

1 **Title:** The riverine bioreactor: an integrative perspective on biological decomposition of  
2 organic matter across riverine habitats

3 **Running title:** Organic matter decomposition by the riverine bioreactor

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69 **Abstract**

70 Riverine ecosystems can be conceptualized as ‘bioreactors’ (the riverine bioreactor)  
71 which retain and decompose a wide range of organic substrates. The metabolic  
72 performance of the riverine bioreactor is linked to their community structure, the  
73 efficiency of energy transfer along food chains, and complex interactions among biotic and  
74 abiotic environmental factors. However, our understanding of the mechanistic  
75 functioning and capacity of the riverine bioreactor remains limited.

76  
77 We review the state of knowledge and outline major gaps in the understanding of biotic  
78 drivers of organic matter decomposition processes that occur in riverine ecosystems,  
79 across habitats, temporal dimensions, and latitudes influenced by climate change.

80  
81 We propose a novel, integrative analytical perspective to assess and predict decomposition  
82 processes in riverine ecosystems. We then use this model to analyse data to demonstrate  
83 that the size-spectra of a community can be used to predict decomposition rates by analysing  
84 an illustrative dataset. This modelling methodology allows comparison of the riverine  
85 bioreactor’s performance across habitats and at a global scale.

86  
87 Our integrative analytical approach can be applied to advance understanding of the  
88 functioning and efficiency of the riverine bioreactor as hotspots of metabolic activity.  
89 Application of insights gained from such analyses could inform the development of  
90 strategies that promote the functioning of the riverine bioreactor across global  
91 ecosystems.

92  
93 **Keywords:** Body mass-abundance scaling, biodegradation, latitude, metabolic theory,  
94 riverine ecosystems, regulating ecosystem service.

## 103 **1. Introduction**

104 Riverine ecosystems have the capacity to store, transform, and transfer inorganic  
105 nutrients, organic matter (OM), sediments and metabolites to adjacent ecosystems, such  
106 as marine environments and riparian forests (Battin et al., 2008; Benstead and Leigh,  
107 2012). They can thus be conceptualized as bioreactors sustained and maintained by active  
108 communities (Krause et al., 2009; Peralta-Maraver et al., 2018). The habitats of riverine  
109 ecosystems include their surface water, streambeds, floodplains and alluvial aquifers,  
110 which are closely interconnected by energy and matter fluxes across bioactive interfaces  
111 (Krause et al., 2011a, 2011b, 2017). Rivers distribute decomposition over time and space,  
112 i.e. longitudinally, laterally and vertically, promoting the processing of a wide range of  
113 organic substrates, from highly recalcitrant particulate OM, such as some leaf litters and  
114 dissolved OM, to dissolved nutrients including pollutants of anthropogenic origin. It is  
115 estimated that riverine ecosystems produce an outgassing flux of 0.75–3.88 GtC yr<sup>-1</sup> as a  
116 result of biological decomposition and chemical weathering (Raymond et al., 2013; Drake  
117 et al., 2018), and of 0.78 GtC yr<sup>-1</sup> due to land-to-ocean transport, in which rivers play a  
118 major role (Friedlingstein et al., 2019). Riverine ecosystems also provide a range of  
119 services essential for human wellbeing, for example by contributing substantially to  
120 natural mitigation of inorganic and organic pollutants (Hill et al., 2014; Peralta-Maraver  
121 et al., 2018) and to the global carbon cycle (Battin et al., 2008; Hotchkiss et al., 2015).

122 Research into the decomposition of OM by riverine communities has experienced  
123 a rise in scientific activity in recent years, spanning disciplines including ecohydrology,  
124 community ecology, environmental pollution and global change science (e.g. Datry et al.,  
125 2018; Schaper et al., 2018, 2019; Tiegs et al., 2019). However, mechanistic understanding  
126 of biologically driven OM decomposition is limited for riverine ecosystems (hereafter, the  
127 riverine bioreactor) at low latitudes, where solar radiation, air and water temperatures,  
128 and rainfall intensity are markedly greater than at high latitudes (reviewed in Boulton et  
129 al., 2008). These major climatic drivers affect the rate at which OM enters aquatic  
130 ecosystems and is processed (Brandt et al., 2007; Wantzen et al., 2008; Tank et al., 2010).

