


Application of the microbial community coalescence concept to riverine networks

India Mansour^{1,2,3,*} , Catherine M. Heppell³, Masahiro Ryo^{1,2} and Matthias C. Rillig^{1,2}

¹*Plant Ecology, Institut für Biologie, Freie Universität Berlin, D-14195 Berlin, Germany*

²*Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany*

³*School of Geography, Queen Mary University of London, London E1 4NS, UK*

ABSTRACT

Flows of water, soil, litter, and anthropogenic materials in and around rivers lead to the mixing of their resident microbial communities and subsequently to a resultant community distinct from its precursors. Consideration of these events through a new conceptual lens, namely, community coalescence, could provide a means of integrating physical, environmental, and ecological mechanisms to predict microbial community assembly patterns better in these habitats. Here, we review field studies of microbial communities in riverine habitats where environmental mixing regularly occurs, interpret some of these studies within the community coalescence framework and posit novel hypotheses and insights that may be gained in riverine microbial ecology through the application of this concept. Particularly in the face of a changing climate and rivers under increasing anthropogenic pressures, knowledge about the factors governing microbial community assembly is essential to forecast and/or respond to changes in ecosystem function. Additionally, there is the potential for microbial ecology studies in rivers to become a driver of theory development: riverine systems are ideal for coalescence studies because regular and predictable environmental mixing occurs. Data appropriate for testing community coalescence theory could be collected with minimal alteration to existing study designs.

Key words: microbial ecology, fungi, bacteria, hyporheic zone, estuary, headwaters, metacommunity, meta-ecosystem, network.

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* Address for correspondence (Tel: +49 30 838 53146; E-mail: india.mansour@gmail.com).

I. INTRODUCTION

Lotic ecosystems hold some of the richest biodiversity on the globe (Tockner & Stanford, 2002; Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010). River systems are particularly unique as hierarchical dendritic networks of ecological corridors, influenced by directional connectivity that links processes across scales longitudinally, latitudinally, and vertically (Ward, 1989; McCluney *et al.*, 2014). Local aquatic communities are influenced by the interaction between local habitat conditions and factors at the regional scale (Heino, 2011), such as interactions with adjacent riparian ecosystems and material and energy transport within dendritic networks from upstream to downstream. These processes are driven by the temporally dynamic nature of river discharge (Poff *et al.*, 1997), maintaining spatio-temporally heterogeneous microbial community structures.

Microorganisms play fundamental ecological roles in rivers: they are largely responsible for decomposition, drive biogeochemical cycles, interact intimately with both macroscopic organisms and the abiotic environment, degrade pollutants and serve as the base of brown food webs. Through their growth and activities microorganisms exert an influence on all the assessment criteria laid out by the Water Framework Directive that determine the ecological status of a river, namely biological, hydromorphological (e.g. Mardhiah *et al.*, 2014), physicochemical and chemical characteristics. Despite their essential functions, microbial groups comprise only a small percentage of lotic ecological studies since publication of the paradigm-shifting River Continuum Concept (Vannote *et al.*, 1980; Tornwall *et al.*, 2015).

Microbial communities occupy many habitats in riverine ecosystems. In the water column, microorganisms can be free-living bacterioplankton or associated with particulate matter or flocs that provide a heterogeneous habitat and a carbon source, and are sites of high activity (Crump, Baross, & Simenstad, 1998). Organisms inhabiting the water column will be passively moved by flows of water, downstream or into the hyporheic zone for example, where they will encounter other microbial communities. Microbial communities also inhabit benthic and hyporheic sediments, typically forming biofilms (Besemer, 2015; Battin *et al.*, 2016).

Metacommunity theory has been applied to explain lotic community assembly from a multi-scale perspective (Tornwall *et al.*, 2015). This framework is concerned with the dispersal of organisms from a regional pool of diversity to local communities (Leibold *et al.*, 2004). Traditionally, it has been applied to fairly distinct local communities connected by the movement of organisms, seeds or propagules. It has the advantage of integrating regional- and local-scale dynamics, but there are limits and challenges in applying this framework to describe the complexity of biotic patterns in riverine systems (Brown *et al.*, 2011; Liu *et al.*, 2013). Some theoretical advances have been made to expand the application of metacommunity theory to dendritic networks (Brown *et al.*, 2011; Altermatt, 2013). For example, dendritic structures drive higher spatial heterogeneity in community

composition than lattice-cell structures (e.g. terrestrial and lentic systems) (Carrara *et al.*, 2012). While these advances improve predictions about community assembly in dendritic networks, they are still notoriously unpredictable (Altermatt, 2013). The current theoretical framework may be critically lacking to adequately incorporate the movement and mixing of abiotic factors, which often move over similar spatial and temporal scales as microbial communities, and is restricted to the mechanisms occurring within the watercourse while neglecting interactions with adjacent environments (e.g. environmental mixing across ecosystem boundaries).

Rillig *et al.* (2015) proposed a novel ecological framework for environmental microbial assemblages involving a multi-scale approach appropriate for the complexity of microbial community assembly in lotic systems. The concept, community coalescence, is an emerging paradigm unique to microorganisms that considers the wholesale mixing of multiple communities and their surrounding environments, which can occur on a regular or intermittent basis and within an abruptly short period of time (even within a few seconds). Associated biotic and abiotic fluxes (e.g. flowing water carrying a microbial community, carbon resources, and nutrients) are considered simultaneously as interactive predictors of the observed local microbial community structure.

Thus community coalescence asks the same question as metacommunity theory (how do local communities assemble given fluxes of community members across the landscape?) while taking a metaecosystem perspective [what environmental flows and subsidies (*sensu* Polis, Anderson, & Holt, 1997) are occurring in this system?] to ultimately understand how, where, and when entire habitat patches, and their associated microbial communities will collide and what resulting environment and community might arise (Fig. 1). Thus it is in line with theoretical work (Logue *et al.*, 2011) that has called for an integration of meta-ecosystem dynamics into metacommunity studies. However, it is noteworthy that immediate wholesale mixing of communities rarely happens to larger organisms and that community coalescence can occur both within a single ecosystem and across ecosystems, distinguishing community coalescence from metacommunity and meta-ecosystem theory, respectively.

Since the publication of meta-ecosystem framework in 2003 (Loreau, Mouquet, & Holt, 2003), it has been applied to riverine networks – particularly to explain carbon dynamics (Battin *et al.*, 2009; Larned *et al.*, 2010). When flows of organisms are included in meta-ecosystem studies, they are often broadly classed as ‘organic matter’ or ‘nutrient sources’ rather than described with the phylogenetic and functional precision necessary to understand compositional and trait-space changes following their dispersal – rather this is the territory of metacommunity theory. While meta-ecosystem theory is concerned with dynamic resource flows across the landscape, metacommunity studies often consider abiotic conditions to be static in a local habitat and consider dynamic biotic flows across the landscape. By contrast, the community coalescence concept is concerned with the alteration of both biotic and abiotic components as

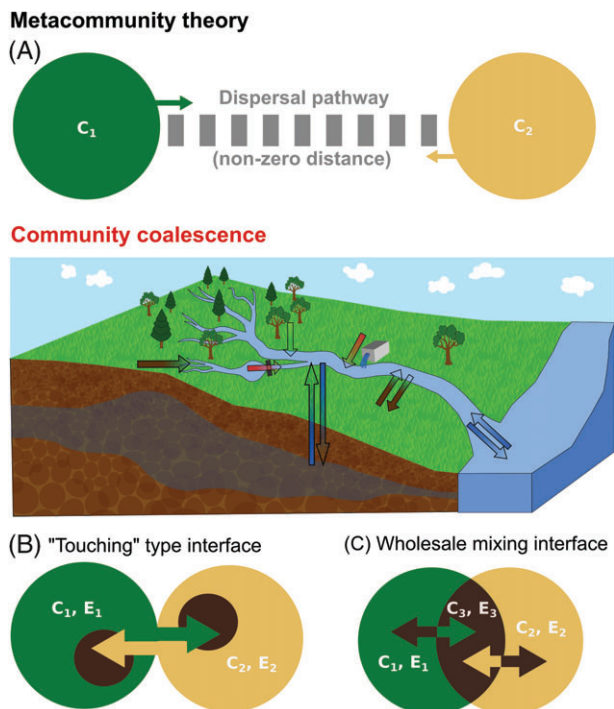


Fig. 1. A generalized visual scheme for community interactions in space. C_i represents different communities (each with a different species composition) and E_i represents environmental constituents, consisting of various resources or other abiotic factors. Metacommunity theory (A) envisages that exchanges are a subset of C_i (i.e. a few species move by dispersal rather than entire communities), and it does not consider movement of environmental factors (E). On the other hand, during community coalescence entire patches collide and all biotic (C_i) and environmental (E_i) components mix. Depending on the types of environmental pieces that are mixing, communities and environmental constituents may initially contact one another through a 'touching' type interface (B) or in a wholesale mixing scenario (C). This mixing is driven by environmental flows, illustrated by multicoloured arrows in the landscape (blue: hydrological flows; green: biological flows; red: anthropogenic flows; brown: precipitation-driven flows).

a result of environmental mixing and in turn, the resultant changes in the microbial community.

The community coalescence concept has been theoretically developed using a top-down (communities as integrated units) modelling approach (Tikhonov, 2016). It has also been experimentally applied in restoration ecology: deterministic processes were found to drive coalescence outcomes in a soil microbial community transplant study (Calderón *et al.*, 2016). An investigation of microbial dynamics in anaerobic digesters found that mixing multiple methanogenic communities increased methane production efficiency, and that the most efficient initial community dominated following community coalescence (Sierocinski *et al.*, 2017). In rivers, consideration of mixing of entire microbial communities has been lacking as an explanation for community assembly, even though interchange between several environmental bodies, including surface water, groundwater, soil, leaves,

wastewater plant effluent, and saltwater – and the microbes inhabiting them – occur on a regular basis. Thus, riverine systems are apt for theoretical and experimental application of the community coalescence concept.

Herein we present a holistic view of microbial community assembly in rivers and floodplain habitats through the lens of the community coalescence concept and discuss hydrological, chemical and physical characteristics that drive or could influence the outcome of the coalescence event. First, we discuss community coalescence events along a longitudinal gradient from headwaters to estuaries. The second part takes a cross-sectional view of the river and considers environmental mixing resulting from lateral and vertical flows (e.g. floodplain to/from river and groundwater–surface water interactions). Lotic hydrologists and ecologists have previously utilized similar hydrological frameworks for theoretical work (Vannote *et al.*, 1980; Boulton *et al.*, 1998) and study designs (Savio *et al.*, 2015).

