









## FOCUS ARTICLE

# Streambed migration frequency drives ecology and biogeochemistry across spatial scales

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## Abstract

The bed of fluvial ecosystems plays a major role in global biogeochemical cycles. All fluvial sediments migrate and although responses of aquatic organisms to such movements have been recorded there is no theoretical framework on how the frequency of sediment movement affects streambed ecology and biogeochemistry. We here developed a theoretical framework describing how the moving-resting frequencies of fine-grained sediments constrain streambed communities across spatial scales. Specifically, we suggest that the most drastic impact on benthic and hyporheic communities will exist when ecological and biogeochemical processes are at the same temporal scale as the sediment moving-resting frequency. Moreover, we propose that the simultaneous occurrence of streambed patches differing in morphodynamics should be considered as an important driver of metacommunity dynamics. We surmise that the frequency of patch transition will add new dimensions to the understanding of biogeochemical cycling and metacommunities from micro-habitat to segment scales. This theoretical framework is important for fluvial ecosystems with frequent sediment movement, yet it could be applied to any other dynamic habitat.

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**KEYWORDS**

benthic and hyporheic communities, environmental filtering, hierarchical spatial and temporal scaling, process time scale, sediment transport frequency

## 1 | THE IMPORTANCE OF STREAMBEDS IN FLUVIAL ECOSYSTEMS

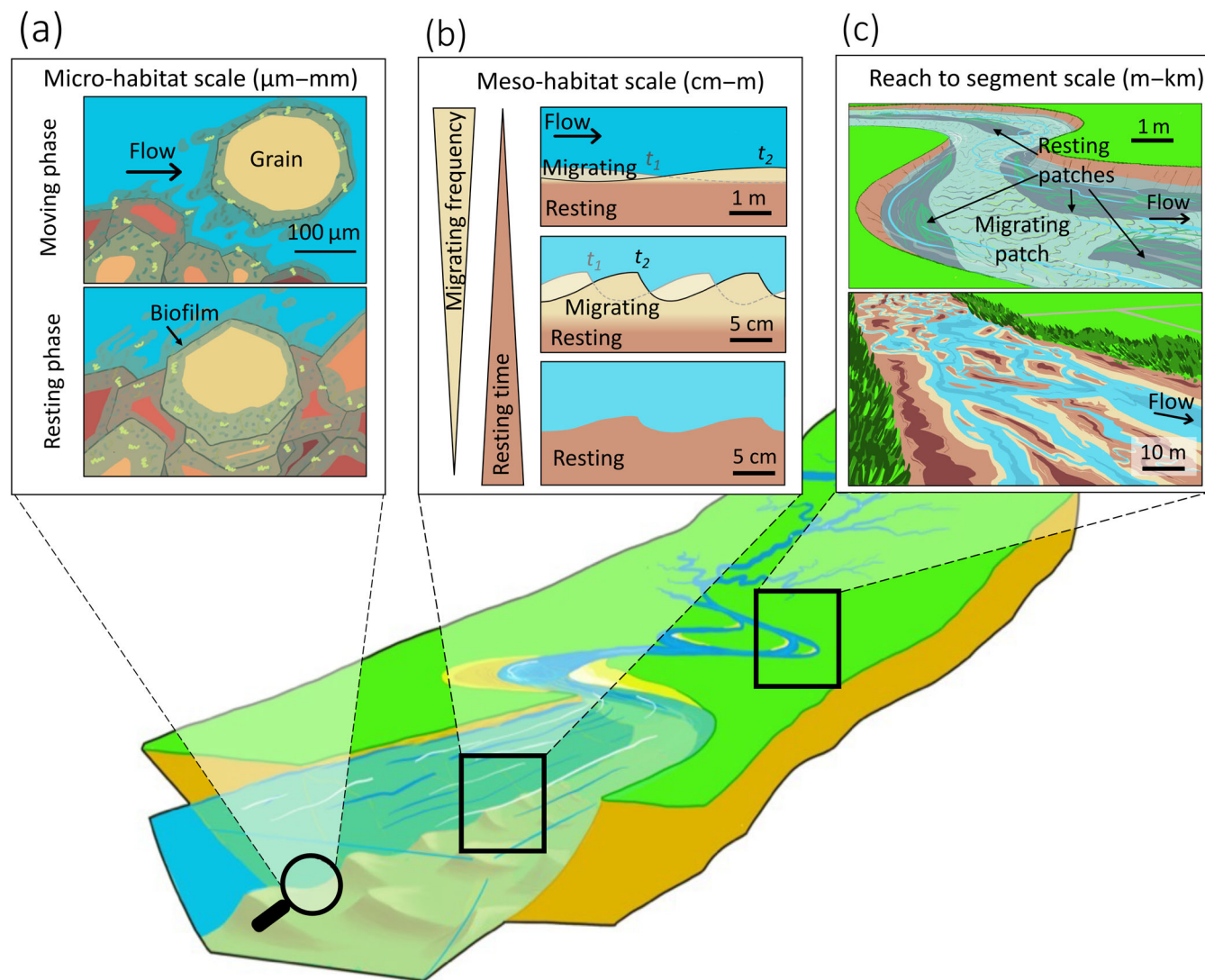
The metabolic hotspots of fluvial ecosystems often occur at and below the water–sediment interface, making the bed of streams and rivers an important zone for global biogeochemical transformation processes (Battin et al., 2016; Krause et al., 2017; Peralta-Maraver et al., 2021). Streams and rivers (hereafter streams) have a disproportionate impact on global biogeochemical cycles given their small surface area relative to other aquatic and terrestrial environments (Cole et al., 2007; Drake et al., 2018). Emission of carbon dioxide related to streams was recently estimated to range between 2% and 7% (1.1–3.9 Pg C year<sup>-1</sup>) of terrestrial emissions (54 Pg C year<sup>-1</sup>), even though streams cover only 0.6% of the non-glaciated land surface (Allen & Pavelsky, 2018; Regnier et al., 2013). Streams also recycle nutrients at much higher rates than other aquatic systems, as they are imported from terrestrial environments and rapidly mineralized by diverse benthic and hyporheic communities (Battin et al., 2016; Romani et al., 2008).