131 Key gaps in our understanding of how biotic and abiotic drivers of the riverine  
132 bioreactor vary across latitudinal gradients and the transferability of concepts among  
133 regions. A unified analytical framework quantifying how OM decomposition responds to  
134 environmental constraints and ecological community structure is needed to assess these  
135 gaps. In addition, riverine ecosystems are increasingly exposed to multiple stressors  
136 driven by anthropogenic activities in a context of ongoing climate change, and such a

137 framework might also indicate how the riverine bioreactor will respond to different  
138 stressor combinations.

139 We review how OM decomposition by the riverine bioreactor varies in response to  
140 latitude in longitudinal (headwater streams to lowland rivers), vertical (surface waters to  
141 aquifers), lateral (channel to floodplains and wetlands) and temporal dimensions. In  
142 doing so, we outline major anthropogenic stressors affecting bioreactor functioning. We  
143 also compare the state of understanding of riverine bioreactor functioning in temperate  
144 and low-latitude (tropical and subtropical) regions. We then propose an integrative  
145 analytical perspective to assess biologically driven OM decomposition processes, based  
146 on established concepts from the metabolic theory of ecology (Brown et al., 2004). Our  
147 work follows a hierarchical stepwise progression and establish solid knowledge  
148 foundations at every step before addressing the complex functioning of the riverine  
149 bioreactor (Fig 1). Our ultimate goal is to provide a foundation on which to base further  
150 crosscutting research into the riverine bioreactor, by promoting interdisciplinary  
151 collaborations.

152

## 153 **2. Decomposition of particulate organic matter in running waters**

154 Rivers are generally heterotrophic ecosystems from source to mouth and across latitude  
155 (Vannote et al., 1980; Ewards and Meyers 1987; Howarth et al., 1996; Wetzel, 2001;  
156 Follstad Shah et al., 2017), their functioning depending largely upon inputs of OM from  
157 autotrophic ecosystems, in particular leaf litter from the surrounding forested catchment.  
158 Thus, energy fluxes to riverine ecosystems are compromised by anthropogenic  
159 deforestation of riparian zones (Sponseller & Benfield, 2001), which reduces leaf litter  
160 and woody debris inputs. Riparian deforestation also limits shading, increasing solar  
161 radiation and water temperatures (Kelly et al., 2003; Johnson and Jones, 2000; Sweeney  
162 et al., 2004), which can reduce the diversity and metabolic activity of stream communities,  
163 resulting in lower decomposition rates (e.g. Silva-Araújo et al., 2020). This is of particular  
164 concern in tropical systems considering the greater rates of deforestation compared with  
165 temperate counterparts. For example, the Amazon basin has the world's highest rate of  
166 rainforest deforestation due to anthropogenic activities (Lepers et al., 2005; McClain and  
167 Elsenbeer 2001).

168 The rate of leaf litter decomposition is naturally constrained by intrinsic litter  
169 characteristics, such as the concentrations of nutrients and secondary compounds, the  
170 decomposing capacities of aquatic communities across trophic levels, and climatic

171 conditions (Webster and Benfield, 1986; McArthur et al., 1988; Thompson and Bärlocher,  
172 1989; Gessner et al., 1999; Leite-Rossi et al., 2016; Follstad Shah et al., 2017; Peralta-  
173 Maraver et al., 2019a). Leaf litter decomposition pathways in rivers have been described  
174 in detail (e.g. Webster and Benfield, 1986; Gessner et al., 1999). In brief, after leaf litter  
175 falls into water, decomposition starts with the dissolution of labile compounds (leaching)  
176 and continues with microbial conditioning, consumption by invertebrates, fragmentation  
177 and physical abrasion (Webster and Benfield, 1986). These processes gradually  
178 decompose leaf litter into gaseous respiration products such as carbon dioxide (CO<sub>2</sub>),  
179 methane, nitrous oxide and molecular nitrogen (Gessner et al., 1999; Fig. 2a). POM  
180 decomposition typically depends on initial microbial conditioning by prokaryotes, fungi  
181 and protists, and later consumption by invertebrate shredders (e.g. Graça, 2001; Peralta-  
182 Maraver et al., 2019a). Leaf litter can accumulate on the streambed and is thus mostly  
183 decomposed by benthic communities (Peralta-Maraver et al. 2019a). However, leaf litter  
184 is buried and stored within the streambed sediments (i.e. the hyporheic zone; Cornut et  
185 al., 2010). Subsurface communities can be less active during leaf litter processing than  
186 benthic organisms (Peralta-Maraver et al., 2019a) and POM may thus accumulate in  
187 deeper sediments.