Community coalescence in riverine systems may include a broad range of organisms, including but not limited to prokaryotes, viruses, fungi, diatoms, algae and protists (e.g. Livingston *et al.*, 2013) because of their size in relation to the environmental components that they inhabit. The scope of this review has been limited to only bacteria, archaea and fungi. We were interested in studies investigating microbial community dynamics in zones of mixing in rivers or streams. To target these studies, we conducted a systematic review. First, we made an *a priori* list of potential mixing zones based on river ecology and hydrology (i.e. headwaters, litter fall, etc.) and searched for field studies investigating microbial community structures in these compartments or during these events (e.g. flooding, litter fall). Search strings used were: bacteria OR fungi OR archaea OR microbial AND river OR stream AND community AND [compartment/event] in *Google Scholar*; the literature search concluded in December 2016. We excluded review papers, theoretical works and laboratory/mesocosm-based experiments. With this subset of field-based studies, we further applied criteria to determine if the minimum requirements to study community coalescence were met (i.e. reporting the community composition of both initial communities as well as the resultant community) and if so, whether evidence was found supporting the occurrence of community coalescence. Results of the 79 studies (see online supporting information, Table S1) included in this review are presented in Figs 2 and 3. It is noteworthy that few fungal studies met the criteria to make inferences about community coalescence (Fig. 2), and that a sixth of the 79 studies met these criteria and provided evidence for community coalescence (Fig. 3).

II. LONGITUDINAL COMMUNITY COALESCENCE

Microbial community coalescence occurs along the length of the river, across the terrestrial–aquatic interface from upslope soils to headwaters and downstream to estuaries

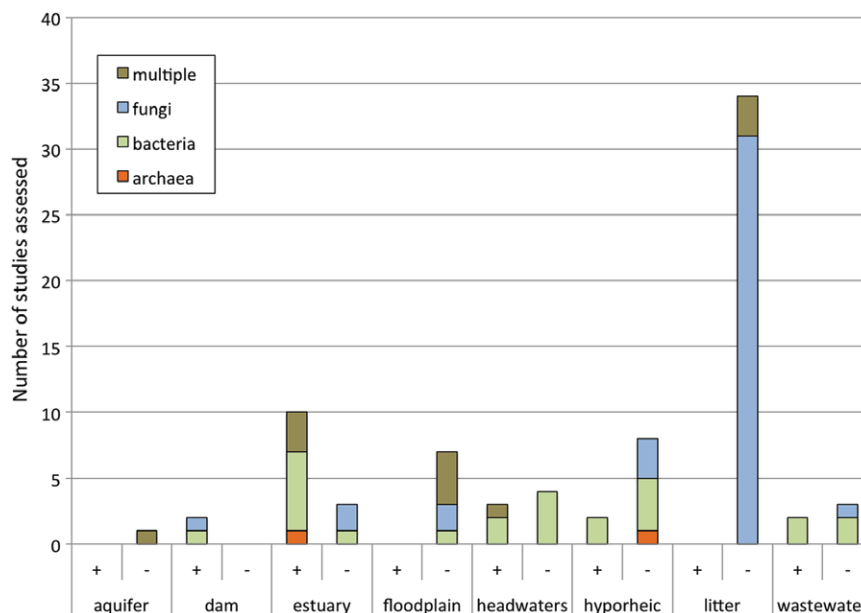


Fig. 2. Number of studies included in this review by organism group and riverine compartment ($N = 79$). + indicates those studies meeting the criteria to study community coalescence and – indicates that criteria were not met. The minimum criteria to make inferences about community coalescence dynamics were that the study reported the community composition of all of the initial communities and the resultant community following mixing.

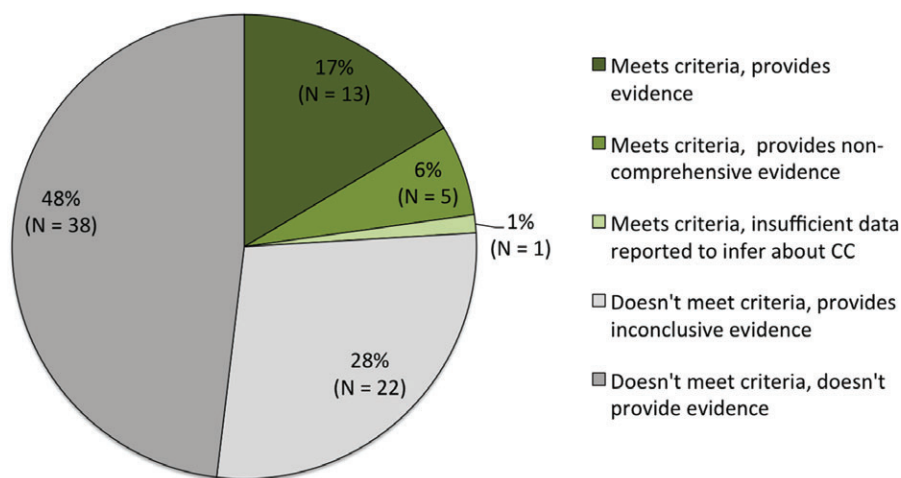


Fig. 3. Percentage of studies meeting criteria to assess community coalescence and the degree of evidence provided or not provided by the studies reviewed ($N = 79$; see Table S1). CC, community coalescence.

(Fig. 4). Coalescence events are conceptually organized from upstream to downstream in this section. This perspective harkens to the meta-ecosystem perspective of the River Continuum Concept (Vannote *et al.*, 1980), which postulates that there is a relationship between carbon processing and biological communities along a longitudinal continuum. In the case of runoff and litter entering low-order streams, microbial communities are concomitantly transported to the freshwater environment. From highly diverse headwaters, these communities shift in composition and become less diverse as they travel downstream (Besemer *et al.*, 2013; Savio *et al.*, 2015).

These shifts may occur in part because of increasingly recalcitrant carbon resources and a changing chemical environment further downstream, but also involve the ability of the component taxa to compete in a freshwater environment. Hydrological events (e.g. large storms, snowmelt) may transport large quantities of particulate organic matter (POM) into riverine systems in a short time period, which is quickly shunted downstream due to increased discharge (Raymond, Saiers, & Sobczak, 2015). Microbial communities are transported along with POM – the concurrent increase in velocity during a pulse-shunt event may allow otherwise uncompetitive

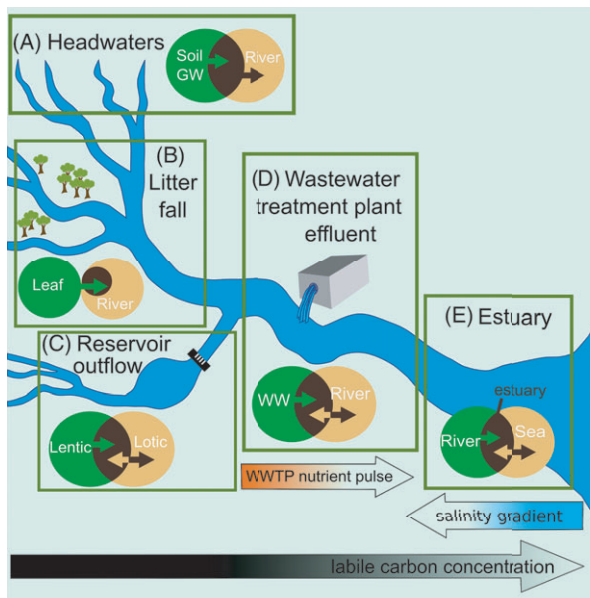


Fig. 4. A longitudinal view of riverine community coalescence events; from headwaters (A) to estuary (E). The collision of two communities and their inhabiting environments are illustrated by two circles in each box (green and yellow). The brown area represents the mixture of source communities and environmental components, and arrows indicate the direction of community exchange (*cf.* Fig. 1). GW, groundwater; WW, wastewater; WWTP, wastewater treatment plant.

microorganisms protected by particulate matter to survive for quite some distance along the longitudinal gradient. Such a longitudinal perspective also offers a means by which these communities might be studied: because the coalescence events discussed in this section occur in compartments along a longitudinal gradient in a moving water body, to study the resultant microbial community, it is necessary to examine samples upstream and downstream of the site of coalescence and consider the driving force of hydrology.

(1) Community coalescence in headwaters

Microbial community coalescence can occur when microorganisms of terrestrial origin enter rivers and streams *via* runoff and mix with aquatic microorganisms (Fig. 5). In a permeable system the majority of runoff will first be filtered through soil (Sophocleous, 2002), where many microorganisms will be lost *via* sorption to soil particles and some gained *via* detachment (Buchan & Flury, 2004). By contrast, in less-permeable systems (e.g. clay-dominated geology), given the same rainfall event, a proportionally greater volume of water is likely to flow over the surrounding floodplain soil, picking up soil particles and associated microorganisms before reaching a receiving stream or river. Microbial size (Gannon, Manilal, & Alexander, 1991) and cell surface characteristics, as well as soil properties (Huysman & Verstraete, 1993) and the presence of preferential flow pathways in the soil such as macropores (Martins *et al.*, 2013) could affect the size and composition of the transported

community. In addition to geology, magnitude and duration of rainfall event, and time of year are also important; greater volumes of runoff will enter streams following high-intensity and/or long-duration storm events especially when antecedent soil moisture deficit is low (Heppell *et al.*, 2002).

Coalescence of terrestrial with freshwater communities may be particularly important in headwaters and low-order streams due to the relatively high proportion of soil-derived water entering the stream. Several recent studies in tundra (Crump, Amaral-Zettler, & Kling, 2012), boreal (Ruiz-González, Niño-García, & del Giorgio, 2015) and temperate (Besemer *et al.*, 2013; Read *et al.*, 2015) ecosystems as well as along the entire length of the Danube River (Savio *et al.*, 2015) have observed considerable abundances of terrestrial microorganisms in headwater microbial communities. Some studies also assessed microbial diversity in soils upslope of the headwaters and found that the majority of taxa in headwaters and downstream sites were first detected in soil or soil water (Crump *et al.*, 2012; Ruiz-González *et al.*, 2015), providing evidence for the coalescence of terrestrial and aquatic communities.

However, other source communities that coalesce in headwaters, such as those associated with groundwater-fed springs, were not assessed in these studies. Savio *et al.* (2015) indirectly accounted for the contribution of groundwater-derived microorganisms (*via* comparison of river-derived microorganisms to a database of groundwater-associated microorganisms) and Read *et al.* (2015) mentions the contribution briefly. Neither studied groundwater communities prior to coalescence in headwaters directly, and no studies considered litter as an additional source of headwater microbial diversity.

A majority of microbial community members found in higher order streams in these longitudinal studies were also detected in headwaters and upslope soils. Thus, community coalescence in headwaters is a defining event in riverine microbial diversity downstream. Further downstream some new taxa are introduced (Crump *et al.*, 2012; Ruiz-González *et al.*, 2015), but what largely shapes the community are shifts in abundance of taxa detected in headwaters – those microorganisms that are introduced and survive in the highly diverse headwater environment are likely going to be the major downstream players. Because coalescence in headwaters is such an important event for the microbial biodiversity of the entire river, it is imperative to investigate potential controls on the process of microbial community assembly here. Framing these investigations within the community coalescence concept may lead to new and insightful research questions, for example: how is the headwater community shaped by runoff-to-groundwater mixing ratios? How do anthropogenic activities affect source communities and their propagation downstream?

