Spatial microbial flows: hidden fluxes of detritus, diversity, and function in meta-ecosystems

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Keywords: community assembly, dispersal, ecosystem functioning, meta-ecosystem, metacommunity, microbial ecology, terrestrial-aquatic linkages

Abstract

Ecosystems are linked by spatial flows of energy, nutrients, and organisms across ecosystem boundaries, forming a meta-ecosystem. The study of spatial flows has typically focused on fluxes of materials (e.g., nutrients or organic matter) and conspicuous organisms (e.g., fish or insects). However, recent evidence from field studies has suggested that numerically significant spatial flows of microorganisms occur across ecosystem boundaries, particularly across the terrestrial-aquatic interface. These spatial microbial flows may be particularly relevant for meta-ecosystem dynamics because the potentially high dispersal rates of microorganisms could exert spatial controls on biodiversity and redistribute microbially mediated ecosystem functions. While understudied empirically, the magnitudes of spatial microbial flows could be quite large in some meta-ecosystems. Estimates of dispersal from terrestrial to aquatic systems have been on the order of 10^{20} bacterial cells per year in some lakes, but microbial spatial flows likely vary widely in strength and direction through time and space, raising questions about their ecological significance. Much of this uncertainty stems from our lack of understanding of the fate and activity of individual microbial dispersers, which are difficult to track and measure *in situ*. Microbial spatial flows could sustain biodiversity and ecosystem functions in recipient ecosystems if dispersers typically have high survival and metabolic activity (potentially sustained by co-transport of available material flows); or they may serve as a spatial flow of materials if survival is lower, primarily having indirect effects on diversity and functioning. The fate of microbial dispersers depends on properties of donor and recipient ecosystems, the biotic and abiotic flows that connect them, and the broader spatial and temporal variation across the landscape. Meta-ecosystem ecology can help further integrate microbial movement into our understanding of ecosystem dynamics at the landscape scale.

Introduction

Ecosystems are open to spatial flows of materials and organisms across their boundaries (Likens and Bormann 1974, Polis et al. 1997, 2004, Gounand et al. 2018b, Harms et al. 2021, Allen et al. 2024). Extensive exploration of the causes and consequences of these flows has coalesced into a set of related perspectives that includes the study of spatial subsidies, terrestrial-aquatic linkages, allochthony, eutrophication, and dispersal. For generality, I will refer to this set of topics by the term "spatial flows" to describe any translocation of nutrients, energy, or organisms from one ecosystem to another (while acknowledging that that these fields address different questions from different perspectives). Spatial flows can occur between any combination of ecosystem types and can lead to a number ecological responses across scales (Gounand et al. 2018a). Spatial flows can form linkages between nearby aquatic (e.g., riverine-to-marine) or terrestrial (e.g., forest and grassland exchanges) ecosystems (Fig. 1), but perhaps the most studied spatial flows are terrestrial-aquatic linkages (Fig. 2). Spatial flows may not necessarily lead to a subsidy if they do not enhance production (Kelly et al. 2014), possibly due to limits on the consumption of resource flows in recipient ecosystems that prevent subsidized production at higher trophic levels (Allen et al. 2024). Spatial flows can exhibit a wide range of variation across time, space, and ecosystem types, but the spatial flows discussed here are broadly applicable across collections of any ecosystem type linked by the movement of materials or organisms.

The collection of ecosystems linked by spatial flows of materials and organisms is known as a meta-ecosystem (Loreau et al. 2003, Gounand et al. 2018a, Guichard and Marleau 2021). Meta-ecosystem ecology has helped synthesize decades of empirical studies on spatial flows within a theoretical framework built on food web ecology, metacommunity theory, ecosystem ecology, and spatial ecology (Massol et al. 2011). In this paper, I argue that meta-ecosystem ecology should build on recent field studies finding that microorganisms often disperse across ecosystem boundaries in nature (Crump et al. 2012, Ruiz-González et al. 2015, Wisnoski et al. 2020, Stadler and del Giorgio 2022). Due to fact that microorganisms have high dispersal rates, exhibit wide metabolic flexibility, and exert disproportionate control over biogeochemical cycles, spatial microbial flows are highly relevant for meta-ecosystems in theory and practice. There have been calls in meta-ecosystem ecology for a more careful consideration of the organisms that consume detritus (Gounand et al. 2014), such as heterotrophic microorganisms. Incorporating these additional spatial flows can generate new patterns and dynamics arising from feedbacks between microbial metacommunity dynamics and fluxes of detritus and nutrients within and between ecosystems.

Microorganisms as mediators of spatial flows

Studies of spatial flows have certainly included a focus on microorganisms, but this focus has primarily been on their ability to stimulate primary and secondary production in the food web. That is, microorganisms in these systems have typically been viewed as transformers of material flows, either in donor systems prior to export or in recipient systems after import (Figs. 1-2, dashed "t" arrows). In lakes, for example, carbon derived from the surrounding terrestrial ecosystem often supports consumer biomass across multiple trophic levels (Carpenter et al. 2005), and can alter water chemistry and ecosystem functioning in ways that may reduce primary production through browning (Solomon et al. 2015). An important pathway by which terrestrial-derived carbon enters aquatic food webs is through bacterial biomass, whereby grazers consume bacteria growing on labile carbon sources and rapidly transfer energy up to higher trophic levels (Berggren et al. 2010). By stimulating bacterial production, spatial flows of carbon can also influence ecosystem functioning through excess respiration (Lennon 2004). Autotrophic and heterotrophic microorganisms can also transform spatial flows of other nutrients like nitrogen or phosphorus, which can support recipient food webs even at great distances between donor and recipient ecosystems (Rabalais et al. 2002). In general, studies from a variety of systems have demonstrated that microbial pathways are critical for processing spatial material flows and making them available to other organisms in the recipient ecosystem (Hall and Meyer 1998, Moore et al. 2004, Jansson et al. 2007, Berggren et al. 2010, Benstead et al. 2021).