Despite the rigidity of individual sediment grains, most streambeds migrate continuously or episodically when the shear stress of flow exceeds the force needed to move individual grains (Bridge, 2003). Most streambeds migrate, but sediment transport is expected to be much more frequent in lowland streams with sizes of grain that range between fine sand to very fine gravel (0.063–4 mm, respectively), defined herein as “fine sediments” (Buffington & Montgomery, 2021; Frings, 2008; Kondolf et al., 2016). Sediment grains spend variable amounts of time moving (rolling, saltating, or suspended) and resting under different flow conditions. Consequently, the structure of stream channels and floodplains develops through the long-term effects of geology (e.g., sediment inputs), hydrology (e.g., water flow), and biology (e.g., stabilization by vegetation) (Buffington & Montgomery, 2021; Dietrich & Perron, 2006; Kondolf et al., 2016; Montgomery & Buffington, 1997; Perucca et al., 2007). Hereafter we refer to periods where streambed sediments are in motion as the “moving phase” and when not in motion as the “resting phase” (Nikora et al., 2002; Zhang et al., 2012).

The ecological and biogeochemical consequences of morphodynamics are well recognized and have generated several scientific concepts on disturbance (Lake, 2000; Resh et al., 1988) and ecological memory (Ortmann-Ajkai et al., 2014). However, the concept of disturbance in stream ecology focuses primarily on catastrophic flood events that occur infrequently (recurrence interval of years or decades) and over large spatial scales (typically catchment scales). This binary view of normal low flow (resting phase) versus infrequent disturbance (moving phase) is overly simplistic and does not capture processes occurring in streams with frequent movement of fine sediments (Kondolf et al., 2016; Ryo et al., 2019; Segura et al., 2011). Here we extend this concept of disturbance in stream ecology to streambeds with fine sediments, and introduce a new theoretical framework on how moving-resting frequency affects stream ecology and biogeochemistry. We first describe the physical environment in migrating streambeds. Afterwards we discuss the ecological and biogeochemical consequences of sediment migration across a range of frequencies and spatial scales by incorporating insights from freshwater and marine environments. Finally, we explore new research perspectives that this viewpoint generates.