(2) Terrestrial/freshwater coalescence *via* litter fall

Microorganisms of terrestrial origin can enter lotic systems through litter fall. In northern, temperate systems, the majority of litter fall enters rivers during autumnal senescence

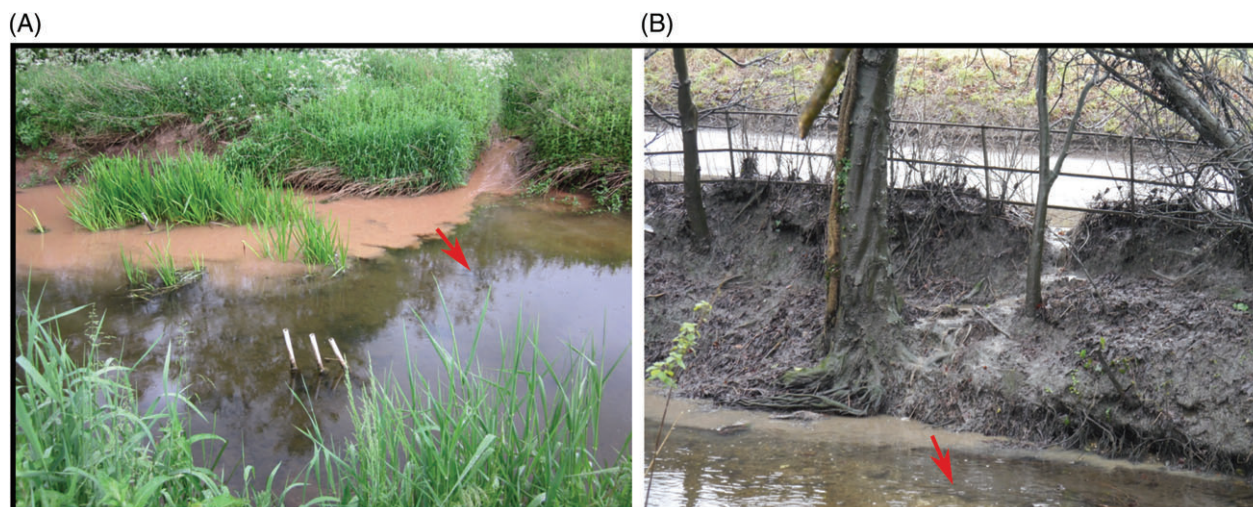


Fig. 5. Runoff events in response to rainfall. River Leith, Cumbria, UK (A) and River Chess, Hertfordshire, UK (B); photographs by Catherine M. Heppell (A) and Paul Jennings (B). The red arrows indicate likely areas where community coalescence occurs between terrestrial and riverine communities in a wholesale-mixing scenario (*cf.* Fig. 4A).

and in headwaters and low-order streams (Abelho, 2001). On trees, leaf surface (phyllosphere) communities are dominated by bacteria, and also include archaea, filamentous fungi and yeasts (Lindow & Brandl, 2003). Studies of cultivated plants and tree species have observed Actinobacteria, Firmicutes, Bacteroides and Proteobacteria to be the most dominant bacterial phyla, and bacterial community structure has been shown to correlate with plant host, geographical location and climate (Lindow & Brandl, 2003; Bulgarelli *et al.*, 2013; Meaden, Metcalf, & Koskella, 2016). Following senescence, litter from riparian trees can enter streams and rivers, where coalescence of terrestrial microbial phyllosphere communities and freshwater microbial communities occurs.

While leaves on trees in terrestrial environments are numerically dominated by bacterial taxa, fungi are the most abundant group following stream incubation (Das, Royer, & Leff, 2007; Manerkar, Seena, & Bärlocher, 2008). The best-studied group of leaf-colonizing fungi in running freshwaters is aquatic hyphomycetes; this group of fungi is largely responsible for microbial decomposition of leaf litter in streams (Krauss *et al.*, 2011). Aquatic hyphomycete growth is typically highest at 15–25°C (Krauss *et al.*, 2011) and reduced diversity has been reported from studies artificially raising stream (Bärlocher *et al.*, 2008) and microcosm (Fernandes *et al.*, 2012) temperatures. Stream pH also significantly affects aquatic hyphomycete communities: both species richness and activity are reduced in acidified streams (Krauss *et al.*, 2011; Clivot *et al.*, 2014). A small meta-analysis of studies comparing pairs of control and human-impacted streams reported that eutrophication and mining consistently reduced aquatic hyphomycete richness, while changes in riparian vegetation (e.g. forestry or plant invasion) did not (Lecerf & Chauvet, 2008).

Because of the importance of allochthonous carbon dynamics in many river systems, litter decomposition rates and decomposer communities inhabiting leaf litter are well

studied. Investigations of litter microbial communities over time report that fungal diversity and evenness is highest in the first few days following submersion, while one or two fungal decomposer species typically dominate after a few weeks of incubation (Nikolcheva, Cockshutt, & Bärlocher, 2003). One explanation offered to explain this phenomenon is that terrestrial taxa are present during the first days of litter incubation and decline in abundance resulting from competition with aquatic hyphomycetes (Nikolcheva *et al.*, 2003).

It does not appear that coalescence of phyllosphere and freshwater microbial communities has been studied directly: in all studies reviewed here, litter microbial communities were only assessed after days to weeks of in-stream incubation. However, the incorporation of the phyllosphere community into the catchment microbiome was recently suggested (Battin *et al.*, 2016). Further investigating the mechanisms behind community assembly on leaf litter is warranted: when and why do terrestrial taxa persist on leaf litter in streams and what is their ecological function? How do anthropogenic activities affect phyllosphere/freshwater coalescence events, and what are the functional consequences?

(3) Serial discontinuities: anthropogenic/freshwater coalescence events

Community coalescence occurs not only as a result of natural events but also at artificial discontinuous points along the river, such as when dam release and wastewater effluent are discharged into running waters. Both wastewater and reservoirs formed by dams have microbial communities and abiotic conditions that differ from running waters. These point-source discrete influences are considered within the context of the Serial Discontinuity Concept (Ward & Stanford, 1983, 2001), which predicts a decrease in the biodiversity of regulated rivers.

Artificial reservoirs frequently associated with man-made dams create a lentic habitat that fragments the river continuity, with inherently different chemical and thermal conditions from the lotic continuum (Friedl & Wüest, 2002). Consequently new bacterial and archaeal lineages, not detected upstream, can appear in the reservoir (Dumestre *et al.*, 2002). Upon dam release, the microbial community in the reservoir water will mix with the lotic community downstream. Physical properties of the dam, such as size and operational rules, may govern whether a unique microbial community is formed in the reservoir (and therefore whether a downstream coalescence event is likely to occur) (Mašín *et al.*, 2003) by determining hydraulic retention time and the associated biophysical alterations (Poff & Hart, 2002).

Another man-made structure that may influence riverine microbial communities is a wastewater treatment plant. The contribution of wastewater effluent to the volume of stream water may range widely and in some cases contributes to 90% or more of instream flow (Brooks, Riley, & Taylor, 2006). The proportion of effluent to stream discharge affects the mixing ratio of the transported (effluent) and receiving (stream) microbial communities, and therefore could influence the outcome of the coalescence event. Wastewater effluent contains nutrients, such as nitrogen and phosphorous, as well as antimicrobials and pharmaceuticals, that can all impact microbial community composition (Rubin & Leff, 2007; Barra Caracciolo, Topp, & Grenni, 2015) and affect the success of various taxa following mixing.

Two recent studies provide evidence for lotic/wastewater effluent coalescence. In one case, seasonal differences in the outcome of lotic/wastewater effluent coalescence were observed: higher abundances of wastewater-derived taxa were observed in downstream sites in autumn and winter (García-Armisen *et al.*, 2014). In another study, a lineage of ammonia-oxidizing bacteria (AOB) introduced in wastewater effluent represented 40% of all AOB further downstream in the estuary (Cebon *et al.*, 2004). This group of bacteria is responsible for a rate-limiting step in the nitrogen cycle, so this result indicates the potential for coalescence events to affect organisms that drive ecosystem functions. Shifts in benthic microbial communities downstream of wastewater treatment plants have also been observed (Wakelin, Colloff, & Kookana, 2008; Drury, Rosi-Marshall, & Kelly, 2013), but the wastewater effluent community was not assessed in these cases and community differences were attributed solely to physicochemical mechanisms. Thus whether established benthic communities are as strongly influenced as planktonic communities by wastewater effluent communities is an open question.

Studying wastewater effluent/lotic community coalescence could provide insight about how lotic communities with altered functional and biological properties arise. From a public health perspective, the presence of antimicrobial compounds in wastewater may result in the proliferation of organisms containing antibiotic-resistance genes originating from the wastewater effluent community (Kristiansson *et al.*, 2011). The coalescence of wastewater communities and lotic

communities could result in the transfer of resistance genes to native lotic organisms. In this context it is important to consider wastewater treatment processes, particularly the use of chlorination or other tertiary treatments, as these will preferentially select resistant taxa and decrease microbial abundance in wastewater effluent. Microorganisms have been shown to survive even chlorination treatment and regrow in environmental waters (Bolster, Bromley, & Jones, 2005).

(4) Estuaries: mixing of freshwater and marine microbial communities

Located at the end of the longitudinal gradient from headwaters downstream are estuaries, where freshwater from rivers and marine waters meet. Mixing of freshwater and marine water creates a salinity gradient exerting a strong influence on microbial community composition (Lozupone & Knight, 2007). Across studies, salinity has been linked to community composition and/or abundance of bacterial (Bouvier & del Giorgio, 2002; Fortunato *et al.*, 2012), archaeal (Crump & Baross, 2000; Webster *et al.*, 2015) and ammonia-oxidizing (Mosier & Francis, 2008) taxa. This type of coalescence is continually occurring, dominantly driven by river inflow and the tide. River inflow relative to tidal intrusion also affects the temporal variability of the salinity gradient (Wolanski, 2007), thus the mixing ratios of the microbial communities and the chemical environment in which they meet are linked to hydrology. Microbial community structure in estuaries is frequently attributed to the mixing of riverine and coastal microbial communities, i.e. community coalescence.

