Evans et al., 2017). Community distance decreased in simulations with higher dispersal rates, yet stochastic assembly was more prevalent under conditions of stronger selection, highlighting an important relationship between selection and dispersal. Conversely, drought stress shifted microbial community assembly to more deterministic processes (Chase, 2007). Under scenarios of environmental stress, we can imagine how the consequences of dispersal will also depend on what microbes and their associated traits are dispersing, their relative fitness, and their adaptive potentials.

3.2. Dispersal and dormancy

An accurate estimate of microbial dormancy in soils is critical to understanding how community assembly processes shape soil biodiversity and to extrapolating the impact of dispersal on community function. Seed banks constructed of dormant microorganisms, many of which are members of the rare biosphere, are important contributors to generating and maintaining soil microbial diversity (Jones and Lennon, 2010, Lennon and Jones, 2011, Aanderud et al., 2015). Furthermore, ecosystem models indicate dormancy dynamics are important for predicting biogeochemical nutrient cycling (Stolpovsky et al., 2011, Wang et al., 2015). Dormancy also has the potential to shape population genetics and fundamental evolutionary processes (Shoemaker and Lennon, 2018).

There is a strong theoretical grounding for the hypothesis that dormancy shapes patterns of microbial biogeography by enhancing dispersal, but empirical evidence has been harder to come by (Epstein, 2009). Mestre and Höfer (Mestre and Höfer, 2020) outline a compelling conceptual framework, the Microbial Conveyor Belt, for surmising how dormancy, dispersal, and resuscitation interact to shape marine microbial community structure and function at the global scale. The Theory of Island Biogeography likewise indirectly supports the link between dormancy and dispersal, where modeling exercises show that increasing the dormancy rate (expressed as a dampening of extinction rates over time) increases community richness (Lennon and Jones, 2011). Some of the first direct evidence linking microbial dormancy and dispersal limitation to microbial biogeography shows that dormancy dampens environmental and spatial distance-decay relationships for microbes in forested ponds (Locey et al., 2020). Another recent study found that both resuscitation of local dormant cells and regional dispersal of active cells contribute to soil community resilience following a period of thermal stress (Sorensen and Shade, 2020). This study poses the question, what are the long-term outcomes of dormant versus active cellular dispersal in natural systems?

3.3. Dispersal outcomes on community function

The outcomes of dispersal on community function depend on the interplay between microbial traits associated with dispersers and the strength of local environmental filtering. Dispersal-colonization tradeoffs may structure microbial trait distributions across the spatial and environmental landscape (Smith et al., 2018). In a recent wood decomposition study spanning sites along a forest/non-forest ecotone, dispersal limitation of traits associated with rapid wood-degradation shaped community composition and function such that fungal communities farther from forests decomposed wood blocks more slowly (Smith and Peay, 2021). Independent of forest proximity, there was also a significant negative relationship between alpha-diversity (shaped by stochastic dispersal) and decomposition due to interspecific competition, linking dispersal to independent drivers of community function in this system (Smith and Peay, 2021).

An intuitive hypothesis is that dispersal can mitigate microbial responses to environmental stress by introducing stress-tolerant microbes, but this prediction depends on the regional pool of microbial traits, their adaptive potential, and the extent of functional redundancy. In an experimental evolution experiment, dispersal elevated community growth under ambient conditions but hindered growth in a warming treatment (Lawrence et al., 2016), suggesting that dispersal may dampen the ability of microbial communities to adapt to environmental change by introducing maladapted individuals. In another study looking at the interaction between dispersal and drought, dispersal altered the community composition to a greater extent under drought conditions but also resulted in loss of community function, which was contrary to the hypothesis that dispersal could mitigate drought stress by introducing tolerant microbes (Evans et al., 2020). In a common garden experiment across a natural precipitation gradient, enhanced dispersal had no effect on community composition, which was the strongest predictor of functional responses to changes in moisture (Waring and Hawkes, 2018). However, under certain conditions, dispersal can enhance community stability in the face of environmental change for both acute and more gradual disturbances (Evans et al., 2019, Sorensen and Shade, 2020).

The order and timing of dispersal events can also influence dispersal outcomes. For instance, the release of fungal spores during day versus night influences dispersal longevity and survival (Oneto et al., 2020). Historical contingencies are past biological interactions or environmental conditions, whose order and timing impact the trajectory of a community response. Priority effects are a specific example of a biotic historical contingency where the early or late arrival of a species determines community assembly outcomes (Fukami, 2015). The important of historical contingencies (Hawkes and Keitt, 2015) and priority effects (Sprockett et al., 2018, Hiscox et al., 2015, Svoboda et al., 2018) on microbial community assembly has been demonstrated across a range of habitats.

4. Traits-based approach for predicting dispersal outcomes

Traits are increasingly invoked as the key parameters to understand ecosystem function. Traits include the physiological, life history, and behavioral characteristics of organisms that underlie ecosystem function (Martiny et al., 2015). Because traits more directly relate to ecosystem function, and most traits are phylogenetically conserved to some degree, traits are a valuable tool in linking microbial biogeography to ecosystem function (Green et al., 2008, Nelson et al., 2016, Fierer et al., 2012). Quantification of traits related to dormancy and dispersal should also be valuable to understanding their interaction, but current attempts are hampered by the breadth of traits that contribute to these processes.