## 2 | MORPHODYNAMICS OF FINE-GRAINED FLUVIAL ECOSYSTEMS

Streambed habitat reflects the physical structure and dynamics from a single sediment grain to the whole channel morphodynamics over spatial scales from micrometers to kilometers (Figure 1). Modeling frameworks evaluate sediment transport of single grains in terms of the frequency, intensity, and duration of moving versus resting phases (Figure 1a) (Nikora et al., 2002; Zhang et al., 2012). Sediment grains are mobilized at the streambed–water interface via turbulent eddies or collision with other moving grains. At meso-habitat scale (1 cm to 100 m), coupling between flow, sediment transport, and channel produces migrating bedforms such as upper stage plane bed, ripples, dunes and bars (Figure 1b), which can be classified based on the grain size, bed and water level slope, water depth, flow velocity, and degree of lateral channel confinement (Andreotti et al., 2012; Garcia, 2008; Montgomery & Buffington, 1997; Rinaldi et al., 2016). Single sediment grains within migrating bedforms experience a moving-resting cycle with specific migration frequency and resting duration. High migration frequency and short resting duration are typical for an upper stage



**FIGURE 1** Morphodynamics of fine sediments (fine sand to very fine gravel) at different spatial scales. (a) Micro-habitat scale ( $\mu\text{m}$  to  $\text{mm}$ ) where the colonization of a single sediment grain by biofilms may have a large impact on the grain scale environment and migration. These sediment grains can move (top panel) or rest (bottom panel) according to the flow regime. (b) Meso-habitat scale ( $\text{cm}$  to  $\text{m}$ ) highlights that bedforms are established at a specific range of flow velocities and sediment grain sizes. Migration frequency and resting duration of sediment grains are consequences of bedform dynamics. The panels illustrate the sideview of the streambed at the upper stage plane bed (top panel), where a thin layer of grains is almost continuously in saltation and bounce over the streambed that undulates in waves (few  $\text{mm}$  in height), migrating ripples and dunes (central panel), where the mobile streambed layer corresponds to the height of the bedform (about  $1\text{ cm}$  in height), and the resting streambed sediments without a mobile layer (bottom panel). Bedform height is not to scale and displayed higher than in reality. (c) Streambed heterogeneity at reach to segment scale ( $\text{m}$  to  $\text{km}$ ) often constitutes a mosaic of migrating and resting sediment patches. This streambed heterogeneity is controlled by the history of sediment inputs, flow conditions, and lateral interactions within the active channel and between the channel, banks, and floodplain.

plane bed, in which the surficial sediment grains are almost continuously in saltation and bounce downstream (Naqshband et al., 2017), while lower migration frequency and intermediate resting duration typically occurs in ripples and dunes, in which sediment grains become buried and remobilized by the passage of bedforms (Buffington & Montgomery, 2021; Kondolf et al., 2016; Raudkivi, 2006).

Stream velocity varies both laterally and longitudinally, producing patches of different migrating bedforms that evolve over time at the reach scale ( $100\text{ m}$  to  $\text{km}$ ). Even small changes of discharge generate fluctuations in the size and spatial distribution of the migrating and resting patches (Figure 1c). The proportion of the streambed in motion is modulated by in-stream features such as boulders and woody debris providing local streambed stability (Krause et al., 2014).

At the segment scale (10–100 km), resting times of sediments in the range of months to decades are set by the frequency of large flood events, which are sometimes described as channel-forming flows (Phillips & Jerolmack, 2014; Tockner et al., 2003). These infrequent events yield large-scale morphodynamic processes extending over the entire channel such as deep sediment relocation, meander scrolling, and channel avulsion (David et al., 2017; Venditti et al., 2017). During such high flow events, grains can be transported between the active stream channel and the floodplain, as well as within the main channel (Buffington & Montgomery, 2021; Frings, 2008; Lewin et al., 2017).