188 At the global scale, annual litterfall is notably higher in tropical rainforests than in  
189 both temperate deciduous broad-leaved and evergreen coniferous forests (Fig. 2a; Zhang  
190 et al., 2014). In contrast to the seasonal changes in temperature and leaf litter inputs that  
191 characterize temperate and boreal rivers, those in tropical and subtropical regions  
192 experience consistently warm temperatures and year-round OM inputs shed by highly  
193 productive riparian plants (Morellato et al., 2000). These riparian inputs are more  
194 abundant and diverse than those in temperate and boreal rivers (Bastian et al. 2007,  
195 Boyero et al. 2011a), in particular during periods of high rainfall. Higher temperatures at  
196 low latitudes also stimulate metabolic activity, microbial and invertebrate-mediated  
197 decomposition of OM compared to higher latitude systems (Taniwaki et al., 2017).

198 Species in stream communities at mid and high latitudes are adapted to marked  
199 seasonal inputs of litterfall from deciduous vegetation (Fig. 2a). The activity of  
200 detritivores adapted to autumnal litterfall pulses may explain the positive relationship  
201 between decomposition rates and absolute latitude, which accounts for the effect of  
202 temperature (Follstad Shah et al., 2017). Also, the abundance of relatively large-bodied  
203 detritivores and their contribution to leaf litter breakdown generally increase with  
204 latitude (Boyero et al., 2011a, 2011b). Thus, quantitative and/or qualitative differences

205 in POM decomposition should occur along global latitudinal gradients, due to distinct  
206 climatic conditions and associated differences in riparian vegetation inputs (Boyero et al.,  
207 2009) and thus detritivore community composition, activity and dietary preferences  
208 (Boyero et al., 2009; Follstad Shah et al., 2017; Majdi and Traunspurger, 2017).

209 Species diversity of riparian litter inputs are negatively related to latitude (Benson  
210 and Pearson, 1993; Wright, 2002; Bastian et al., 2007), resulting in greater variability in  
211 the chemical characteristics and palatability of leaf litter in subtropical and tropical  
212 climates (Wantzen and Wagner, 2006). Because of the generalist feeding behavior of  
213 many invertebrate taxa, the importance of consumers that feed on leaf litter but are not  
214 classified as shredders might have been overlooked in tropical regions (Kelly et al., 2002;  
215 Leite-Rossi et al., 2016; Mendes et al., 2017). Additionally, the more diverse and abundant  
216 large-sized consumers inhabiting tropical streams, such as shrimps, crabs and  
217 'herbivores' fish, might act as leaf litter consumers and directly influence decomposition  
218 rates (Boulton et al., 2008; Costa et al., 2016), and thus require consideration in litter  
219 breakdown modelling.

220 There is considerable intra-regional variability in the role of detritivores in leaf  
221 litter decomposition at low latitudes (Boyero et al., 2014). For example, streams in the  
222 vast, savanna-like Brazilian Cerrado ecoregion are characterized by unpalatable leaf litter  
223 and thus a scarcity of invertebrate shredders (Gonçalves et al., 2007). In addition, tropical  
224 soils typically export low concentrations of inorganic nutrients such as nitrogen and  
225 phosphorous to rivers, these nutrients being common factors limiting microbial activity  
226 in freshwaters (e.g. Pringle et al., 1986; Tank and Webster, 1998; Wold and Hershey,  
227 1999). These nutrients probably limit decomposition rates in Cerrado streams by  
228 constraining the length of food chains. In contrast, the abundant shredders in some South  
229 American streams of the Atlantic Forest, Amazonian and Andean mountains process more  
230 OM, even in streams in which microorganisms make little contribution to leaf litter  
231 decomposition (Graça et al., 2016).