Many studies in estuaries meet the minimum criteria to assess the consequences of community coalescence; namely microbial diversity is frequently assessed in both upstream freshwaters and downstream marine waters as well as in the zone of mixing, i.e. the estuary. Reports suggest that estuarine microbial communities are comprised of members of the upstream and downstream communities (Crump, Armbrust, & Baross, 1999; Crump & Baross, 2000; Crump *et al.*, 2004; Fortunato *et al.*, 2012). Compared to proximal sampling locations, both high and low diversity in the zone of mixing has been reported in studies employing next-generation sequencing (Campbell & Kirchman, 2012; Fortunato *et al.*, 2012). Particle-associated and free-living estuarine communities may behave quite differently in community coalescence situations. For example, free-living bacterial communities were found to be more similar to proximal river and marine (source) samples than particle-associated communities, which the authors attributed to the longer residence time of particles than water in the estuary (Crump *et al.*, 1999). While many studies assess bacterial and archaeal communities in estuaries, to our knowledge, no studies exist in which fungal community composition was assessed in hydrologically connected freshwater and marine waters and the zone of their mixing.

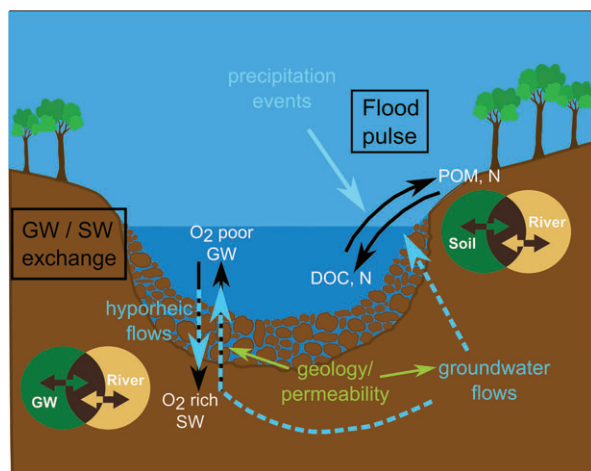


Fig. 6. A cross-sectional view illustrating lateral (overland flow) and vertical flows of groundwater (GW) and surface water (SW). Both lateral and vertical flows introduce wholesale mixing of communities and environmental components from adjacent microbial habitats (green and yellow circles; cf. Fig. 1C). Mixing events resulting in community coalescence are shown with black arrows and text. Chemistry likely to impact the outcome of the community coalescence event is shown in white (Tockner *et al.*, 1999). Hydrological flows driving the events are in blue and physical controls on the hydrology in green. DOC, dissolved organic matter; POM, particulate organic matter.

III. LATERAL AND VERTICAL COMMUNITY COALESCENCE

Processes driven by the longitudinal movement of water downstream were considered in Section II. Now our perspective will shift and consider flows in the remaining two dimensions of the river (Fig. 6). Lateral movement of water onto floodplains and vertical exchange of surface water and groundwater communities in the hyporheic zone will be discussed.

(1) Overbank flooding: a soil/freshwater community coalescence event

Freshwater and terrestrial microbial communities mix during overbank flooding. River-derived particulate matter and floodplain-derived soil particles and litter are exchanged, thus community coalescence occurs in both habitats. Floodplain inundations resulting from heavy precipitation are more likely to occur in impermeable or minimally permeable (e.g. clay-rich) systems where precipitation cannot infiltrate the soil before reaching the recipient stream, and river levels rise rapidly in response to rainfall (Sophocleous, 2002). In more permeable systems, rising groundwater and/or growth of autochthonous vegetation (in highly vegetated systems) can displace water onto banks, where aquatic and soil communities likely interact for longer periods of time than in flashier impermeable systems. The flood pulse concept predicts that flood duration and predictability (timing) correlate with organismal adaptations

to exploit the aquatic/terrestrial transition zone created by flood pulses (Junk, Bayley, & Sparks, 1989). It is likely that community coalescence outcomes would differ in short and irregularly flooded systems compared to regularly flooded streams with longer flood duration.

Some mesocosm studies have been conducted to investigate the impact of flooding on community composition (Drenovsky *et al.*, 2004; Wilson *et al.*, 2011). Deionized water lacking a natural microbial community was used to simulate floodwater and thus no coalescence event took place in these studies. However, in both cases, shifts in soil microbial community composition were observed, indicating that the chemical and physical impacts of flooding are influential and likely to affect the community coalescence outcome. One manipulative field study investigated the effects of flooding and observed a decrease in microbial biomass and bacterial-to-fungal ratio in the stagnant flooding treatment (Unger, Kennedy, & Muzika, 2009) – conversely, a field study across short-, intermediate- and long-term flooded soils found no fungal marker in the long-term flooded site (Rinklebe & Langer, 2006). While hydrologic connectivity has been reported to influence floodplain microbial activity and microbial community structure (Freimann *et al.*, 2015), further investigation is necessary to resolve the influence of abiotic factors on floodplain microbial communities and to clarify the extent to which microorganisms are exchanged between floodplain and stream.

Studying this exchange by applying the community coalescence framework in floodplains might provide insight into dispersal or survival tactics by particular groups, i.e. some microorganisms may be able to take advantage of floods temporarily moving them out of their ‘typical’ habitat (e.g. Chauvet *et al.*, 2016). For example, terrestrial sites may serve as a reservoir for taxa whose preferred stream habitat is always moving them further downstream. In one study, aquatic hyphomycete species were identified on leaves submerged within and proximal to a Canadian stream (Sridhar & Bärlocher, 1993). The highest number of species was observed on litter from within the stream, followed by litter in occasionally flooded sites, and the fewest in never-inundated sites. Conversely, typically terrestrial taxa may take advantage of running waters for dispersal, as has been proposed for plants (Gurnell *et al.*, 2007). For example, mycorrhizal fungal spores have been observed in freshly deposited flood sediments (Harner *et al.*, 2011).

(2) Hyporheic zone: freshwater/groundwater community coalescence

The hyporheic zone is the interface of surface water and groundwater in riverine systems, and thus a site of vertical exchange between surface water and groundwater microbial communities. At the catchment scale, rivers can be categorized as ‘gaining’ or ‘losing’ depending on the net surface water volume gained from or lost to groundwater, and most river systems are dependent to some extent on base flow (upwelling groundwater) (Boulton & Hancock, 2006). On the reach scale, however, the riverbed has both

upwelling and downwelling zones, for example in riffle-pool sequences (Hendricks, 1993), termed hyporheic exchange flows. Such flows may shape distinct microbial communities within meters of one another: distinct hyporheic bacterial communities inhabited upwelling and downwelling zones in a gravel bar (Lowell *et al.*, 2009).

Organisms tolerant of low-oxygen conditions will likely be more competitive in zones of upwelling of oxygen-depleted, dissolved organic matter (DOM)-poor and sometimes nutrient-rich groundwater, whereas aerobes and decomposers would have an advantage in zones of intrusion of DOM-rich, oxygenated surface water (Hendricks, 1993; Boulton *et al.*, 1998). A variety of studies have investigated controls on hyporheic bacterial community structure and report that nutrients (Lowell *et al.*, 2009; Febria *et al.*, 2012), carbon quality and availability (Lowell *et al.*, 2009; Febria *et al.*, 2012; Wagner *et al.*, 2014) and temperature (Febria *et al.*, 2012) are influential. Physical filtering of microbial communities controlled by sediment characteristics and bed permeability could affect the density and composition of the transported community in downwelling zones. For example, sediment grain size and conidia morphology have been found to limit fungal dispersal into hyporheic sediment (Cornut *et al.*, 2014).

To our knowledge, only one study has directly assessed the mixing of surface water and groundwater microbial communities and the resultant community composition in the hyporheic zone (Stegen *et al.*, 2016). The authors attributed compositional changes along the groundwater-to-surface water gradient to both organismal dispersal *via* hyporheic flows and to changes in the resource environment (e.g. organic carbon concentrations). This study is a good model for further community coalescence studies in the hyporheic zone: samples were collected across different river-stage conditions, organic carbon was well characterized, indices of community compositional change were calculated and mechanistic hypotheses to explain their observations linked ecology, chemistry and hydrology (i.e. flows of resources and communities).

IV. WHY AND HOW TO STUDY COMMUNITY COALESCENCE

Application of the microbial community coalescence concept in riverine systems may help target relevant sampling locations and explain the microbial community assembly by considering the influence of the intermingling of microbial communities from multiple sources within this dynamic environment. In addition to providing valuable ecological information, riverine systems are ideal habitats for testing community coalescence and further theory development.

(1) Why? Structure/function, altered ecosystems, and theory development

Attributing variation in community assembly patterns to particular factors is often difficult in the field due to a

multitude of concurrently acting environmental factors. The amount of variance between observed communities explained by measured environmental variables is often quite low (i.e. how well the metacommunity paradigm of 'species sorting' explains observed community structure): a recent analysis found the mean variance explained across >300 ecological studies to be 26% and to be particularly low for decomposers (Soininen, 2014). Including mixing-related parameters (e.g. direction and volume of groundwater flow, time since last flood) may improve the amount of variance explained. This may prove easily accomplished as often these hydrological and climatic variables are already monitored. Assessment of other source communities that may mix with stream communities could also improve predictions about how microbial communities will change in time and space along the river continuum.

This is important, because ecosystem function is linked with community composition. For example, in estuaries bacterial community composition has been linked to functions including CO₂ production, CH₄ flux, nitrification and enzyme activities (Reed & Martiny, 2013). The functional capacity of a community is dependent upon the traits of the taxa comprising that community, i.e. the trait space. Following community coalescence, the functional trait space of the resultant community may expand or contract, and the maintenance of functions carried out by specialized groups of organisms will depend on the success of those groups following mixing.

The community coalescence framework makes explicit the potential for environmental mixing to serve as an additional driver of microbial community structure, and one that may be particularly important in places where mixing frequently occurs, like in rivers. As a result, application of the microbial community coalescence concept leads to new types of hypotheses and study designs that may improve our ability to make predictions about microbial community structure in the field. At the catchment scale (e.g. how microbial communities are assembling and changing from headwaters downstream to estuaries), zones or time periods where/when environmental mixing is occurring may correlate with points in space and/or time where large shifts in microbial communities occur as a result of community coalescence. These points in space/time will be specific to a particular river system, but are often easily observable. Sampling before/after these points may resolve some of the shifts in community structure along the river continuum. For example, a hypothesis that could be posited is that large shifts in microbial community structure along the river continuum will occur following environmental mixing events.

At the reach scale, applying this framework might improve the amount of variance explained between different observed local communities or identify easily measurable environmental parameters that correlate with local community structure. For example, a comparison of application of the species sorting paradigm with community coalescence in the hyporheic zone: in both cases, local communities inhabiting hyporheic sediments would be sampled and local

environmental variables of interest (e.g. O₂ concentrations, nutrient status) would be measured. In the species sorting paradigm, the ‘metacommunity’ would be subjectively defined by the researcher, and may simply include the other local hyporheic communities. Often, variance partitioning is applied to determine the environmental variables predictive of the local observed communities. By contrast, the community coalescence framework explicitly considers the forces of environmental mixing that drive passive dispersal of new microorganisms to these local communities. So, departing from metacommunity theory, these ‘source’ communities (i.e. surface water, groundwater) would also be sampled, and the driver of the environmental mixing, i.e. hyporheic flows, would also be quantified. Some additional hypotheses that arise could be, for example: (i) the direction and volume of hyporheic flows are predictive of local microbial community structure in hyporheic sediments because they drive passive dispersal of new microorganisms to these sediments and control fluxes in local physicochemical conditions; (ii) surface water assemblages with characteristics X and Y are competitive in hyporheic sediments and therefore are likely to make up a significant proportion of the hyporheic community in downwelling zones.