### 3 | ECOLOGICAL IMPLICATIONS OF MOVING AND RESTING PHASE AT MICRO-HABITAT SCALE

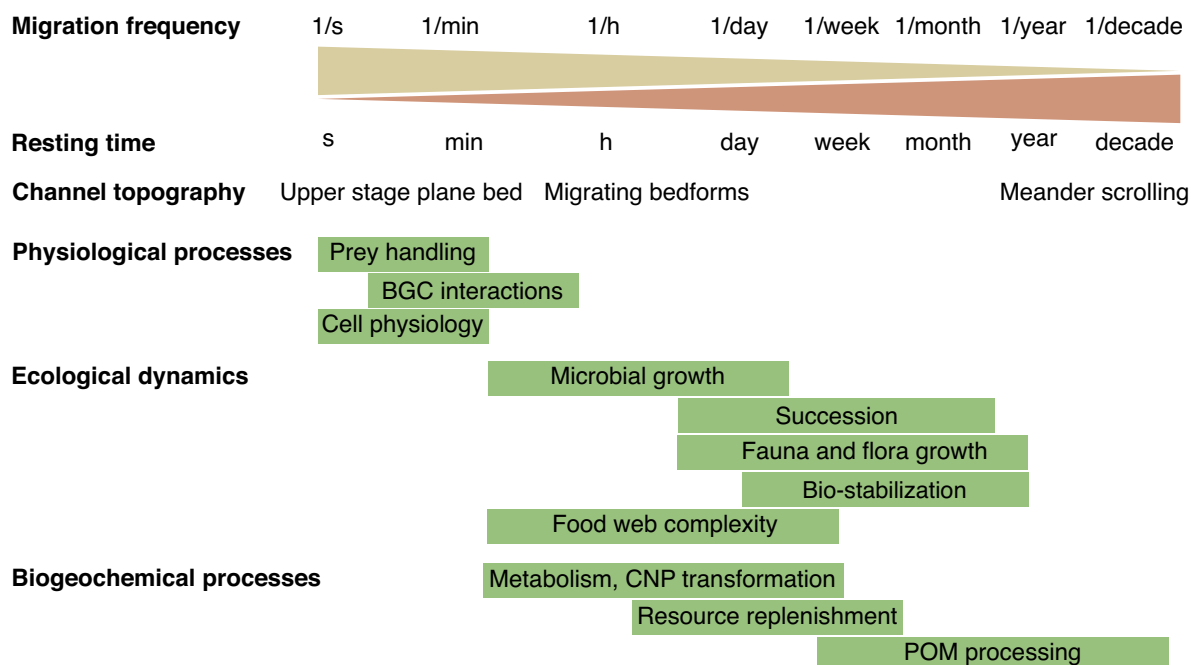
Phototrophic and heterotrophic microbes (including both prokaryotes and protists) are the building blocks of biofilms that grow on all types of aquatic surfaces (micro-habitat scale; Figure 1a). Stability of sediment grains during the resting phase enables the growth and succession of biofilms in the benthic and hyporheic zone (Figure 1a), which in turn supports diverse food web interactions. Phototrophic and heterotrophic microbes utilize the available resources from the sediment pore water, such as oxygen, nutrients and dissolved organic carbon, which are then transferred to micro-grazers such as protists (Augspurger et al., 2008; Norf et al., 2009; Risse-Buhl et al., 2012). Metazoa, including both meio- and macrofauna, contribute to food web interactions during prolonged resting phases, when they have time to reproduce (Majdi & Traunspurger, 2015; Weitere et al., 2018). In turn, grazing promotes energy transfer and boosts microbial activity by keeping the community in a productive state (Oprei et al., 2019; Peralta-Maraver et al., 2019; Risse-Buhl et al., 2015).

Excessive microbial growth that includes secretions of extracellular polymeric substances (EPS) during prolonged resting phases (weeks to months) stabilizes the streambed, reduces the frequency of sediment remobilization and decreases the exchange of resources between the overflowing water and the streambed (Caruso et al., 2017; Cook et al., 2020; Mendoza-Lera & Mutz, 2013). The processes of bio-stabilization and bio-clogging are caused not only by bacterial biofilms and algal mats, which produce multicellular networks and EPS (Gerbersdorf et al., 2020; Malarkey et al., 2015; Paterson et al., 2018), but also by macrofaunal structures such as mucus, silk secretions, cases and nets (Albertson et al., 2019; Majdi et al., 2014).

The biofilm community colonizing single sediment grains can endure significant changes in environmental conditions as migration frequencies change. Migration frequency of once per minute to once per day occurring in migrating bedforms affects both structure and growth rates of the benthic and hyporheic communities (Scheidweiler et al., 2021; Zlatanović et al., 2017). Microbial doubling times are generally in the range of minutes to days (Aufrecht et al., 2019; Bar-Zeev et al., 2012; Sinsabaugh et al., 2015; Zlatanović et al., 2017; Figure 2). Consequently, microbial growth will be inhibited when growth rates are longer than the sediment migration frequency, owing to the physical disturbance of the growing community. As growth rates are species-specific, sediment migration results in the selection of species with growth rates shorter than migration frequency and a shift in the benthic and hyporheic community structure compared to resting streambed patches. Furthermore, diatom frustules, biofilms as well as benthic and hyporheic fauna endure mechanical damages and dispersal by abrasion when colliding with moving grains (Delgado et al., 1991; Luce et al., 2010; Luce et al., 2013; Miller, 1989; Probandt et al., 2018). Motile bacteria and diatoms are mainly found to colonize fissures and crevices of sand grains, where they are subject to lower mechanical forces (Ahmerkamp et al., 2020; Jewson et al., 2006; Krejci & Lowe, 1986; Miller et al., 1987; Weise & Rheinheimer, 1978). The mechanical forces thus act as an environmental filter constraining the community to the habitable area of sediment grains.