The impact of spatial organismal flows on recipient ecosystems may be mediated partly by microorganisms. Dispersal between ecosystems is commonly observed (Leibold and Chase 2018, Guzman et al. 2019, Schlägel et al. 2020). For example, a recurrent, seasonal phenomenon is the emergence of aquatic insects and their subsequent dispersal into nearby terrestrial ecosystems, where they die due to abiotic constraints or are consumed by terrestrial predators (Nakano and Murakami 2001, Gratton and Zanden 2009). These aquatic-derived prey then contribute to terrestrial stocks of living consumer biomass, detritus (as uneaten insects or after assimilation into terrestrial predators), and inorganic nutrients after decomposition by resident microorganisms (Dreyer et al. 2012, 2015). Spatial flows of organisms may be recycled through the food web (if they are consumed), eventually becoming detritus that is processed by microorganisms (Hairston and Hairston 1993, Wetzel 1995). After microbial processing, these resources can then be incorporated into local biomass or contribute to spatial flows of resources across the meta-ecosystem (e.g., Fig. 2, dashed “t” arrows). In this scenario, microorganisms are again playing a processing role, transforming materials before or after translocation across the boundary.

Spatial material flows between ecosystems can be direct or indirect (Gravel et al. 2010), with microbial metabolic pathways playing central roles in connecting different pools and fluxes (Kayler et al. 2019). Direct flows reflect the translocation of inorganic materials between ecosystems. In a direct flow, materials move from donor to recipient ecosystem without being transformed. These translocated materials can then be processed in the recipient habitat by uptake by primary producers. In contrast, indirect flows reflect the translocation of organic materials between ecosystems. In an indirect flow, inorganic materials move between ecosystems bound up in organic materials like organisms or detritus. After translocation, these organic materials must be consumed or decomposed back to inorganic forms in the recipient ecosystem (Wetzel 1995). Both direct and indirect flows are inefficient, resulting in the loss of materials due to sorption (Groeneveld et al. 2020), uptake (Mineau et al. 2016, Peipoch et al. 2016, Tank et al. 2018), or organismal death. Indirect flows may incur additional losses, such as respiration and excretion, due to metabolic processes that consume energy during decomposition or secondary production. Materials may be lost from the entire meta-ecosystem (e.g., respired carbon that is not fixed again within any ecosystem), or they could be reintegrated back into the actively cycling channel by physical or microbial processes.

In these scenarios, microorganisms feature prominently in their interactions with the detrital component of the food webs, serving as an energy shunt up the food web bypassing primary producers. It is often implicitly assumed that the microbial communities that will process incoming spatial material flows are already established, but the composition and functional capacity of microbial communities in recipient ecosystems can vary widely over time and space (Martiny et al. 2006, Hanson et al. 2012). Understanding ecosystem functions then may benefit from studying microbial community assembly processes, which include environmental and biotic filters as well as stochastic processes and dispersal from the broader metacommunity (Fukami 2010, Nemergut et al. 2013, Leibold and Chase 2018, Langenheder and Lindström 2019). While the link between microbial community structure and ecosystem functioning is often complex and difficult to predict (Allison and Martiny 2008, Krause et al. 2014, Louca et al. 2018, Sanchez et al. 2023), dispersal can be an important process in facilitating or disrupting ecosystem functioning in microbial systems (Venail et al. 2008, Lindström and Östman 2011, Székely and Langenheder 2017, Graham and Stegen 2017, Evans et al. 2020, Walters et al. 2022).

Spatial microbial flows: dispersal between ecosystems

Dispersal is a central process guiding the assembly of microbial communities, and in many habitat types, dispersing microorganisms may frequently arrive from regional pools beyond the focal ecosystem (Lindström et al. 2006, Dodds et al. 2020). This cross-boundary movement of microorganisms can be considered as a spatial microbial flow (Figs. 1-2, dashed "d" arrows). Spatial microbial flows are a subset of other organismal flows but are worth distinguishing because of their potentially large magnitudes and ability to translocate taxonomic and functional diversity that can interact closely with material flows. Of course, not all terrestrial-derived bacteria can persist in aquatic ecosystems, and microbial taxa with broader niche breadth or more specialized persistence traits may be better able to survive across ecosystem boundaries than others (Barcina et al. 1997, Wisnoski et al. 2020). Several recent studies have found an abundance of terrestrial-derived bacteria in aquatic ecosystems, suggesting they may contribute substantially to aquatic biodiversity (Crump et al. 2012, Ruiz-González et al. 2015, Hermans et al. 2020, Wisnoski et al. 2020, Caillon and Schelker 2020, Caillon et al. 2021, Stadler and del Giorgio 2022).

Some of the most compelling evidence for spatial microbial flows has come from terrestrial-aquatic linkages in freshwater ecosystems. A series of studies from an Arctic landscape showed that dispersal from terrestrial ecosystems can gradually shape aquatic microbial community structure (Crump et al. 2007). Aquatic microbial diversity resembled the composition of nearby soil communities from the surrounding watershed, and this compositional similarity was highest in aquatic samples near the terrestrial-aquatic interface, suggesting a key role for dispersal (Crump et al. 2012). The localization of terrestrial influence near the terrestrial-aquatic interface may have resulted from the combination of high immigration rates of terrestrial-derived bacteria and the concentrated influx of terrestrial-derived organic matter and nutrients near the interface. Transplant experiments showed that aquatic communities were less productive when grown in inlet water hypothesized to contain more terrestrial-derived materials (Adams et al. 2014). These hypotheses were further supported by more recent work from a temperate region, suggesting spatial material flows interact with microbial dispersal (Bambakidis et al. 2024).