### 232 233 **3. Decomposition of dissolved organic matter by the riverine bioreactor**

234 Riverine ecosystems receive considerable dissolved OM from their catchments (Regnier  
235 et al., 2013) including significant anthropogenic inputs (Fig. 2b; Vitousek et al., 1997), and  
236 play an important role in transporting these allochthonous dissolved substances through  
237 landscapes. They also contribute to the retention and decomposition of dissolved OM,  
238 modifying the chemical forms and concentrations of dissolved compounds during

239 transport (Rahm et al., 2016). For example, approximately two thirds of the dissolved  
240 carbon transported by rivers is estimated to be decomposed and mineralized before  
241 reaching the sea (Cole et al., 2007). Around 50% of the total dissolved nitrate maybe  
242 processed during early stages of transport in headwater streams (Peterson et al., 2001),  
243 and 10–30% of soluble reactive phosphorous can be retained in riverine sediments  
244 (reviewed in Withers and Jarvie, 2008). Abiotic factors such as geology and pH are  
245 important influences on the transformation and mineralization of dissolved OM (House  
246 et al., 2003; Refsgaard et al., 2014).

247 Planktonic microorganisms such as heterotrophic bacteria are key players in the  
248 decomposition of dissolved OM in freshwater (Seitzinger et al., 2006; Berggren and del  
249 Giorgio, 2015), due to their high extracellular enzymatic activity (Cunha et al., 2010). They  
250 support the flux of biomass and energy to higher trophic levels in surface water (Weitere  
251 et al., 2005) and bacterial respiration in the water column is a major contributor to  
252 dissolved organic carbon processing in inland waters (Raymond et al., 2013). Although  
253 bacterial respiration varies widely across global-scale, latitudinal gradients and rates are  
254 higher towards the equator (Aufdenkampe et al., 2011). Increasing dissolved inorganic  
255 nutrient concentrations enhance bacterial densities and biomass, which in turn promotes  
256 dissolved OM decomposition (Reche et al., 1998). Incorporation of dissolved organic  
257 carbon into microbial biomass is regulated by its concentrations and quality, and the  
258 abiotic conditions such as temperature (Findlay et al., 2001; Lennon and Cottingham  
259 2008; Williams et al., 2010). Lastly, chemical and thermal pollution can simplify microbial  
260 communities and increase or decrease their metabolic rates (Cherry et al., 1974;  
261 Schneider and Topalova, 2009; Wang et al., 2011). For example, microbial decomposition  
262 can increase along pollution gradients in response to inorganic nutrient availability  
263 (Pascoal et al., 2005) despite a decline in community diversity (Liao et al., 2018).

264 Significant quantities of dissolved compounds are also biologically processed by  
265 microbial biofilms attached to sediment particles (Battin et al., 2016). The high surface  
266 area provided by sediment particles within the streambed represents an active zone with  
267 a high capacity to decompose dissolved organic compounds (Fig. 2b; Krause et al., 2017;  
268 Peralta-Maraver et al., 2018). In particular for nitrogen organic compounds, streambed  
269 sediments can be hotspots of biological processing, such as biological assimilation  
270 (Alexander et al., 2000; Peterson et al., 2001). The intrinsic potential of the streambed to  
271 process nitrates, phosphates and organic carbon is well understood in temperate regions  
272 (e.g. Lewandowski et al., 2011), while it remains unexplored in tropical regions. In



273 addition, the streambed can decompose emerging organic contaminants (EOCs,  
274 Lewandowski et al., 2011; Schaper et al., 2018; Posselt et al., 2020). However,  
275 channelization (the modification of a channel's banks and/or bed) suppresses the vertical  
276 connectivity between the surface and the streambed (Cleven, 2003) and decreases the  
277 frequency of floodplain inundations (Nilsson et al., 2005), resulting in potential detriment  
278 of the riverine bioreactor functioning.