We expect biological traits such as small cell size, motility, robust shells or diatom frustules, as well as greater adhesion (e.g., via stalks and EPS) to be advantageous for the colonization of moving grains in migrating patches because of the greater mechanical challenge associated with this habitat (DeJonge, 1985; Delgado et al., 1991; Hou et al., 2018; Risse-Buhl et al., 2014). High shear forces cause changes in EPS properties (e.g., stiffer and more adhesive polysaccharides) and production (e.g., over production of polysaccharides), resulting in stronger cohesion and surface adhesion (Chew et al., 2014; Hou et al., 2018; Stoodley et al., 2002). Despite this protective mechanism, sediment migration can impair cell–cell interactions (Remis et al., 2010; Rivera-Yoshida et al., 2018), and consequently limit interactions between microbial species. Important limitations could include: impaired quorum sensing when flow causes autoinducer molecules to disperse (Kim et al., 2016), decreased proximity of fungi and bacteria repressing transfer of nutrients (Arnon et al., 2010; Lock et al., 1984), and decreased bacterial utilization of labile DOC released by phototrophic protists (Romaní et al., 2004).

Doubling times of meio- and macro-fauna and -flora range from weeks to months (Olsen & Townsend, 2005; Riis & Sand-Jensen, 2006; Utz & Hilderbrand, 2011), impairing the ability of these organisms to colonize migrating sediments with shorter resting phases. However, larger organisms use strategies such as burrowing, adhesion or clinging to



**FIGURE 2** Time scales of the migration frequency and resting duration of sediments at which they impact different physiological processes, ecological dynamics and biogeochemical processes. Biogeochemical (BGC) interactions include inter-species communications (e.g., bacterial quorum sensing) as well as multi-species interaction (e.g., exchange of labile DOC components, competition). Temporal scales at which sediment migration may affect the different cellular, ecological, and biogeochemical processes are indicated by the green boxes.

surfaces, and case construction to resist the effects of mechanical forces, allowing them to survive in such conditions (de la Fuente et al., 2018; Kryvokhyzhyna et al., 2022; Swan & Palmer, 2000; Wood et al., 2010). Indeed, these strategies might act to stabilize the streambed and reduce sediment transport as pointed out above. Similarly, excessive development of biofilms, density-dependent growth of macrophytes (e.g., Heffernan, 2008), or regrowth of macrophytes from rhizomes resulting in bio-stabilization and bio-clogging of sediments. As a consequence, this process causes longer sediment resting duration and accelerates community recovery from streambed migration. Thus, ecological mechanisms of resistance and resilience to sediment migration at micro-habitat scale introduce non-linearity into the relationship between migration frequency at meso-habitat scale and ecological processes.

#### 4 | CONCEPT OF MIGRATION FREQUENCY AT MESO-HABITAT SCALE

Based on the current state of knowledge related to migrating streambeds, we hypothesize that physiological processes, ecological dynamics and biogeochemical processes are affected primarily when their time scale and the migration frequency of the sediment coincide (Figure 2). The different migration frequencies and resting durations of the sediment grains considered in Figure 2 can be aligned with the channel topography of fine sediment streambeds at meso-habitat scale (Figure 1b). Migration frequency acts synergistically as an environmental filter (Poff, 1997) for the establishment of streambed communities and their associated biogeochemical functions. Considering physiological processes at the cellular level (Figure 2), prey handling time of flagellates (heterotrophic protists) ranges between 2 and 300 s (Boenigk & Arndt, 2002) indicating inhibition of food uptake at sediment migration frequencies in the range of 1/s and 1/min. Thus, at shorter resting phases, inter-species interactions in food webs or during succession and biological modification of habitat are likely to be less important relative to mechanical challenges.