Community coalescence may also provide insight into altered ecosystems, a critical topic in the context of global change and increasing anthropogenic pressure on riverine systems. For example, terrestrial fungal taxa were found to make a large contribution to fungal diversity on leaf litter in an acidic, polluted stream compared to an unpolluted stream where typical freshwater taxa dominated (Clivot *et al.*, 2014). This illustrates an unintended consequence of community coalescence: typically the terrestrial taxa present on leaf litter do not persist long on leaves in the aquatic environment; however, in the presence of mining pollution they persisted. Because aquatic fungi are largely responsible for in-stream litter decomposition (Krauss *et al.*, 2011), this could have functional consequences.

In addition to providing a framework for studying microbial communities in both natural and altered riverine systems, the community coalescence concept also provides the opportunity for riverine microbial ecology studies to drive theory development. Riverine systems are uniquely suited for community coalescence studies because of the regular and often predictable mixing that occurs (as compared to mixing that would be present within terrestrial systems). Many studies examine the influence of riverine mixing events on various biological and chemical parameters; therefore, suitable study designs are already employed (e.g. litter bag studies, sampling in mixing zones) or require only slight alteration.

(2) How? Source/resultant communities and methodologies

Perhaps more so in rivers than in other habitats (e.g. soils) microbial ecologists are already (and necessarily) considering environmental mixing as it relates to community assembly. However, inhabited pieces of the environment are often considered in a strictly abiotic sense. For example, studies

investigating aquatic microbial communities on leaf litter often take the perspective of the leaf as a substrate for decomposition by the aquatic community and do not consider the microbial community associated with that leaf prior to its entry in the stream, or the leaf as a source of microbial cells for the river. In longitudinal studies of microbial communities, hydrology is related to the temporal dynamics of community shifts from headwaters to estuary within the watercourse, but groundwater and upwelling hyporheic samples are often overlooked as additional sources of microbial communities themselves.

To study community coalescence, minimally the source (starting) and resultant (final) communities must be characterized. Methodologies differentiating living/active from dead organisms are critical (e.g. Campbell & Kirchman, 2012), as community changes can occur rapidly in response to changing biotic and environmental conditions following mixing, but imprints of dead organisms very likely persist as environmental DNA (Carini *et al.*, 2016). Additionally, key environmental variables that characterize mixing events should be quantified. Many of these variables are already measured in lotic microbial ecology studies, e.g. mixing ratios, nutrient contents, etc.; however, the composition of source communities is often overlooked. Collecting this additional data would allow testing of hypotheses that explicitly consider how conditions created by environmental mixing govern the composition of the resultant community. Runoff and groundwater mixing ratios, for example, may be the best predictive parameters for headwater microbial diversity because these ratios control the abundance of the source communities as well as the chemistry of the headwaters. This could be tested statistically by calculating community dissimilarity measures among the initial and resultant communities and then determining if the measures are correlated with the relative proportion of mixing and/or the values of abiotic factors of the associated communities. If several headwaters with differing mixing ratios are tested, the importance of this ratio for headwater community structure could be resolved using ordination techniques.

For those compartments where little or no evidence has been reported supporting community coalescence dynamics, field investigations are an appropriate first step. Field studies will elucidate the degree to which community coalescence dynamics may or may not help to explain differences in community variation. Mixing is likely to play a larger role in community assembly in certain compartments than others and some mixing-related predictor variables may be more easily measured or ascertained than others – e.g. wastewater treatment plant effluent volumes *versus* estimating the amount of litter entering a stream. It is important to ensure that native microbial communities are not altered during manipulative studies in the field – i.e. leaf litter should not be extensively handled or autoclaved before litter bag experiments intending to investigate community coalescence dynamics.

In compartments where evidence for coalescence has been observed in the field (e.g. estuaries, wastewater

treatment plant effluent), experimental microcosm studies may be appropriate for testing mechanistic hypotheses. Mixing ratios could easily be manipulated (e.g. to simulate various wastewater effluent volumes) and different source communities (e.g. wastewater subjected to different treatment regimes) could be tested. Mechanisms that could drive changes in ecosystem function following the community coalescence event (e.g. horizontal gene transfer or shifts in functional gene abundance) could be investigated without the confounding effects of the other environmental variables present in the field. Additionally, mechanistic hypotheses about community assembly could be tested, such as the influence of priority effects, mixing ratios (Rillig *et al.*, 2015), and number of communities (Sierocinski *et al.*, 2017) on the resultant community.

Some established ecological theories could provide mechanisms for the outcome of microbial community coalescence events in different lotic habitats. Priority effects explain how an established biofilm might inhibit immigration by members of a transported community by occupying advantageous patches and utilizing carbon and nutrients. Particle-associated microbial communities might be described by nestedness: resulting from proximity and utilization of common resources, the inhabitants of a floc or a leaf are more likely to interact with one another than with other inhabitants of the water column. Oligotrophs may be likely to persist following coalescence in the water column of higher-order rivers, whereas copiotrophs may prevail after freshwater coalescence with nutrient-rich wastewater effluent.

Ecological mechanisms explain part of the story of community assembly following environmental mixing but to get the whole picture we must ask not only how the communities are interacting with one another, but also how their changing environment is acting upon them. What are the resultant chemical characteristics of the new environment created by mixing (e.g. shifts in O₂, N, or labile carbon concentrations) and does it confer a competitive advantage to a particular source community or subset of organisms (i.e. species sorting)? Has regularly occurring mixing 'primed' one or both source communities for persistence following coalescence?

V. CONCLUSIONS

(1) The recently proposed, microbial-specific community coalescence concept provides a holistic framework to examine microbial community assembly in rivers, departing from the classical metacommunity framework. The ecology of all source microbial communities and the physicochemical properties of the environmental bodies that are mixing are considered in concert, discussed here in the context of the physical and hydrological controls constraining the occurrence of communities and environmental factors in space and time.

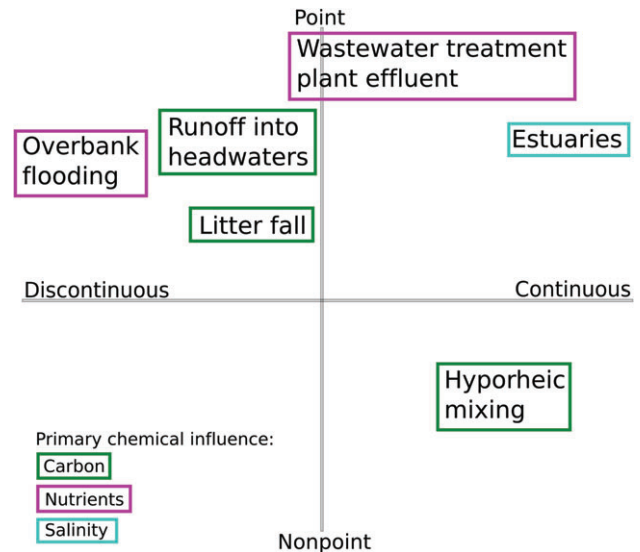


Fig. 7. Conceptual diagram illustrating putative connections between chemistry, hydrology, and temporality in community coalescence events along temporal (x) and spatial (y) axes.

(2) Studies of wastewater treatment plant outflow, as well as research in headwaters, estuaries, and the hyporheic zone provide preliminary evidence for community coalescence. The influence of environmental mixing on flood-influenced habitats and phyllosphere communities has not yet been investigated.

(3) It seems very likely that the hydrological and chemical environment as well as spatial and temporal controls influence the ecological outcome of microbial community coalescence events (Fig. 7), but the process as a whole and the relative contributions of the components in explaining composition and diversity requires more integrated studies. Riverine systems are ideal for the experimental and theoretical development of the community coalescence concept.

(4) This framework may aid in identifying spatiotemporally relevant sampling points where potential community shifts occur. Further, defining the environmental mixing events of interest for the community under study dictates the appropriate spatial scale and timing of sample collection and narrows the scope of physical and chemical parameters of interest.

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VII. REFERENCES

References marked with asterisk have been cited within the supporting information.