The evidence for spatial microbial flows can also be found at broader spatial extents. Across a boreal landscape of hundreds of lakes, a similar pattern was detected: a gradual transition from dominance by bacteria of terrestrial origin to bacteria of aquatic origin with increased distance from the terrestrial-aquatic interface (Ruiz-González et al. 2015). Terrestrial-derived bacteria were hypothesized to face increasingly strong environmental and biotic filtering with increased residence time in the aquatic environment. This process would gradually select for a bacterial community better suited to aquatic conditions along the hydrologic flowpath (Read et al. 2015, Savio et al. 2015, Ruiz-González et al. 2015, Niño-García et al. 2016). These and other studies have repeatedly found bacteria of suspected terrestrial origin in aquatic ecosystems at local and regional scales, but the processes that regulate their arrival and persistence are still unclear more generally.

A possible mediating factor in colonization success is the metabolic activity of immigrating bacteria. The ability to enter dormancy, a reversible state of reduced metabolic activity that can buffer against unfavorable environmental conditions, is widespread across the microbial tree of life and is an especially common strategy employed by bacteria in terrestrial soils (Lennon and Jones 2011, Lennon et al. 2021). If a large proportion of terrestrial soil bacteria are inactive, their persistence in aquatic ecosystems may be aided by this inactivity. This hypothesis was explored in a survey of bacterial diversity along a terrestrial-to-aquatic gradient in a small, north-temperate reservoir (Wisnoski et al. 2020). Consistent with previous work, many terrestrial-derived taxa were detected in the aquatic ecosystem. Aquatic richness and compositional similarity to soils decreased with increased distance from the terrestrial-aquatic interface, suggesting a role for dispersal. However, many terrestrial-derived taxa appeared to be metabolically inactive, which may have enhanced their ability to persist in a less favorable aquatic habitat (Wisnoski et al. 2020). Contemporaneous work from the same ecosystem has shown that dormancy helps promote persistence of some taxa in the face of seasonal environmental variation, particularly by preserving bacterial diversity in winter (Wisnoski and Lennon 2021). In combination, these two studies suggest that terrestrial-derived bacteria disperse into aquatic systems, survive initially through dormancy, reactivate later, with persistent taxa affecting the recipient aquatic community and ecosystem functioning. Thus, dormancy may alleviate some environmental constraints on successful establishment between donor and recipient ecosystems, expanding the influence of spatial microbial flows.

A broader spatial survey across boreal lakes at higher latitudes found slightly different results. In the boreal system, terrestrial-derived bacteria were not only present in aquatic environments, but also appeared to be metabolically active across much of the region (Stadler and del Giorgio 2022). In this study, terrestrial bacteria made up a dominant proportion of the active bacterial communities in all aquatic ecosystems except for the estuaries. There was also a temporal dimension to terrestrial-aquatic connectivity. High hydrological connectivity during spring increased the relative importance of spatial microbial flows and helped maintain terrestrial-derived bacteria in aquatic ecosystems; this connectivity was diminished during summer months, when reduced spatial microbial flows allowed local environmental conditions to shape aquatic bacterial communities still containing a large proportion of active bacteria of terrestrial origin (Stadler and del Giorgio 2022). Thus, in this example, dispersal was important for providing an initial source, but continued dispersal (and possibly dormancy) may have been less necessary for allowing terrestrial-derived bacteria to persist in the aquatic ecosystem.

I focused on these spatial microbial flows between terrestrial and freshwater ecosystems because they have been explicitly studied in the context of meta-ecosystems, but it is conceivable that similar dynamics play out in other combinations of habitat types that have received less attention (Dodds et al. 2020). When all these studies are considered together, it becomes clear that spatial microbial flows occur in nature and can influence recipient ecosystems, at least in terms of their apparent taxonomic diversity, but the effects of such flows may differ greatly depending on their magnitude, timing, and activity levels. If microorganisms were previously viewed as processers of materials exchanged across the interface, it is now becoming clear that they are also exchanged between ecosystems. The degree to which allochthonous microorganisms process allochthonous versus autochthonous materials remains to be seen, however. A meta-ecosystem perspective could integrate microbial flows and their effects on recipient and source ecosystems at different spatial scales.

A meta-ecosystem view of spatial microbial flows

Now consider spatial microbial flows alongside existing views of material and (macro)organismal flows (Figs. 1-2). An important theme here is the ability of moving microorganisms to not only influence patterns of microbial diversity, but to also perform ecosystem functions that transform local materials, which can have meta-ecosystem scale effects depending on how materials are transformed before or after translocation between ecosystems. A recent framework describes three main ways that spatial flows can impact recipient ecosystem functioning: through functioning by dispersers in the recipient ecosystem, by causing a change in recipient ecosystem diversity and functioning, or by modifying donor ecosystem functions that have consequences for recipient ecosystem functioning (Scherer-Lorenzen et al. 2022). Spatial microbial flows can influence meta-ecosystems through all three pathways.

Microorganisms may play functionally different roles than other consumers typically considered in meta-ecosystems. Microbial communities respond to the local environment, regulate resource availability, and are consumed by higher trophic levels, but their controls on resource availability via nutrient recycling can have different effects on the flow of energy than the primarily consumptive effects of non-microbial members of the food web. Microorganisms regulate many ecosystem functions, such as the decomposition of organic matter and the cycling of nutrients (Falkowski et al. 2008, Krause et al. 2014). The presence of microbial taxa in an ecosystem has the potential to influence internal cycling, but also play a direct role in controlling the products leaving an ecosystem. Microbes may produce certain molecular compounds or otherwise modify the composition of materials that flow into recipient ecosystems (Battin et al. 2008, Liang et al. 2017, Sokol et al. 2022). In addition, microbial necromass itself can constitute a detrital component locally recycled or deposited in recipient ecosystems (Liang et al. 2019). Modifications to the quality and quantity of resource flows can have effects on recipient ecosystem functioning by mediating spatial functional complementarity (Osakpolor et al. 2023, Pichon et al. 2023). When these local controls on material cycles are combined with microbial dispersal, key microbial taxa may track favorable conditions across the landscape and redistribute key ecosystem functions.