Considering ecological dynamics (Figure 2), the frequency of sediment migration generally correlates negatively with biofilm biomass (Luce et al., 2010). We expect a shift in microbial community composition from eukaryotic phototrophs to prokaryotic phototrophs and heterotrophs with increasing migration frequency. Biofilms regrowing within hours can colonize migrating streambed patches (Aufrecht et al., 2019), while macrophytes with a slower growth rate (doubling

time of aboveground biomass 10–100 days) require long periods of sediment stability to re-establish following floods (Nielsen & Sand-Jensen, 1991; Riis & Sand-Jensen, 2006). Microcrustacean densities are higher in low shear stress patches (and thus lower frequency of sediment movement) where they also recover faster after a flood, than in high shear stress patches (Robertson et al., 1995). Slower growth rates of some meio- and macro-fauna species are expected to truncate food webs, reducing diversity and ecological interactions in migrating sediments compared to resting sediments (Hatton et al., 2019; Xuehua et al., 2009). Biogeochemical processes are differentially affected by migration frequency depending on their processing time or bioavailability, microbial and fauna growth (Figure 2). These examples draw on existing ecological knowledge of biota and sediment morphodynamics. To our knowledge there are no studies explicitly designed to provide proof of our postulated theoretical framework on the ecological and sediment morphodynamic time scales, calling for further complementary research.

## 5 | CONCEPT OF MIGRATING-RESTING PATCH TRANSITION AT LARGER SCALE

Frequent migrating and resting sediment patches occur simultaneously at larger spatial scales (Figure 1c) and should be considered as an important driver of metacommunity dynamics. Within the streambed metacommunity (Leibold et al., 2004), sediment migration horizontally homogenizes the landscape, thus, reducing meiofauna species diversity (Schratzberger & Larcombe, 2014), while supporting their passive horizontal displacement (Levin & DiBacco, 1995). Simultaneously, sediment migration enhances the vertical mixing of benthic and hyporheic interstitial communities (Kryvokhyzhyna et al., 2022). Phototrophs as well as small vermiform meio- and macro-fauna actively move and burrow deeper into the streambed to take refuge avoiding the mechanical challenges in the upper migrating sediment layers (Dole-Olivier et al., 1997; Fegley, 1987; Gaudes et al., 2010; Robertson & Wood, 2010). In addition to the passive displacement and active movement within the streambed, organisms that are unable to burrow might be dispersed into the water column, either as individual organisms or aggregates of streambed sediments and biofilms (protobiofilms), and consequently drift downstream with the flow (Bar-Zeev et al., 2012; Risse-Buhl et al., 2014; Shimeta et al., 2003). Drifting organisms and protobiofilms generally settle in areas of low flow and resting sediment (James et al., 2009; Palmer, 1992) and rapidly recolonize the streambed within minutes to days (Arndt et al., 2003; Bar-Zeev et al., 2012; Robertson, 2000). Thus, the local communities of distinct streambed patches are connected both via downstream drift and dispersal within the streambed. Hence, the heterogeneous distribution of migrating and resting patches within the streambed are expected to increase  $\beta$ -diversity at reach to segment scale.

Species-specific requirements, local patch-specific factors (environmental filters) and dispersal processes all drive  $\beta$ -diversity (Bo et al., 2020; Soininen & Teittinen, 2019; Tolonen et al., 2018). We hypothesize that metacommunity dynamics are structured by the distribution of migrating and resting patches in the reach that includes their spatial arrangement and areal coverage as well as the frequency of migrating-resting patch transition. Consequently, it is likely that benthic and hyporheic communities will experience transport-resting cycles at nested spatio-temporal scales: (1) The moving-resting cycle of single sediment grains occurs at a gradient of frequencies at meso-habitat scale, and (2) the transition of migrating-resting patches occurs at a much lower frequency driven by larger-scale fluvial constraints such as discharge variability, water depth and sediment load at reach to segment scale. The nestedness of spatio-temporal scales highlights the need for cross-scale observations in future research.