279 Current knowledge on the natural functioning of the riverine bioreactor comes  
280 from temperate-zone studies that focus on organic compound transformation in the  
281 surficial streambed sediments (e.g. Lewandowski et al., 2011; Schaper et al., 2018) and  
282 combine techniques at the interface of hydrology, biochemistry, microbiology and  
283 community ecology (e.g. Jaeger et al., 2019; Mechelke et al., 2019; Schaper et al., 2019a;  
284 Posselt et al., 2020). Degradation of dissolved OM may also occur in deeper groundwater  
285 systems (Jurado et al., 2012), creating a vertical chain of biochemical breakdown  
286 processes through river sediments to groundwater ecosystems.

287 The metabolic activity of organisms inhabiting rivers in temperate regions  
288 contributes to active degradation of dissolved OM, elimination of pathogens, and nutrient  
289 cycling in surface water, streambed and groundwater systems (Deng et al., 2014; Griebler  
290 and Avramov, 2015; Meckenstock et al., 2015; Hose and Stumpp, 2019; Reiss et al., 2019).  
291 Prokaryotes form biofilms with high enzyme activity, which enables their decomposition  
292 of a wide range of natural substrates (Battin et al. 2016). But also, they possess the  
293 potential to decompose new chemicals by developing new metabolic pathways  
294 (Kolvenbach et al., 2014). Prokaryotes often congregate in multi-species biofilms,  
295 maximizing the range of dissolved compounds that can be decomposed and the rate at  
296 which this degradation occurs (e.g. Foght, 2008).

297 Streambed and groundwater invertebrates (both meiofauna and  
298 macroinvertebrates) indirectly contribute to OM decomposition within the streambed  
299 (Peralta-Maraver et al., 2018). In temperate regions, macroinvertebrates directly  
300 influence the hydraulic properties of sediments through bioturbation and bioirrigation  
301 (Fig. 2c, d; Baranov et al., 2016a, 2016b; Hose and Stumpp, 2019;). In addition, the mucus  
302 and silk secretions of benthic flatworms and caddisfly juveniles, respectively, stabilize  
303 sediments, and contribute to OM decomposition by enhancing biofilm development and  
304 invertebrates colonization (Majdi et al., 2014; Albertson et al., 2019). Groundwater  
305 macroinvertebrates may promote the abundance of Protozoa inhabiting interstitial pore  
306 spaces (Weitowitz et al., 2019), where protozoans swimming and grazing on biofilms

307 promote water mixing, potentially increasing biofilm area and stimulating bacterial  
308 activity (Fig. 2e; Peralta-Maraver et al., 2018). These complex biotic interactions may  
309 enhance decomposition by the bioreactor, but the mechanisms behind this stimulatory  
310 response remains unknown.

311 Further studies need to explore global patterns in the biologically mediated  
312 decomposition of dissolved organic matter and the metabolic capacity of communities  
313 inhabiting streambed sediments. In temperate regions, the distribution of surface water  
314 and groundwater macroinvertebrate taxa (Sket, 1999; Danielopol et al., 2000; Gibert et  
315 al., 2009; Robertson et al., 2009) is reasonably well understood (Maurice and Bloomfield,  
316 2012; Domisch et al., 2013), but our knowledge of microbial and protozoan population is  
317 rudimentary. The understanding of groundwater ecosystems functioning in tropical and  
318 subtropical regions lags even further behind that of temperate environments (Moosdorf  
319 et al., 2015; Adyasari et al. 2018). The mechanisms driving transformations of dissolved  
320 nutrients and contaminants in groundwater systems and the taxonomic groups related to  
321 decomposition processes require further study. For example, information on the  
322 distribution of surface water and groundwater macroinvertebrates in tropical regions is  
323 patchy, and much of our current limited knowledge of their role during decomposition  
324 processes derives from temperate regions. However, the relative contribution of different  
325 taxa may vary considerably across global latitudinal gradients due to differences in their  
326 metabolic rates and energy flow through trophic levels. Filling this knowledge gap is  
327 especially important given the occurrence of large-scale environmental accidents in  
328 tropical regions that pollute both surface and subsurface systems (e.g. Escobar, 2015;  
329 Cionek et al., 2019).