Compared to a simplified framework of two coupled ecosystems (e.g., Figs. 1-2), a meta-ecosystem approach has greater generality and flexibility to explore more complex spatial processes (Fig. 3). This is key because spatial flows span a range of spatial configurations (Marleau et al. 2014). These can range from small aquatic ecosystems embedded in a terrestrial landscape (Wisnoski et al. 2020, Caillon et al. 2021, Malazarte et al. 2022), to patchy distributions of many aquatic and terrestrial ecosystems with heterogeneous spatial connectivity across a larger spatial extent (Crump et al. 2007, Ruiz-González et al. 2015, Stadler and del Giorgio 2022). A meta-ecosystem perspective can incorporate fluxes between neighboring ecosystems as well as irregular connectivity networks across multiple ecosystems (Fig. 3). In other words, a meta-ecosystem perspective is flexible enough to study unidirectional subsidies between two ecosystems (e.g., terrestrial-aquatic linkages) as well as connections spanning multiple ecosystem types across a landscape (Soininen et al. 2015, Gounand et al. 2018a, Collins et al. 2020). The combination of organismal and material flows in meta-ecosystems can lead to emergent feedbacks within and among ecosystems that affect diversity and ecosystem functioning at different spatial scales (Marleau and Guichard 2019, Peller et al. 2022). The congruence between microbial diversity and resources could influence functioning and the flow of energy up through the food webs (Kayler et al. 2019). Spatial microbial flows can create external controls on local nutrient recycling (or other functions) regulated by dispersal rates, with microbial colonization dependent on spatial material flows.

Meta-ecosystem controls on microbial fate

One important factor regulating the impacts of spatial microbial flows is the fate of microorganisms after dispersal into a recipient ecosystem (Székely et al. 2013, Wisnoski et al. 2020). If dispersed microorganisms survive, they constitute a spatial organismal flow that could directly interact with the recipient community and modify its functioning (Fig. 4). If they die, they instead serve as a spatial material flow that influences the recipient detrital pool and indirectly shapes microbial and macrobial communities and the ecosystem functions they perform. The fate of microorganisms, and thus the effective impact of spatial microbial flows in the meta-ecosystem, can depend on how spatial material flows and local nutrient recycling influence environmental conditions in the recipient ecosystem. Abiotic and biotic conditions in the meta-ecosystem may inhibit establishment of microbial dispersers, support a persistent population, or maintain a sink population via continued dispersal.

Microbial fate may be influenced by spatial material flows, which vary widely in the type and magnitudes of their effects (Massol et al. 2017, Gounand et al. 2018a). Flows between similar environments (e.g., a forest and a shrubland) may have weaker apparent effects on the underlying spatial heterogeneity since both ecosystems share similar resources, detritus, and possibly diversity, unless flux rates were strongly asymmetrical. Spatial flows between dissimilar environments (e.g., an urban or agricultural region and a nearby estuary) could provide an influx of new potential resources that may fuel productivity, shift community composition, and increase niche opportunities in the recipient ecosystem (Stedmon et al. 2006, Soares et al. 2018, Bambakidis et al. 2024, Crump and Bowen 2024). Consequently, they may have larger consequences for microbial fate. Depending on the strength of these material flows at the meta-ecosystem scale, the landscape could expand or contract in its suitability for dispersing organisms, shifting patterns of diversity and function if material and organismal flows are at least partially aligned in orientation.

Microbial fate also depends on whether dispersing microorganisms consume materials derived primarily from the donor or recipient ecosystem. The composition of dissolved organic matter can structure microbial communities (Muscarella et al. 2019, Bambakidis et al. 2024), and may therefore influence the persistence of dispersing microorganisms. If dispersing microbes primarily consume materials from their source ecosystem, whether they disperse along with materials could determine not only microbial persistence but also energetic fluxes up the food web. Regardless of their origin, bacteria can provide a relatively rapid transfer of terrestrial-derived carbon to higher trophic levels primarily through the breakdown of low molecular weight organic carbon sources (Berggren et al. 2010). More recalcitrant compounds tend to accumulate due to their molecular complexity and because they gradually become too dilute to find, both of which make them inaccessible to heterotrophic microorganisms (Zhang et al. 2018, Kothawala et al. 2021). The supply of accessible compounds could subsidize microbial heterotrophs and help stabilize their populations and functions. It is not clear whether the microbial decomposers responsible for facilitating the transfer of terrestrial-derived organic matter to aquatic food webs are maintained via dispersal from nearby terrestrial landscapes. If dispersal were to contribute to decomposition of terrestrial-derived carbon, this would represent external controls on both biodiversity and ecosystem functioning via coupled microbial and material flows.

Coupling between microbial and material flows (e.g., co-transport) can enhance microbial persistence and functioning in recipient ecosystems. For example, in the Pacific Northwest (USA), red alder leaves fall into nearby rivers and are decomposed by aquatic organisms. Experiments have shown that the bacterial communities involved in this process exhibit consistent successional dynamics that contribute to faster decomposition of leaf litter from nearby trees than conspecific litter from trees located further away (i.e., a home-field advantage), partly owing to the presence of endophytic bacteria in the leaves prior to entering the aquatic ecosystem (Jackrel et al. 2019). In other words, leaves were transported from terrestrial to aquatic ecosystems with their intact microbiome, and this co-transport enhanced recipient ecosystem function (i.e., decomposition). In addition to the co-transport of leaf litter and litter-associated microorganisms (Marks 2019), there are likely many other scenarios where spatial microbial flows are coupled with spatial material flows, but the implications of co-transport across a broader array of meta-ecosystems have not been as well described yet.

Compared to macroorganisms, the fate of microorganisms in recipient ecosystems may be more difficult to predict. Microorganisms may be somewhat flexible in the range of conditions they can tolerate, which may be further complicated by their ability to switch into dormant states. Dormancy could increase the lag time between arrival and growth stage in the recipient ecosystem, which may be useful since dispersal can introduce organisms to environments that are not yet favorable for growth. Interactions between dispersal and dormancy could allow organisms to integrate across spatiotemporal variation in habitat suitability, promoting regional persistence of important taxa (Buoro and Carlson 2014, Brendonck et al. 2017, Wisnoski et al.