For example, range size correlates to genomic and phenotypic attributes of dust-associated microbes, suggesting that these traits may be related to dispersal capabilities (Choudoir et al., 2018). For AM fungi, a recent study showed that small spore size was positively associated with aerial dispersal (Chaudhary et al., 2020), while another study found spore size to be a poor predictor of AM fungal range size (Kivlin, 2020). It's clear we are far from understanding physiological traits that determine dispersal outcomes. Since atmospheric dispersal is important to both plants and microbes, looking to decades of studies in plant ecology for inspiration about traits related to dispersal will likely yield fruitful insights (Thomson et al., 2010, Tamme et al., 2014). Once traits are identified, analyses developed for genome-wide association studies (GWAS) (Eriksson et al., 2010, San et al., 2020) may offer useful insights for identifying genetic variation related to common traits associated with dormancy and/or dispersal.

Ultimately, we need to develop a predictive framework for implementing dispersal traits into changes in ecosystem function. One suggestion is implementation of the response-effect framework (Lavorel and Garnier, 2002), where response traits determine community structure (indirect drivers) and effect traits influence ecosystem function (direct drivers). This framework has been previously applied to fungal systems (Crowther et al., 2014, Koide et al., 2014), and while it can be challenging to parse indirect versus direct effects on ecosystem function, there is predictive power when response and effect traits are correlated. Using this framework, microbial dormancy and dispersal traits are response traits which control microbial community structure directly (and ecosystem function indirectly), as separate from effect traits that govern ecosystem function directly. Another approach could implement a tradeoff framework, such as the yield-resource acquisition-stress (Y-A-S) traits framework developed as a microbial analog to Grime's competitor-stress tolerator-ruderal (C-S-R) framework (Grime, 1977, Malik et al., 2020). For example, dormancy could be invoked as a measure of community stress response. A third approach could implement dormancy or dispersal as a performance filter along an ecological gradient overlaying other system traits (Webb et al., 2010). These frameworks could be high-level conceptualizations to be combined with statistical modeling. For example, the relative contribution of dispersal to ecosystem function can be estimated using generalized nonlinear models, with microbial traits as potential fixed effects screened in model selection. Structural equation modeling (SEM) can be employed downstream to define direct and indirect drivers of ecosystem function.

5. Road map and research recommendations

To improve our predictions of structure-function relationships in soils, we need to apply and evaluate a more precise, yet adaptable conceptualization of microbial dispersal. We propose a reframing of microbial dispersal into active, dormant, and acellular modes. The ecological, spatial, and temporal restraints vary between cellular and acelluar dispersal (Figure 1), with genetic dispersal potentially decoupled from environmental filtering and organismal identity. We are not the first to frame patterns of biogeography through the lens of genetic dispersal. For example, Baltrus (Baltrus, 2020) discusses the dynamics of genetic element dispersal and the contributions to the biogeography microbial pathways. We also encourage researchers to contemplate the limits of this thinking. Can microbial dispersal always be sufficiently represented as genetic dispersal, or is it sometimes more important to consider the individual organisms harboring these genes?

To close current knowledge gaps, we recommend starting with these research directions. First, we need to develop a quantitative theoretical framework that integrates microbial dispersal, dormancy, and environmental filtering. A new model describes the interactions between dispersal and dormancy and outcomes on community diversity across scales (Wisnoski and Shoemaker, 2021). This model considers multiple dormancy traits (*i.e.* survival and germination rates) and how these processes interact with dispersal to create nonlinear effects on metacommunity diversity across local and regional spatial scales. Models that capture dispersal and dormancy dynamics will continue to improve as we better measure these phenomena, both as ecosystem processes and as microbial traits.

Second, we need to develop more accurate methods for quantifying, and accounting for, microbial dispersal and dormancy. Golan and Pringle (Golan and Pringle, 2017) provide a comprehensive framework for considering fungal long distance dispersal that entails mathematical models, genetic inference, and direct quantification based on spore capture. We also need improved tools to quantify genetic dispersal (Brito, 2021). We recommend incorporating dispersal and dormancy explicitly into soil structure-function studies. A typical structure-function analysis neglects the influence of dispersal from a regional pool, and also assumes that all recovered DNA sequences are representative of active (or potentially active) organisms. Incorporating dispersal might mean a no-dispersal or enhanced-dispersal treatment as part of the experimental design, or accounting for new taxa from the atmosphere at regional scales or along fungal highways at local scales. Incorporating dormancy might mean including a resuscitation treatment (*e.g.* bacterial resuscitation factor Rpf, see (Kuo et al., 2021)), or filtering taxa based on microbial activity. Although at present our methods for quantifying active versus non-active fractions are imperfect. If we knew how to differentiate active versus inactive rRNA, we'd be a lot closer to estimating true dormancy rates. Cell-resolved metabolomics might offer a promising solution (Walsh et al., 2018).

Finally, we need to better qualify and quantify traits related to dormancy and dispersal. This may require different strategies for different microbial lineages. For example, identifying a taxon-specific sporulation gene, or an environmental signal that is associated with entering dormancy or the resuscitation of a particular microbe. New research on the homeostasis of ribosomes in *Methanococcus* during energy limitation underscores the need for alternative traits that accompany activity and dormancy (Müller et al., 2021). We as microbial ecologists need to support research that focuses on specific members of a microbial community (*e.g.* revitalization of microbial cultivation efforts (Carini, 2019)). In understanding the trees, we may finally be able to see the forest.

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7. Author Contributions

M.J.C and K.M.D conceptualized and investigated the perspective. M.J.C and K.M.D wrote and revised the manuscript.

8. Declaration of Interests

The authors declare no competing interests.

9. Inclusion and Diversity

One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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