- ABELHO, M. (2001). From litterfall to breakdown in streams: a review. *The Scientific World Journal* **1**, 656–680.
- *ALMEIDA, J. M. G. C. F. (2005). Yeast community survey in the Tagus estuary. *FEMS Microbiology Ecology* **53**, 295–303.
- ALTERMATT, F. (2013). Diversity in riverine metacommunities: a network perspective. *Aquatic Ecology* **47**, 365–377.
- *BÄRLOCHER, F. & GRAÇA, M. A. S. (2002). Exotic riparian vegetation lowers fungal diversity but not leaf decomposition in Portuguese streams. *Freshwater Biology* **47**, 1123–1135.
- BÄRLOCHER, F., SEENA, S., WILSON, K. P. & DUDLEY WILLIAMS, D. (2008). Raised water temperature lowers diversity of hyporheic aquatic hyphomycetes. *Freshwater Biology* **53**, 368–379.
- BARRA CARACCILO, A., TOPP, E. & GRENNI, P. (2015). Pharmaceuticals in the environment: biodegradation and effects on natural microbial communities. A review. *Journal of Pharmaceutical and Biomedical Analysis* **106**, 25–36.
- *BATISTA, D., PASCOAL, C. & CÁSSIO, F. (2012). Impacts of warming on aquatic decomposers along a gradient of cadmium stress. *Environmental Pollution* **169**, 35–41.
- BATTIN, T. J., KAPLAN, L. A., FINDLAY, S., HOPKINSON, C. S., MARTI, E., PACKMAN, A. I., NEWBOLD, J. D. & SABATER, F. (2009). Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience* **2**, 595–595.
- BATTIN, T. J., BESEMER, K., BENGTTSSON, M. M., ROMANI, A. M. & PACKMANN, A. I. (2016). The ecology and biogeochemistry of stream biofilms. *Nature Reviews Microbiology* **14**, 251–263.
- *BAUDOIN, J. M., GUÉROLD, F., FELTEN, V., CHAUVET, E., WAGNER, P. & ROUSSELLE, P. (2008). Elevated aluminium concentration in acidified headwater streams lowers aquatic hyphomycete diversity and impairs leaf-litter breakdown. *Microbial Ecology* **56**, 260–269.
- *BALDY, V., CHAUVET, E., CHARCOSSET, J. & GESSNER, M. (2002). Microbial dynamics associated with leaves decomposing in the mainstem and floodplain pond of a large river. *Aquatic Microbial Ecology* **28**, 25–36.
- BESEMER, K. (2015). Biodiversity, community structure and function of biofilms in stream ecosystems. *Research in Microbiology* **166**, 774–781.
- BESEMER, K., SINGER, G., QUINCE, C., BERTUZZO, E., SLOAN, W. & BATTIN, T. J. (2013). Headwaters are critical reservoirs of microbial diversity for fluvial networks. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131760–20131760.
- BOLSTER, C. H., BROMLEY, J. M. & JONES, S. H. (2005). Recovery of chlorine-exposed *Escherichia coli* in estuarine microcosms. *Environmental Science and Technology* **39**, 3083–3089.
- BOULTON, A. J. & HANCOCK, P. J. (2006). Rivers as groundwater-dependent ecosystems: a review of degrees of dependency, riverine processes and management implications. *Australian Journal of Botany* **54**, 133–144.
- BOULTON, A. J., FINDLAY, S., MARMONIER, P., STANLEY, E. H. & VALETT, H. M. (1998). The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* **29**, 59–81.
- BOUVIER, T. C. & DEL GIORGIO, P. A. (2002). Compositional changes in free-living bacterial communities along a salinity gradient in two temperate estuaries. *Limnology and Oceanography* **47**, 453–470.
- *BRABLCOVÁ, L., BURIÁNKOVÁ, I., BADUROVÁ, P., CHAUDHARY, P. P. & RULÍK, M. (2015). Methanogenic archaea diversity in hyporheic sediments of a small lowland stream. *Anaerobe* **32**, 24–31.
- BROOKS, B. W., RILEY, T. M. & TAYLOR, R. D. (2006). Water quality of effluent-dominated ecosystems: Ecotoxicological, hydrological, and management considerations. *Hydrobiologia* **556**, 365–379.
- BROWN, B. L., SWAN, C. M., AUERBACH, D. A., CAMPBELL GRANT, E. H., HITT, N. P., MALONEY, K. O. & PATRICK, C. (2011). Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *Journal of the North American Benthological Society* **30**, 310–327.
- *BRUDER, A., CHAUVET, E. & GESSNER, M. O. (2011). Litter diversity, fungal decomposers and litter decomposition under simulated stream intermittency. *Functional Ecology* **25**, 1269–1277.
- *BUCHAN, G. D. & FLURY, M. (2004). Pathogen transport by water. In *Encyclopedia of Water Science* (eds B.A. Stewart and T.A. Howell), pp. 1–4. Marcel Dekker, New York.
- BULGARELLI, D., SCHLAEPPI, K., SPAEPEN, S., VAN THEMAAT, E. V. L. & SCHULZE-LEFERT, P. (2013). Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology* **64**, 807–838.
- *CAI, L., JI, K.-F. & HYDE, K. D. (2006). Variation between freshwater and terrestrial fungal communities on decaying bamboo culms. *Antonie Van Leeuwenhoek* **89**, 293–301.
- CAMPBELL, B. J. & KIRCHMAN, D. L. (2012). Bacterial diversity, community structure and potential growth rates along an estuarine salinity gradient. *The ISME Journal* **7**, 210–220.
- CARINI, P., MARSDEN, P. J., LEFF, J. W., MORGAN, E. E., STRICKLAND, M. S. & FIERER, N. (2016). Relic DNA is abundant in soil and obscures estimates of soil microbial diversity. *Nature Microbiology* **2**, 16242.
- CARRARA, F., ALTERMATT, F., RODRIGUEZ-ITURBE, I. & RINALDO, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proceedings of the National Academy of Sciences* **109**, 5761–5766.
- CEBRON, A., COCI, M., GARNIER, J. & LAANBROEK, H. J. (2004). Denaturing gradient gel electrophoretic analysis of ammonia-oxidizing bacterial community structure in the lower Seine river: impact of Paris wastewater effluents. *Applied and Environmental Microbiology* **70**, 6726–6737.
- CHAUVET, E., CORNUT, J., SRIDHAR, K. R., SELOSSE, M.-A. & BÄRLOCHER, F. (2016). Beyond the water column: aquatic hyphomycetes outside their preferred habitat. *Fungal Ecology* **19**, 112–127.
- CLIVOT, H., CORNUT, J., CHAUVET, E., ELGER, A., POUPIN, P., GUÉROLD, F. & PAGNOUT, C. (2014). Leaf-associated fungal diversity in acidified streams: insights from combining traditional and molecular approaches. *Environmental Microbiology* **16**, 2145–2156.
- *CORNUT, J., ELGER, A., LAMBRIGOT, D., MARMONIER, P. & CHAUVET, E. (2010). Early stages of leaf decomposition are mediated by aquatic fungi in the hyporheic zone of woodland streams. *Freshwater Biology* **55**, 2541–2556.
- *CORNUT, J., CLIVOT, H., CHAUVET, E., ELGER, A., PAGNOUT, C. & GUÉROLD, F. (2012). Effect of acidification on leaf litter decomposition in benthic and hyporheic zones of woodland streams. *Water Research* **46**, 6430–6444.
- CORNUT, J., CHAUVET, E., MERMILLOD-BLONDIN, F., ASSEMAT, F. & ELGER, A. (2014). Aquatic hyphomycete species are screened by the hyporheic zone of woodland streams. *Applied and Environmental Microbiology* **80**, 1949–1960.
- *COLAS, F., BAUDOIN, J.-M., CHAUVET, E., CLIVOT, H., DANGER, M., GUÉROLD, F. & DEVIN, S. (2016). Dam-associated multiple-stressor impacts on fungal biomass and richness reveal the initial signs of ecosystem functioning impairment. *Ecological Indicators* **60**, 1077–1090.
- *COUSIN, S. (2009). Flavobacterial community structure in a hardwater rivulet and adjacent forest soil, Harz Mountain, Germany. *Current Microbiology* **58**, 409–415.
- CALDERÓN, K., SPOR, A., BREUIL, M.-C., BRU, D., BIZOUARD, F., VIOLLE, C., BARNARD, R. L. & PHILIPPOT, L. (2016). Effectiveness of ecological rescue for altered soil microbial communities and functions. *The ISME Journal* **11**, 1–12.
- CRUMP, B. C. & BAROSS, J. A. (2000). Archaeoplankton in the Columbia River, its estuary and the adjacent coastal ocean, USA. *FEMS Microbiology Ecology* **31**, 231–239.
- CRUMP, B. C., BAROSS, J. A. & SIMENSTAD, C. A. (1998). Dominance of particle-attached bacteria in the Columbia River estuary, USA. *Aquatic Microbial Ecology* **14**, 7–18.
- CRUMP, B. C., ARMBRUST, E. V. & BAROSS, J. A. (1999). Phylogenetic analysis of particle-attached and free-living bacterial communities in the Columbia river, its estuary, and the adjacent coastal ocean. *Applied and Environmental Microbiology* **65**, 3192–3204.
- CRUMP, B. C., HOPKINSON, C. S., SOGIN, M. L. & HOBBI, J. E. (2004). Microbial biogeography along an estuarine salinity gradient: combined influences of bacterial growth and residence time. *Applied and Environmental Microbiology* **70**, 1494–1505.
- CRUMP, B. C., AMARAL-ZETTLER, L. A. & KLING, G. W. (2012). Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. *The ISME Journal* **6**, 1629–1639.
- *CUDOWSKI, A., PIETRYCZUK, A. & HAUSCHILD, T. (2015). Aquatic fungi in relation to the physical and chemical parameters of water quality in the Augustów Canal. *Fungal Ecology* **13**, 193–204.
- *DANGER, M., CORNUT, J., ELGER, A. & CHAUVET, E. (2012). Effects of burial on leaf litter quality, microbial conditioning and palatability to three shredder taxa. *Freshwater Biology* **57**, 1017–1030.
- DAS, M., ROYER, T. V. & LEFF, L. G. (2007). Diversity of fungi, bacteria, and actinomycetes on leaves decomposing in a stream. *Applied and Environmental Microbiology* **73**, 756–767.
- *DAS, M., ROYER, T. V. & LEFF, L. G. (2008). Fungal communities on decaying leaves in streams: a comparison of two leaf species. *Mycological Progress* **7**, 267–275.
- DRENOVSKY, R. E., VO, D., GRAHAM, K. J. & SCOW, K. M. (2004). Soil water content and organic carbon availability are major determinants of soil microbial community composition. *Microbial Ecology* **48**, 424–430.
- DRURY, B., ROSI-MARSHALL, E. & KELLY, J. J. (2013). Wastewater treatment effluent reduces the abundance and diversity of benthic bacterial communities in urban and suburban rivers. *Applied and Environmental Microbiology* **79**, 1897–1905.
- *DUARTE, S., PASCOAL, C. & CÁSSIO, F. (2008). High diversity of fungi may mitigate the impact of pollution on plant litter decomposition in streams. *Microbial Ecology* **56**, 688–695.
- *DUARTE, S., BÄRLOCHER, F., TRABULO, J., CÁSSIO, F. & PASCOAL, C. (2015). Stream-dwelling fungal decomposer communities along a gradient of eutrophication unraveled by 454 pyrosequencing. *Fungal Diversity* **70**, 127–148.
- DUDGEON, D., ARTHINGTON, A. H., GESSNER, M. O., KAWABATA, Z.-I., KNOWLER, D. J., LÉVÊQUE, C., NAIMAN, R. J., PRIEUR-RICHARD, A.-H., SOTO, D., STIASNY, M. L. J. & SULLIVAN, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163.