2019, Wisnoski and Shoemaker 2022). Inputs of terrestrial-derived materials could further interact with dispersal and dormancy to shape the composition of the metabolically active portion of the bacterial community and overall resilience (Muscarella et al. 2016). In a meta-ecosystem context, these impacts may become more entangled due to feedbacks with the abiotic environment.

The magnitude of spatial microbial flows may also be relevant, as the number of microorganisms exchanged between ecosystems could be high enough to generate persistence (e.g., mass effects). Metacommunity theory has shown that dispersal rates can have strong implications for community structure and compositional differences across the landscape, with high rates of movement having a homogenizing effect on community structure and potentially a detrimental effect on ecosystem functioning (Mouquet and Loreau 2003, Grainger and Gilbert 2016, Thompson et al. 2020). Empirical estimates of microbial flows across the terrestrial-aquatic interface are rare, but evidence suggests they might be quite high, nearing 10^{20} cells/yr. in a large Swedish lake (Bergström and Jansson 2000). This numerically important flux is likely to differ across meta-ecosystems but indicates the potential for many possible colonization attempts arising through microbial linkages.

Landscape context of microbial flows

Meta-ecosystems are distributed across landscapes that vary in their degrees of spatial heterogeneity (Forman and Godron 1981, Pickett and Cadenasso 1995, Biswas and Wagner 2012). With increasing spatial heterogeneity, different ecosystem types are more likely to share boundaries with one another along which spatial flows could occur. Depending on the differences between donor and recipient ecosystems, ecosystem boundaries might represent gradual (e.g., grassland-to-forest) or steep (e.g., terrestrial-to-aquatic) environmental gradients between ecosystems (Terborgh 1971). Landscapes with lower spatial autocorrelation may also have more ecosystem boundaries relative to ecosystem area due to a higher density of interfaces. These ecosystem interfaces may also be sites where the mixing of resources and organisms alleviates resource limitation and increases productivity (Wetzel 1990, Naiman and Décamps 1997, Krause et al. 2017). While not typically considered in patch-based perspectives on meta-ecosystems, interface/ecotone habitats may be important sources of organismal and material flows in the meta-ecosystem. Newer modeling techniques may offer potential ways to incorporate these ecotones into the broader meta-ecosystem (Harvey et al. 2023). The overall spatial heterogeneity in the meta-ecosystem (e.g., between all donor-recipient pairs) is likely to influence the degree of spatial microbial flows at the landscape scale (Mony et al. 2020, 2022).

The mapping between spatial heterogeneity and meta-ecosystem dynamics depends on the spatial configuration of ecosystems across the landscape. Spatial connectivity influences the collection of donor-recipient ecosystem pairs in the meta-ecosystem because similar ecosystems may have stronger or weaker connectivity depending on their distribution on the landscape and the network of spatial flows that connect them (Little and Altermatt 2018, Peller et al. 2024). Likewise, once the spatial network of connectivity is determined, spatial flows can vary in direction (e.g., unidirectional, bidirectional, reciprocally alternating) and magnitude depending on the processes that generate them (Nakano and Murakami 2001, Bartels et al. 2012, Leroux and Loreau 2012, Fritz and Whiles 2021). Given the primary vectors of microbial dispersal (Comte et al. 2017, Custer et al. 2022, Choudoir and DeAngelis 2022, Grupstra et al. 2022, Chaudhary et al. 2022), the directionality of microbial flows may track the directionality of major air currents, hydrological flowpaths, and animal/plant movement in relation to meta-ecosystem structure on the landscape.

Ecosystems also vary through time in several properties that contribute to microbial community dynamics. Fluctuations in temperature, resource inputs, salinity, or other factors can drive fluctuations in the suitability of recipient ecosystems for successful colonization by dispersing microorganisms. More spatially synchronous environmental fluctuations may promote direct spatial microbial flows that contribute to diversity and ecosystem function in recipient habitats, supported by dispersal from the donor system. Such spatial synchrony can promote spatially synchronous fluctuations in ecosystem functioning, which could be a destabilizing process for regional-scale ecosystem functioning (Wang and Loreau 2014, 2016, Lamy et al. 2021, Patrick et al. 2021). With respect to timing, spatial flows could be pulsed (Anderson et al. 2008, Piovia-Scott et al. 2019) or occur at a steady rate (Walters et al. 2018), spanning a range of possible amplitudes, frequencies, and regularity. Depending on spatial flows and local fluctuations, ecosystems could go through phases of spatial synchrony and asynchrony at different timescales (Walter et al. 2017, Luo et al. 2021). The timing of exchanges relative to the growth and survival rates of organisms that depend on these flows could be relevant because pulses that are too short or infrequent to affect either donor or recipient ecosystem may have minimal effects in the long run.

Open questions

Many questions remain about the viability, long-term persistence, and functional contributions of externally derived microorganisms in recipient ecosystems. There are also opportunities to merge ideas from the meta-ecosystem framework with complementary insights from the community coalescence framework, which focuses on microbial and environmental mixing (Rillig et al. 2015, Mansour et al. 2018, Rocca et al. 2021, Custer et al. 2024). In addition, analytical approaches from movement ecology may be helpful for considering how fluxes of individuals scale across space and organizational hierarchies, aggregating individual movement into implications at the community and ecosystem scales (Wisnoski and Lennon 2023). These perspectives differ in their scope and range of processes but will likely yield new insights for a more microbially compatible meta-ecosystem ecology.

A major outstanding question relates to whether microbial spatial flows are large enough to have measurable impacts on recipient ecosystems. In the case of terrestrial-derived microorganisms in aquatic ecosystems, one might ask whether bacteria maintained by dispersal from the watershed help decompose complex forms of organic matter and cycle carbon back into higher levels of the aquatic food web. Meta-ecosystem experiments (Scherer-Lorenzen et al. 2022, Châtillon et al. 2023) may help uncover the conditions under which eliminating microbial spatial flows may reduce functioning locally and at the meta-ecosystem scale. To understand these functional implications, it will be important to better characterize the fate of microbial dispersers across a range of donor-recipient ecosystem pairs, investigating temporal dynamics, microbial compositional shifts, and multiple ecosystem functions.