330

#### 331 **4. Organic matter breakdown in aquatic-terrestrial ecotones**

332 Ecotones are transition or buffer zones between adjacent structurally different  
333 communities and habitat types, having a set of characteristics defined by space and time  
334 scales (di Castri et al. 1988). Riverine ecosystems encompass habitats that shift between  
335 wet and dry states in space and time, acting as ecotones that support both aquatic and  
336 terrestrial communities. These dynamic aquatic-terrestrial ecosystems are distributed  
337 across river networks on all continents and in all climates, including temperate  
338 (Stubbington et al., 2017) and tropical (Barbosa et al., 2012) regions. Notably, an  
339 estimated half of the global river network comprises temporary streams, which  
340 experience partial or complete streambed drying (Tooth and Nanson, 2000; Datry et al.,

341 2014). Furthermore, the number and length of temporary rivers is increasing globally due  
342 to increased water abstraction and higher intra-annual rainfall variability as a  
343 consequence of climate change (Jackson et al., 2001; Larned et al., 2010). Ecological  
344 functioning changes considerably between wet and dry states, but our understanding of  
345 organic matter processing during dry phases remain largely unexplored (Datry et al.,  
346 2017a).

347       Expansion and contraction of aquatic and terrestrial habitats also occur laterally  
348 in perennial systems, in particular floodplain environments, which are among the most  
349 productive and biochemically active systems in the world (Junk et al., 1989). In the middle  
350 and lower river sections, flooding of the main channel and tributaries typically creates a  
351 mosaic of aquatic and terrestrial habitats on floodplains. Even though river–floodplain  
352 systems may maintain water flow throughout the year, their aquatic–terrestrial transition  
353 zones remain dry for all or most of the low during the low water season (Junk et al., 1989).  
354 Floodplains support the functioning of riverine bioreactor, as they act as sediment traps,  
355 sinks for dissolved nutrients and chemicals, and as large carbon stores (Baigún et al.,  
356 2008; Walalite et al., 2016), and supply channels with a diversity of organic substrates  
357 and associated microbial decomposers (O’Connell et al., 2000).

358       Dynamic aquatic–terrestrial habitats including temporary rivers and floodplains  
359 have different characteristics to those of adjacent riparian, purely terrestrial and fully  
360 aquatic habitats, and support unique communities, including inundation-tolerant  
361 terrestrial colonists (Tockner and Stanford, 2002; Steward et al., 2011) and desiccation-  
362 tolerant aquatic organisms (Stubbington and Datry, 2013; Datry et al., 2017b) during dry  
363 phases. During transitions from aquatic to terrestrial phases, drivers of organic matter  
364 decomposition such as leaching and aquatic decomposers, are gradually replaced by  
365 physical photodegradation and terrestrial colonists, such as soil fauna and fungi (Fig. 2f;  
366 Austin and Vivanco, 2006; Corti et al., 2011; Acre et al., 2019). These transitional aquatic-  
367 terrestrial dynamics promote organic matter decomposition and mineralization process  
368 in inland waters (Datry et al., 2018). Organic matter decomposition might be also  
369 enhanced if biofilm activity increases in response to sediment reworking by terrestrial  
370 soil invertebrates (Fig. 2f; Prather et al., 2013).

371       The timing, frequency, duration and magnitude of wet and dry phases defines the  
372 structure and metabolic capacity of communities inhabiting aquatic–terrestrial channels  
373 and floodplains (Adis and Junk, 2002; Stubbington et al., 2017; Colls et al., 2019) and  
374 interrupts both decomposition rates and OM quality (Padial and Thomaz, 2006).

375 Consequently, wet phases promote decomposition within floodplains, as in temporary  
376 streams and rivers (Datry et al., 2018; von Schiller et al., 2019). This is because, rewetting  
377 events in temporary systems create ‘hot moments’ of biological activity, initiating pulses  
378 of organic matter decomposition that contribute significantly to carbon cycling (Datry et  
379 al., 2018; Shumilova et al., 2019; von Schiller et al., 2019). Repeated inundation of aquatic-  
380 terrestrial channels and floodplains may be analogous to conditions in floodable soil  
381 aquifer treatment (SAT) systems in wastewater plants. SAT systems release time-  
382 controlled flood pulses of secondary effluents from conventional wastewater treatment  
383 through a recharge basin, with posterior wastewater processing dominated by  
384 biodegradation in the sediments (Amy and Drewes, 2007; Arye et al., 2011). During dry  
385 phases, terrestrial colonists such as, nematodes, annelids and arthropods (e.g. ants), can  
386 transform plant litter and fine POM into constituent nutrients by consumption and  
387 egestion, and thus support particulate nutrient cycling in the whole river ecosystem (Bush  
388 et al., 2019).