- DUMESTRE, J., CASAMAYOR, E., MASSANA, R. & PEDRÓS-ALIÓ, C. (2002). Changes in bacterial and archaeal assemblages in an equatorial river induced by the water eutrophication of Petit Saut dam reservoir (French Guiana). *Aquatic Microbial Ecology* **26**, 209–221.
- FAGERVOLD, S. K., BOURGEOIS, S., PRUSKI, A. M., CHARLES, F., KERHERVÉ, P., VÉTION, G. & GALAND, P. E. (2014). River organic matter shapes microbial communities in the sediment of the Rhône prodelta. *The ISME Journal* **8**, 2327–2338.
- *FEBRIA, C. M., BEDDOES, P., FULTHORPE, R. R. & WILLIAMS, D. D. (2012). Bacterial community dynamics in the hyporheic zone of an intermittent stream. *The ISME Journal* **6**, 1078–1088.
- FERIS, K., RAMSEY, P., FRAZAR, C., MOORE, J. N., GANNON, J. E. & HOLBEN, W. E. (2003). Differences in hyporheic-zone microbial community structure along a heavy-metal contamination gradient. *Applied and Environmental Microbiology* **69**, 5563–5573.
- *FERIS, K. P., RAMSEY, P. W., FRAZAR, C., RILLIG, M., MOORE, J. N., GANNON, J. E. & HOLBEN, W. E. (2004). Seasonal dynamics of shallow-hyporheic-zone microbial community structure along a heavy-metal contamination gradient. *Applied and Environmental Microbiology* **70**, 2323–2331.
- FERNANDES, I., PASCOAL, C., GUIMARÃES, H., PINTO, R., SOUSA, I. & CÁSSIO, F. (2012). Higher temperature reduces the effects of litter quality on decomposition by aquatic fungi. *Freshwater Biology* **57**, 2306–2317.
- *FERNÁNDEZ, D., VOSS, K., BUNDSCHUH, M., ZUBROD, J. P. & SCHÄFER, R. B. (2015). Effects of fungicides on decomposer communities and litter decomposition in vineyard streams. *Science of the Total Environment* **533**, 40–48.
- *FERREIRA, V., GULIS, V. & GRAÇA, M. A. S. (2006). Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* **149**, 718–729.
- *FORTUNATO, C. S. & CRUMP, B. C. (2011). Bacterioplankton community variation across river to ocean environmental gradients. *Microbial Ecology* **62**, 374–382.
- *FORTUNATO, C. S. & CRUMP, B. C. (2015). Microbial gene abundance and expression patterns across a river to ocean salinity gradient. *PLoS One* **10**, e0140578.
- FORTUNATO, C. S., HERFORT, L., ZUBER, P., BAPTISTA, A. M. & CRUMP, B. C. (2012). Spatial variability overwhelms seasonal patterns in bacterioplankton communities across a river to ocean gradient. *The ISME Journal* **6**, 554–563.
- FREIMANN, R., BÜRGMANN, H., FINDLAY, S. E. G. & ROBINSON, C. T. (2015). Hydrologic linkages drive spatial structuring of bacterial assemblages and functioning in alpine floodplains. *Frontiers in Microbiology* **6**, 1–15.
- FRIEDL, G. & WÜEST, A. (2002). Disrupting biogeochemical cycles - consequences of damming. *Aquatic Sciences* **64**, 55–65.
- *FROSSARD, A., GERULL, L., MUTZ, M. & GESSNER, M. O. (2013). Litter supply as a driver of microbial activity and community structure on decomposing leaves: a test in experimental streams. *Applied and Environmental Microbiology* **79**, 4965–4973.
- *FRYAR, S. C., YUEN, T. K., HYDE, K. D. & HODGKISS, I. J. (2001). The influence of competition between tropical fungi on wood colonization in streams. *Microbial Ecology* **41**, 245–251.
- *GADANHO, M. & SAMPAIO, J. (2004). Application of temperature gradient gel electrophoresis to the study of yeast diversity in the estuary of the Tagus river, Portugal. *FEMS Yeast Research* **5**, 253–261.
- GANNON, J. T., MANILAL, V. B. & ALEXANDER, M. (1991). Relationship between cell surface properties and transport of bacteria through soil. *Applied and Environmental Microbiology* **57**, 190–193.
- GARCÍA-ARMISEN, T., INCEOĞLU, Ö., OUATTARA, N. K., ANZIL, A., VERBANCK, M. A., BRION, N. & SERVAIS, P. (2014). Seasonal variations and resilience of bacterial communities in a sewage polluted urban river. *PLoS One* **9**, e92579.
- *GULIS, V. & SUBERKROPP, K. (2003). Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* **48**, 123–134.
- GURNELL, A., GOODSON, J., THOMPSON, K., CLIFFORD, N. & ARMITAGE, P. (2007). The river-bed: a dynamic store for plant propagules? *Earth Surface Processes and Landforms* **32**, 1257–1272.
- *HAMONTS, K., RYNGAERT, A., SMIDT, H., SPRINGAEL, D. & DEJONGHE, W. (2014). Determinants of the microbial community structure of eutrophic, hyporheic river sediments polluted with chlorinated aliphatic hydrocarbons. *FEMS Microbiology Ecology* **87**, 715–732.
- *HARNER, M. J., PIOTROWSKI, J. S., LEKBERG, Y., STANFORD, J. A. & RILLIG, M. C. (2009). Heterogeneity in mycorrhizal inoculum potential of flood-deposited sediments. *Aquatic Sciences* **71**, 331–337.
- HARNER, M. J., OPITZ, N., GELUSO, K., TOCKNER, K. & RILLIG, M. C. (2011). Arbuscular mycorrhizal fungi on developing islands within a dynamic river floodplain: an investigation across successional gradients and soil depth. *Aquatic Sciences* **73**, 35–42.
- *HARROP, B. L., MARKS, J. C. & WATWOOD, M. E. (2009). Early bacterial and fungal colonization of leaf litter in Fossil Creek, Arizona. *Journal of the North American Benthological Society* **28**, 383–396.
- HENDRICKS, S. P. (1993). Microbial ecology of the hyporheic zone: a perspective integrating hydrology and biology. *Journal of the North American Benthological Society* **12**, 70–78.
- HEINO, J. (2011). A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology* **56**, 1703–1722.
- HEPPELL, C. M., WORRALL, F., BURT, T. P. & WILLIAMS, R. J. (2002). A classification of drainage and macropore flow in an agricultural catchment. *Hydrological Processes* **16**, 27–46.
- HUYSMAN, F. & VERSTRAETE, W. (1993). Water-facilitated transport of bacteria in unsaturated soil columns: influence of cell surface hydrophobicity and soil properties. *Soil Biology and Biochemistry* **25**, 83–90.
- JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. (1989). The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium*, Canadian Special Publication of Fisheries and Aquatic Sciences (Volume 165, ed. D. P. Dodge), pp. 110–127. Government of Canada Publications, Ottawa.
- *KANE, D. F., TAM, W. Y. & GARETH JONES, E. B. (2002). Fungi colonising and sporulating on submerged wood in the River Severn, UK. *Fungal Diversity* **10**, 45–55.
- *KELLY, J. J., BANSAL, A., WINKELMAN, J., JANUS, L. R., HELL, S., WENCEL, M., BELT, P., KUEHN, K. a., RIER, S. T. & TUCHMAN, N. C. (2010). Alteration of microbial communities colonizing leaf litter in a temperate woodland stream by growth of trees under conditions of elevated atmospheric CO₂. *Applied and Environmental Microbiology* **76**, 4950–4959.
- *KOMINOSKI, J. S., HOELLEIN, T. J., KELLY, J. J. & PRINGLE, C. M. (2009). Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? *Oikos* **118**, 457–463.
- KRAUSS, G.-J., SOLÉ, M., KRAUSS, G., SCHLOSSER, D., WESENBERG, D. & BÄRLOCHER, F. (2011). Fungi in freshwaters: ecology, physiology and biochemical potential. *FEMS Microbiology Reviews* **35**, 620–651.
- KRISTIANSSON, E., FICK, J., JANZON, A., GRABIC, R., RUTGERSSON, C., WEIJDEGÅRD, B., SÖDERSTRÖM, H. & LARSSON, D. G. J. (2011). Pyrosequencing of antibiotic-contaminated river sediments reveals high levels of resistance and gene transfer elements. *PLoS One* **6**, e17038.
- *LIN, X., MCKINLEY, J., RESCH, C. T., KALUZNY, R., LAUBER, C. L., FREDRICKSON, J., KNIGHT, R. & KONOPKA, A. (2012). Spatial and temporal dynamics of the microbial community in the Hanford unconfined aquifer. *The ISME Journal* **6**, 1665–1676.
- LARNED, S. T., DATRY, T., ARSCOTT, D. B. & TOCKNER, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology* **55**, 717–738.
- LINDOW, S. E. & BRANDL, M. T. (2003). Microbiology of the Phyllosphere. *Applied and Environmental Microbiology* **69**, 1875–1883.
- LEGERF, A. & CHAUVET, E. (2008). Diversity and functions of leaf-decaying fungi in human-altered streams. *Freshwater Biology* **53**, 1658–1672.
- *LEGERF, A., DOBSON, M., DANG, C. K. & CHAUVET, E. (2005). Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* **146**, 432–442.
- LEIBOLD, M. a., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J. M., HOOPES, M. F., HOLT, R. D., SHURIN, J. B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.
- LIU, J., SOININEN, J., HAN, B. P. & DECLERCK, S. a. J. (2013). Effects of connectivity, dispersal directionality and functional traits on the metacommunity structure of river benthic diatoms. *Journal of Biogeography* **40**, 2238–2248.
- LIVINGSTON, G., JIANG, Y., FOX, J. & LEIBOLD, M. (2013). The dynamics of community assembly under sudden mixing in experimental microcosms. *Ecology* **94**, 2898–2906.
- LOGUE, J. B., MOUQUET, N., PETER, H. & HILLEBRAND, H. (2011). Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution* **26**, 482–491.
- LOREAU, M., MOUQUET, N. & HOLT, R. D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters* **6**, 673–679.
- LOWELL, J. L., GORDON, N., ENGSTROM, D., STANFORD, J. A., HOLBEN, W. E. & GANNON, J. E. (2009). Habitat heterogeneity and associated microbial community structure in a small-scale floodplain hyporheic flow path. *Microbial Ecology* **58**, 611–620.
- LOZUPONE, C. a. & KNIGHT, R. (2007). Global patterns in bacterial diversity. *Proceedings of the National Academy of Sciences* **104**, 11436–11440.
- MANERKAR, M. a., SEENA, S. & BÄRLOCHER, F. (2008). Q-RT-PCR for assessing archaea, bacteria, and fungi during leaf decomposition in a stream. *Microbial Ecology* **56**, 467–473.
- MARDHIAH, U., CARUSO, T., GURNELL, A. & RILLIG, M. C. (2014). Just a matter of time: fungi and roots significantly and rapidly aggregate soil over four decades along the Tagliamento River, NE Italy. *Soil Biology and Biochemistry* **75**, 133–142.
- MARTINS, J. M. F., MAJDALANI, S., VITORGE, E., DESAUNAY, A., NAVEL, A., GUINÉ, V., DAÍAN, J. F., VINCE, E., DENIS, H. & GAUDET, J. P. (2013). Role of macropore flow in the transport of *Escherichia coli* cells in undisturbed cores of a brown leached soil. *Environmental Science: Processes & Impacts* **15**, 347–356.
- MAŠÍN, M., JEZBERA, J., NEDOMA, J., STRAŠKRABOVÁ, V., HEJZLAR, J. & ŠIMEK, K. (2003). Changes in bacterial community composition and microbial activities along the longitudinal axis of two canyon-shaped reservoirs with different inflow loading. *Hydrobiologia* **504**, 99–113.