Another open question is how variable spatial flows are across space and over time and how such variability affects microbial community dynamics and meta-ecosystem functioning. Early descriptions are primarily snapshots in time and patchily distributed across space (but see Hermans et al. 2020). There may be predictable sources of variation, such as the seasonal variation in hydrological flow that regulates connectivity. For example, river flood plains go through phases of connectivity with nearby ecosystems (Junk et al. 1989), stream networks expand and contract within the watershed (Stanley et al. 1997, Benda et al. 2004), and intermittent ecosystems exhibit phases of spatial isolation (Datry et al. 2014, Butterworth et al. 2023). At broad spatial extents, there may be geographic patterns in the degree of spatial flows between ecosystems (Montagano et al. 2019). Anthropogenic modifications to the landscape may also be introducing long-term shifts in spatial flows over decadal scales, for example, by decreasing connectivity between adjacent ecosystems and severing spatial flows (Wesner et al. 2020). Data collected from a variety of ecosystems can be used to describe variation in the magnitude and directionality of microbial flows, which can influence the range of phenomena analyzed in meta-ecosystem models to generate novel predictions.

Conclusions

The aim of this paper is to describe a potentially overlooked organismal spatial flow in meta-ecosystem ecology arising from cross-boundary microbial dispersal. Microbial spatial flows seem to be common at the terrestrial-aquatic interface, where a substantial portion of aquatic microbial diversity appears to be derived from surrounding terrestrial ecosystems. Across a more general range of ecosystem types, the functional implications of microbial spatial flows are likely to depend on the metabolic activity of allochthonous microorganisms in relation to the local ecosystem conditions that regulate functioning. These can be further modified by other spatial flows across the landscape, which likely depend on spatial configuration of ecosystems and their connectivity, temporal variation within and between ecosystems, and the magnitude and direction of dispersal vectors. Many open questions remain to understand the importance of microbial spatial flows in different ecosystem types, and these questions may be addressed with simulation models and creative lab and field experiments.

Acknowledgments

This project was paid for with federal funding from the U.S. Department of the Treasury, the Mississippi Department of Environmental Quality, and the Mississippi Based RESTORE Act Center of Excellence under the Resources and Ecosystems Sustainability, Tourist Opportunities, and Revived Economies of the Gulf Coast States Act of 2012 (RESTORE Act). The statements, findings, conclusions, and recommendations are those of the author(s) and do not necessarily reflect the views of the Department of the Treasury, the Mississippi Department of Environmental Quality, or the Mississippi Based RESTORE Act Center of Excellence.

Author contributions

NIW conceived of the project and wrote the paper. NIW declares no conflicts of interest.

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Figure captions

Figure 1 – A meta-ecosystem containing two similar ecosystem types with an explicit microbial community. Within each ecosystem, inorganic nutrients (N) are consumed by primary producers (P) and microorganisms (M), both of which are consumed by grazers (G), which are then eaten by carnivores (C). All biotic components contribute to detritus (D). Detritus is converted back into inorganic nutrients at a rate that depends on the composition of the microbial community (dashed “t” arrow). Between ecosystems, spatial flows occur between all compartments (dashed arrows), where microbial dispersal (dashed arrow “d”) relates to the movement of individual taxa between each ecosystem, with each taxon contributing to ecosystem functioning (decomposition rate, shown here).

Figure 2 – A meta-ecosystem containing two contrasting ecosystem types with an explicit microbial community. Within each ecosystem, inorganic nutrients (N) are consumed by primary producers (P) and microorganisms (M), both of which are consumed by grazers (G), which are then eaten by carnivores (C). All biotic components contribute to detritus (D). Detritus is converted back into inorganic nutrients at a rate that depends on the composition of the microbial community (dashed “t” arrow). Between ecosystems, spatial flows (dashed arrows) directly link non-living components (detritus and inorganic nutrients). However, due to dissimilarity between ecosystem types, survival of primary producers, grazers, and carnivores is low, so spatial flows contribute directly to the detrital pool in the other ecosystem. Microbial dispersal (dashed arrow “d”) relates to the movement of individual taxa between each ecosystem, with each taxon contributing to ecosystem functioning (decomposition rate, shown here). Some taxa can survive dispersal across the ecosystem boundary, joining populations in the recipient ecosystem, but

other taxa may not survive and instead get shunted into the detrital pool, where they are then recycled at rates that depend on microbial community composition (dashed “t” arrows).

Figure 3 – Complex spatial configurations of aquatic and terrestrial ecosystems linked by spatial material flows (blue and green arrows) and spatial organismal flows (black arrows). Depicted here is simply an example of the type of connectivity one might observe. (A) A meta-ecosystem representation of the connectivity shown across the landscape in panel (B). Material flows may be aligned with microbial flows or not. Biotic and abiotic components are linked by microbial functions (dashed arrows) that transform materials within ecosystems and allow them to by transported in organic or inorganic forms.

Figure 4 – The fate of microbial dispersers in recipient ecosystems relates to the functional implications of spatial microbial fluxes in the meta-ecosystem. If dispersers survive and remain metabolically active, then they are likely to contribute to contemporary ecosystem functioning. If dispersers survive but remain metabolically inactive, then they exist with the potential to contribute to functioning at some point in the future, should they survive until conditions are more favorable. If dispersers die, they become detritus and do not contribute directly to functioning (but may indirectly support ecosystem functioning as a substrate for decomposers).

Figures

Figure 1.