It is still unknown to what extent individual populations or communities adapt to new conditions after migrating-resting patch transition. Previous studies suggest that communities from migrating ripples can adjust to resting conditions within a few days (Atkinson et al., 2008; Miller, 1989; Zlatanović et al., 2017), although the antecedent sediment transport conditions can affect community responses (Scheidweiler et al., 2021). This behavior suggests that these communities are not only adapted to the most-prevalent environmental conditions of their local habitat, but also to the larger scale frequency of migrating-resting patch transitions of fluvial systems. This idea extends the intermediate disturbance hypothesis that focused on temporal scales (Connell, 1978) to spatio-temporal patterns in streambed habitats driven by larger-scale fluvial processes. Therefore, we suggest that  $\gamma$ -diversity peaks at specific transition frequency and areal coverage of migrating and resting patches, and thus is lower when the whole streambed is composed either of resting or migrating sediment patches.

## 6 | IMPLICATIONS ON BIOGEOCHEMICAL PROCESSES

Availability of resources (e.g., dissolved gases, dissolved and particulate organic matter and nutrients) becomes the primary rate-limiting factor for biological uptake rates during prolonged resting phases at slow flow velocities (Battin

et al., 2003; De Falco et al., 2018; Figure 2). Increasing stream water velocity induces bedform migration and improves resource availability by increasing the advective exchange flux between the flowing water and the streambed (Arnon et al., 2007; Wolke et al., 2020). During bedform migration, porewater exchange is also influenced by the movement of the grains. Porewater is released from the upstream part of the bedform and may be trapped in the downstream part of the bedform. This process is commonly termed “turnover” and may become dominant over advection driven exchange at relatively high bedform migration velocities (Elliott & Brooks, 1997; Packman et al., 2000).

The heterotrophic activity and resource recycling is ultimately affected by a combination of resource availability, porewater exchange and local reaction rates (Zheng et al., 2019). For example, local respiration rates and resource removal decrease as bedform migration velocity increases (Ahmerkamp et al., 2017; Wolke et al., 2020; Zheng et al., 2019). In comparison to resting sediments, lower bacterial abundance in migrating sediments could potentially explain the lower heterotrophic respiration rates (Scheidweiler et al., 2021; Zlatanović et al., 2017). In contrast, suppressed primary production in migrating sediments cannot be explained by changes in phototroph biomass (chlorophyll a) (Scheidweiler et al., 2021). Frequent burial within the bedform and resulting light limitation for the phototrophs (Izagirre et al., 2009; Pilditch & Miller, 2006) might impair primary production.

Migrating sediments are in general well connected with the stream water. Exchange flux increases with stream water velocity and bedform migration velocity. However, delivery of nutrients into deeper streambed layers located below the migrating layer (i.e., the upper layer of the streambed that migrates; Figure 1b) is reduced as compared to non-migrating bedforms. The penetration of water, nutrients and particles is impeded when turnover is becoming dominant under fast bedform migration velocities (Teitelbaum et al., 2022; Zheng et al., 2019). Thus, resource transfer to hyporheic communities below the migrating layer is reduced (Elliott & Brooks, 1997; Wolke et al., 2020; Zheng et al., 2019). At the same time, suspended particulate matter is trapped by migrating sediments and accumulates in the zone below the migrating layer (Dallmann et al., 2020; Dallmann et al., 2021; Harvey et al., 2012; Teitelbaum et al., 2022). This accumulation can lead to clogging of the streambed by clay particles (Teitelbaum et al., 2021) but also to increased biogeochemical activity utilizing organic matter (Phillips et al., 2019).

Most of the recent process-based studies focus on the bedform scale (meso-habitat), yet, bedform migration varies spatially in channel cross-section and longitudinally (Figure 1c). The frequency of migrating-resting patch transition thus adds new dimensions to the understanding of biogeochemical cycling at reach and segment scales. Although it is acknowledged that the transport of fine sediments in fluvial ecosystems is a common phenomenon in lowland alluvial and glacial landscapes, the global distribution and statistics of streambed migration is still unclear. In Germany, approximately 16% of all stream length have sandy sediments (source of data: [https://www.gewaesser-bewertung.de/index.php?article\\_id=11&clang=0](https://www.gewaesser-bewertung.de/index.php?article_id=11&clang=0)) and flow velocities that can cause streambed migration under base flow conditions. Some local studies from England, Wales and US suggest that sandy streambeds are migrating about 50% of the time (Booker & Dunbar, 2008; Verzano et al., 2012), but the impact of streambed migration on biogeochemical processes in

### BOX 1 Future research needs

The major research gaps related to the coupling between fine sediment transport in fluvial ecosystems, dynamics of benthic and hyporheic communities, and biogeochemical processes across spatio-temporal scales are:

1. Estimates of the global distribution and statistics of streambed migration are needed to improve our understanding on how this streambed heterogeneity created by the moving-resting frequency of sediment grains (micro-habitat scale) and migrating-resting patch transitions (meso-habitat and reach scale) can provide important control points for ecosystem biogeochemistry and affect global biogeochemical cycles.
2. The theoretical framework we postulate on the coupling between ecological and biogeochemical consequences across a range of sediment migration frequencies at micro- and meso-habitat scale remains to be demonstrated.
3. Cross-scale observations are needed because nonlinear relationships may exist when the response of ecological dynamics and biogeochemical processes to the frequency of sediment migration at the micro-habitat are scaled up and translated to larger spatial scales where communities experience the transition of migrating-resting patches.

those streams was not evaluated. Global data on the distribution of mobile-bed streams and the frequency of streambed migration in these systems is still lacking, as most prior studies have focused on either morphological classification or total catchment sediment yields. Worldwide agricultural intensification and urban area expansion are substantially increasing catchment erosion and quantities of fine sediments in fluvial ecosystems (Wilkes et al., 2019; Zhang et al., 2014). Climate change is also increasing the frequency of high-flow events that remobilize streambed sediments (Buffington & Montgomery, 2021; Kondolf et al., 2016). Stream ecosystems are particularly sensitive to both of these perturbations (Kondolf et al., 2016; Luce et al., 2013; Ormerod, 2009). Thus, there is a pressing need to improve our understanding on how the moving-resting frequency of sediment grains and migrating-resting patch transitions affect fluvial ecosystems and global biogeochemical cycles (Box 1).

## 7 | CONCLUSION

We here focus on the morphodynamics of fine-grain sediments while identifying their impact on ecological dynamics and biogeochemical processes at the micro to meso-habitat, reach and segment scale. Despite the enormous geophysical, ecological and biogeochemical implications of morphodynamics, a conceptual framework for sediment moving-resting frequency has not yet been developed. The presented concept is an extension of existing ecological theory, that is, the disturbance theory focusing on flood events, toward more frequent movement of fine-grain sediments. Transport-resting cycles affecting benthic and hyporheic communities are nested across spatio-temporal scales: (1) At the micro-habitat scale, sediment grains are moving and resting at different frequencies. We propose that the most severe effect on benthic and hyporheic communities will occur when ecological and biogeochemical processes are at the same temporal scale as the migration frequency of the sediment. In addition, ecological mechanisms introduce non-linearity into the relationship between migration frequency and ecological or biogeochemical processes. (2) At reach to segment scale, migrating and resting patches occur simultaneously and their transition is driven by larger-scale fluvial constraints such as discharge variability, water depth and sediment load. We provide evidence that benthic and hyporheic communities are not only adapted to the most-prevalent environmental conditions of their local habitat, but also to the larger scale frequency of migrating-resting patch transitions. Thus, migrating-resting patch transition adds new dimensions to the understanding of biogeochemical cycling at larger spatial scales. The nestedness of spatio-temporal scales highlights the need for cross-scale observations to improve our understanding of fine-grain fluvial ecosystems and global biogeochemical cycles.

### AUTHOR CONTRIBUTIONS

**Ute Risse-Buhl:** Conceptualization (lead); funding acquisition (equal); project administration (lead); visualization (lead); writing – original draft (lead). **Shai Arnon:** Conceptualization (lead); funding acquisition (equal); visualization (supporting); writing – original draft (lead). **Edo Bar-Zeev:** Conceptualization (lead); funding acquisition (equal); visualization (supporting); writing – original draft (lead). **Anna Oprei:** Conceptualization (supporting); visualization (supporting); writing – original draft (supporting). **Aaron Packman:** Conceptualization (supporting); funding acquisition (equal); visualization (supporting); writing – original draft (supporting). **Ignacio Peralta-Maraver:** Conceptualization (equal); funding acquisition (equal); visualization (lead); writing – original draft (equal). **Anne Robertson:** Conceptualization (equal); funding acquisition (equal); visualization (supporting); writing – original draft (equal). **Yoni Teitelbaum:** Conceptualization (supporting); visualization (supporting); writing – original draft (supporting). **Michael Mutz:** Conceptualization (lead); funding acquisition (equal); visualization (supporting); writing – original draft (lead).

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## CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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