- McCLUNEY, K. E., POFF, N. L., PALMER, M. A., THORP, J. H., POOLE, G. C., WILLIAMS, B. S., WILLIAMS, M. R. & BARON, J. S. (2014). Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Frontiers in Ecology and the Environment* **12**, 48–58.
- MEADEN, S., METCALF, C. J. E. & KOSKELLA, B. (2016). The effects of host age and spatial location on bacterial community composition in the English Oak tree (*Quercus robur*). *Environmental Microbiology Reports* **8**, 649–658.
- MOSIER, A. C. & FRANCIS, C. A. (2008). Relative abundance and diversity of ammonia-oxidizing archaea and bacteria in the San Francisco Bay estuary. *Environmental Microbiology* **10**, 3002–3016.
- *NIKOLCHEVA, L. G. & BÄRLOCHER, F. (2004). Taxon-specific fungal primers reveal unexpectedly high diversity during leaf decomposition in a stream. *Mycological Progress* **3**, 41–49.
- *NIKOLCHEVA, L. G. & BÄRLOCHER, F. (2005). Seasonal and substrate preferences of fungi colonizing leaves in streams: traditional versus molecular evidence. *Environmental Microbiology* **7**, 270–280.
- NIKOLCHEVA, L. G., COCKSHUTT, A. M. & BÄRLOCHER, F. (2003). Determining diversity of freshwater fungi on decaying leaves: comparison of traditional and molecular approaches. *Applied and Environmental Microbiology* **69**, 2548–2554.
- *PASCOAL, C. & CÁSSIO, F. (2004). Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied and Environmental Microbiology* **70**, 5266–5273.
- POFF, N. L. & HART, D. D. (2002). How dams vary and why it matters for the emerging science of dam removal. *Bioscience* **52**, 659–668.
- POFF, L. N., ALLAN, J. D., BAIN, M. B., KARR, J. R., PRESTEGAARD, K. L., RICHTER, B. D., SPARKS, R. E. & STROMBERG, J. C. (1997). The natural flow regime. *Bioscience* **47**, 769–784.
- POLIS, G. a., ANDERSON, W. B. & HOLT, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**, 289–316.
- RAYMOND, P. A., SAIRS, J. E. & SOBCHAK, W. V. (2015). Hydrological and biogeochemical controls on watershed dissolved organic matter transport: pulse-shunt concept. *Ecology* **97**, 5–16.
- READ, D. S., GWEON, H. S., BOWES, M. J., NEWBOLD, L. K., FIELD, D., BAILEY, M. J. & GRIFFITHS, R. I. (2015). Catchment-scale biogeography of riverine bacterioplankton. *The ISME Journal* **9**, 516–526.
- REED, H. E. & MARTINY, J. B. H. (2013). Microbial composition affects the functioning of estuarine sediments. *The ISME Journal* **7**, 868–879.
- RILLIG, M. C., ANTONOVICS, J., CARUSO, T., LEHMANN, A., POWELL, J. R., VERESOGLOU, S. D. & VERBRUGGEN, E. (2015). Interchange of entire communities: microbial community coalescence. *Trends in Ecology & Evolution* **30**, 470–476.
- RINKLEBE, J. & LANGER, U. (2006). Microbial diversity in three floodplain soils at the Elbe River (Germany). *Soil Biology and Biochemistry* **38**, 2144–2151.
- *RINKLEBE, J. & LANGER, U. (2008). Floodplain soils at the Elbe river, Germany, and their diverse microbial biomass. *Archives of Agronomy and Soil Science* **54**, 259–273.
- RUBIN, M. A. & LEFF, L. G. (2007). Nutrients and other abiotic factors affecting bacterial communities in an Ohio River (USA). *Microbial Ecology* **54**, 374–383.
- *RUIZ-GONZÁLEZ, C., PROIA, L., FERRERA, I., GASOL, J. M. & SABATER, S. (2013). Effects of large river dam regulation on bacterioplankton community structure. *FEMS Microbiology Ecology* **84**, 316–331.
- RUIZ-GONZÁLEZ, C., NIÑO-GARCÍA, J. P. & DEL GIORGIO, P. a. (2015). Terrestrial origin of bacterial communities in complex boreal freshwater networks. *Ecology Letters* **18**, 1198–1206.
- SAVIO, D., SINCLAIR, L., IJAZ, U. Z., PARAJKA, J., REISCHER, G. H., STADLER, P., BLASCHKE, A. P., BLÖSCHL, G., MACH, R. L., KIRSCHNER, A. K. T., FARNLEITNER, A. H. & EILER, A. (2015). Bacterial diversity along a 2600 km river continuum. *Environmental Microbiology* **17**, 4994–5007.
- *SEENA, S., WYNBERG, N. & BÄRLOCHER, F. (2008). Fungal diversity during leaf decomposition in a stream assessed through clone libraries. *Fungal Diversity* **30**, 1–14.
- STEGEN, J. C., FREDRICKSON, J. K., WILKINS, M. J., KONOPKA, A. E., NELSON, W. C., ARNTZEN, E. V., CHRISLER, W. B., CHU, R. K., DANCZAK, R. E., FANSLER, S. J., KENNEDY, D. W., RESCH, C. T. & TFAILY, M. (2016). Groundwater–surface water mixing shifts ecological assembly processes and stimulates organic carbon turnover. *Nature Communications* **7**, 11237.
- SOPHOCLEOUS, M. (2002). Interactions between groundwater and surface water: the state of the science. *Hydrogeology Journal* **10**, 52–67.
- SIEROCINSKI, P., MILFERSTEDT, K., BAYER, F., GROSSKOPF, T., ALSTON, M., SWARBRECK, D., HOBBS, P. J., SOYER, O. S. & HAMELIN, J. (2017). A single community dominates structure and function of a mixture of multiple methanogenic communities. *Current Biology* **27**, 3390–3395.e4.
- SOININEN, J. (2014). A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* **95**, 3284–3292.
- SRIDHAR, K. R. & BÄRLOCHER, F. (1993). Aquatic hyphomycetes on leaf litter in and near a stream in Nova Scotia, Canada. *Mycological Research* **97**, 1530–1535.
- *SRIDHAR, K. R., DUARTE, S., CÁSSIO, F. & PASCOAL, C. (2009). The role of early fungal colonizers in leaf-litter decomposition in Portuguese streams impacted by agricultural runoff. *International Review of Hydrobiology* **94**, 399–409.
- *STALEY, C., UNNO, T., GOULD, T. J., JARVIS, B., PHILLIPS, J., COTNER, J. B. & SADOWSKY, M. J. (2013). Application of Illumina next-generation sequencing to characterize the bacterial community of the Upper Mississippi River. *Journal of Applied Microbiology* **115**, 1147–1158.
- *STUTTER, M. I. & RICHARDS, S. (2012). Relationships between soil physicochemical, microbiological properties, and nutrient release in buffer soils compared to field soils. *Journal of Environment Quality* **41**, 400.
- *SUBERKROPP, K. & CHAUVET, E. (1995). Regulation of leaf breakdown by fungi in streams: influences of water chemistry. *Ecology* **76**, 1433–1445.
- TIKHONOV, M. (2016). Community-level cohesion without cooperation. *eLife* **5**. <https://doi.org/10.7554/eLife.15747.001>
- TOCKNER, K. & STANFORD, J. a. (2002). Riverine flood plains: present state and future trends. *Environmental Conservation* **29**, 308–330.
- TOCKNER, K., PENNETZDORFER, D., REINER, N., SCHIEMER, F. & WARD, J. V. (1999). Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology* **41**, 521–535.
- *TOLKKINEN, M., MYKRÄ, H., ANNALA, M., MARKKOLA, A. M., VUORI, K. M. & MUOTKA, T. (2015). Multi-stressor impacts on fungal diversity and ecosystem functions in streams: natural vs. anthropogenic stress. *Ecology* **96**, 672–683.
- TORNWALL, B., SOKOL, E., SKELTON, J. & BROWN, B. (2015). Trends in stream biodiversity research since the river continuum concept. *Diversity* **7**, 16–35.
- UNGER, I. M., KENNEDY, A. C. & MUZIKA, R.-M. (2009). Flooding effects on soil microbial communities. *Applied Soil Ecology* **42**, 1–8.
- VANNOTE, R. L., MINSHALL, G. W., CUMMINS, K. W., SEDELL, J. R. & CUSHING, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137.
- VÖRÖSMARTY, C. J., MCINTYRE, P. B., GESSNER, M. O., DUDGEON, D., PRUSEVICH, A., GREEN, P., GLIDDEN, S., BUNN, S. E., SULLIVAN, C. a., LIERMANN, C. R. & DAVIES, P. M. (2010). Global threats to human water security and river biodiversity. *Nature* **468**, 334–334.
- WAGNER, K., BENGTSOON, M. M., BESEMER, K., SIECZKO, A., BURNS, N. R., HERBERG, E. R. & BATTIN, J. (2014). Functional and structural responses of hyporheic biofilms to varying sources of dissolved organic matter. *Applied and Environmental Microbiology* **80**, 6004–6012.
- WAKELIN, S. A., COLLOFF, M. J. & KOOKANA, R. S. (2008). Effect of wastewater treatment plant effluent on microbial function and community structure in the sediment of a freshwater stream with variable seasonal flow. *Applied and Environmental Microbiology* **74**, 2659–2668.
- WARD, J. V. (1989). The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* **8**, 2–8.
- WARD, J. & STANFORD, J. (1983). The serial discontinuity concept of lotic ecosystems. In *Dynamics of Lotic Ecosystems* (eds T. D. FONTAINE III and S. M. BARTELL), pp. 29–42. Ann Arbor Science, Ann Arbor.
- WARD, J. & STANFORD, J. A. (2001). Revising the serial discontinuity concept. *Regulated Rivers: Research & Management* **17**, 303–310.
- WEBSTER, G., O'SULLIVAN, L. A., MENG, Y., WILLIAMS, A. S., SASS, A. M., WATKINS, A. J., PARKES, R. J. & WEIGHTMAN, A. J. (2015). Archaeal community diversity and abundance changes along a natural salinity gradient in estuarine sediments. *FEMS Microbiology Ecology* **91**, 1–18.
- *WHITFIELD, L., RICHARDS, a. J. & RIMMER, D. L. (2004). Relationships between soil heavy metal concentration and mycorrhizal colonisation in *Thymus polytrichus* in northern England. *Mycorrhiza* **14**, 55–62.
- WILSON, J. S., BALDWIN, D. S., REES, G. N. & WILSON, B. P. (2011). The effects of short-term inundation on carbon dynamics, microbial community structure and microbial activity in floodplain soil. *River Research and Applications* **27**, 213–225.
- WOLANSKI, E. (2007). Estuarine water circulation. In *Estuarine Ecohydrology*, pp. 17–39. Elsevier Amsterdam, The Netherlands.

VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article. **Table S1.** Studies reviewed and included in Figs 2 and 3. CC, community coalescence; Y, yes; N, no; P, non-comprehensive or inconclusive.

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