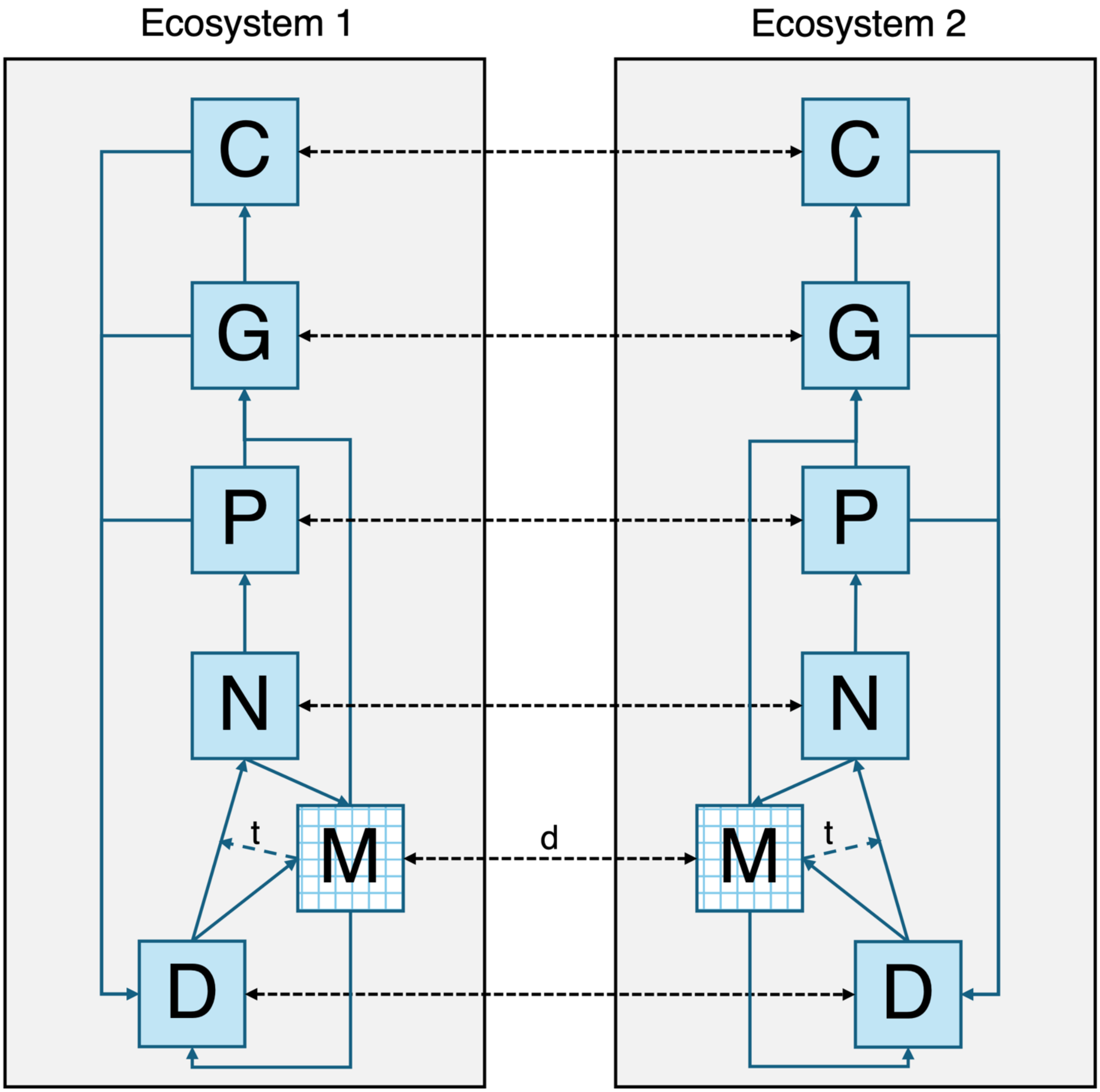


Figure 2.

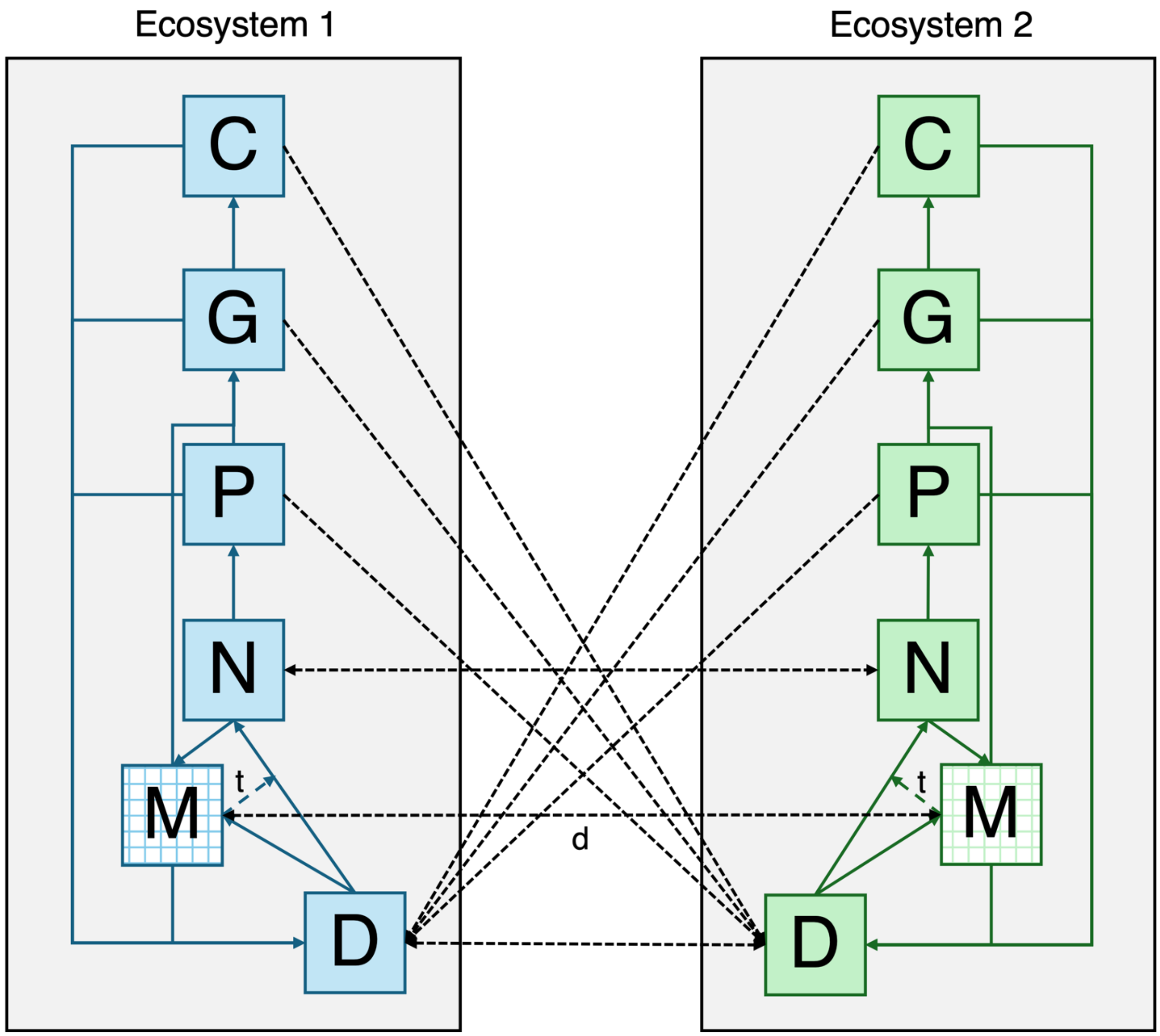


Figure 3.

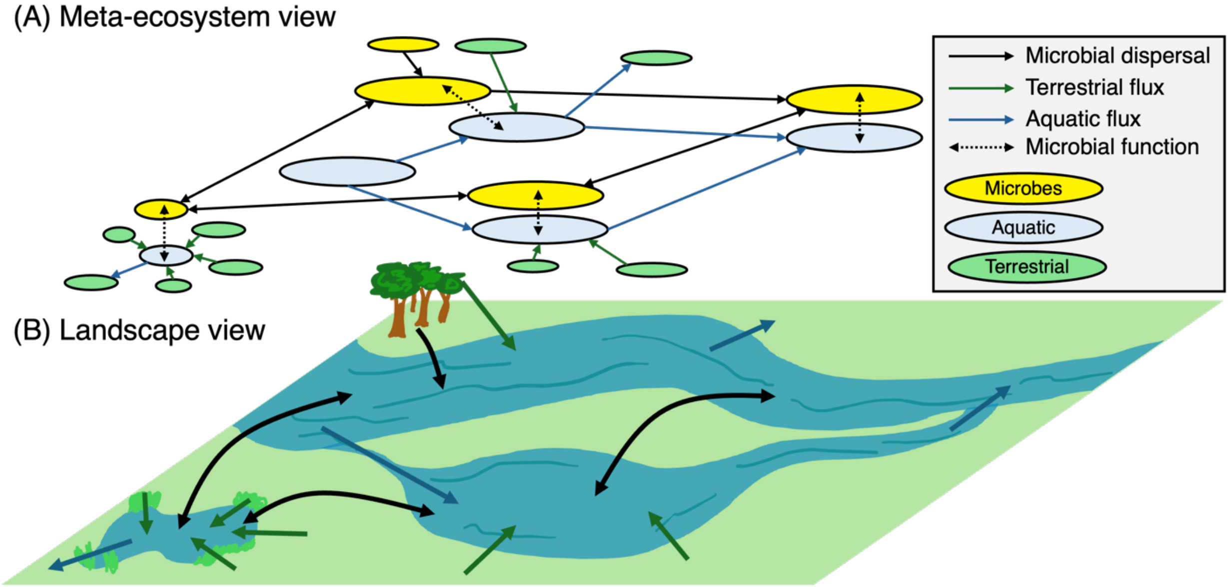
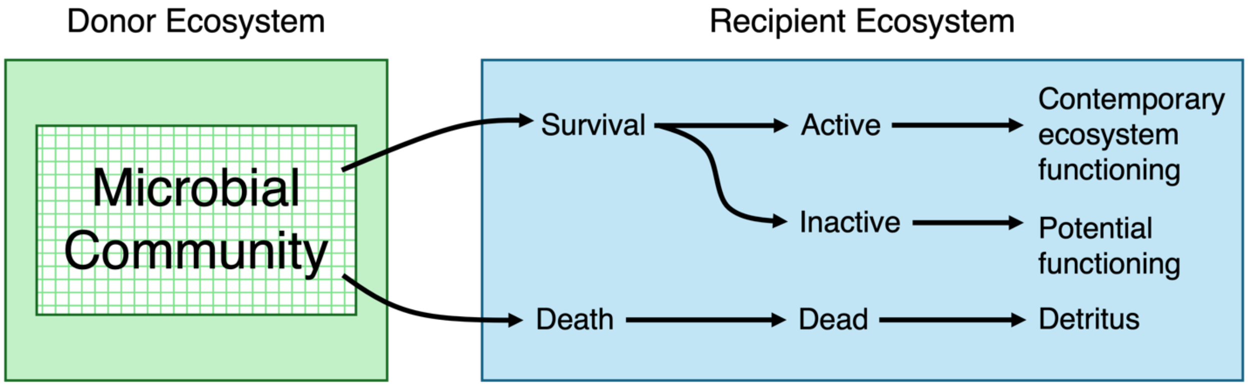

(A) Meta-ecosystem view
Microbial dispersal
Terrestrial flux
Aquatic flux
Microbial function
Microbes
Aquatic
Terrestrial
(B) Landscape view

Figure 4.



Donor Ecosystem
Microbial Community
Recipient Ecosystem
Survival
Active
Contemporary ecosystem functioning
Inactive
Potential functioning
Death
Dead
Detritus