389 Rewetting events vary considerably across latitudinal gradients. In boreal and high  
390 latitude temperate regions, the timing of wet and dry phases can be predictable, in  
391 response to seasonal changes in precipitation and snowmelt (Olsson and Söderström,  
392 1978; Gasith and Resh, 1999) inputs. However, the magnitude of flood pulses could vary  
393 considerably among wet and dry years at mid-latitudes, for example in many  
394 Mediterranean streams (Bonada and Resh, 2013). Flood pulses can be marked and  
395 predictable in some tropical rivers due to the extended wet season (Boulton et al., 2008).  
396 But, the higher annual precipitation in wet subtropical and tropical regions results in  
397 frequent and irregular flood pulses, which structure communities including biofilms  
398 (Taniwaki et al., 2019; Burrows et al., 2020) and benthic macroinvertebrates (Nessimian  
399 et al., 1998). Nonetheless, the higher frequency and magnitude of flood pulses has not  
400 been related to decomposition processes at low latitudes. Global predictions of bioreactor  
401 capacity in aquatic-terrestrial channels and floodplains should seek to integrate the  
402 effects of flood pulses on community structure and energy flow through food webs with  
403 quantified decomposition rates (Shumilova et al. 2019).

404

## 405 **5. Perspective: unifying a theoretical and analytical framework**

406 Throughout this paper, we acknowledge that a wide range of different sized organisms  
407 with different functional roles contribute directly or indirectly to decomposition  
408 processes. For example, consortia of prokaryotes and eukaryotic microorganisms form

409 biofilms and drive initial leaf litter decomposition through extracellular digestion, making  
410 substrates more palatable to macroinvertebrate consumers. In addition, the enzymatic  
411 activity of sediment biofilms and planktonic prokaryotes enables them to process a  
412 breadth of dissolved organic substrates (from macronutrients to pollutants). In addition,  
413 the activity of grazers and burrowers boost microbial activity.

414 Collectively, complex interactions between biotic groups within riverine  
415 communities and their environments mediate the functioning of the riverine bioreactor.  
416 However, research documenting organic matter decomposition typically considers only  
417 certain community groups, which typically have different trophic roles (e.g. microbial  
418 conditioning vs. macroinvertebrate shredding leaf litter). In addition, compared to both  
419 microorganisms and macroinvertebrates, the contribution of meiofauna to organic  
420 matter decomposition in freshwater ecosystems remains poorly characterized (Majdi et  
421 al. 2020, but see Wang et al., 2020). These size biases limit incorporation of quantitative  
422 measurements of energy and biomass flow through communities when studying  
423 decomposition phenomena. In addition, research into decomposition processes has not  
424 characterized variation in community structure and energy transfer across latitudinal  
425 gradients. Integrative analyses that represent entire communities and global-scale  
426 variability are needed to better understand the biologically driven decomposition  
427 processes in riverine ecosystems.

428 Changing temperatures are one of the most conspicuous differences among river  
429 ecosystems along a latitudinal gradient. Environmental temperature is a key influence on  
430 metabolic rates, body size, growth rates, feeding rates and consequently decomposition  
431 rates in aquatic ecosystems (Brown et al., 2004). Thus, incorporating environmental  
432 temperature and the scaling between the metabolic rates and body size of aquatic  
433 ectotherms represents a step towards extrapolation of empirical findings from temperate  
434 ecosystems to processes in lesser-studied tropical ecosystems. In this sense, metabolic  
435 scaling (sensu Brown et al., 2004; Sibly et al., 2012) provides the theoretical and analytical  
436 framework that links the energetic constraints of individuals to ecosystem-level  
437 processes. Thus, this framework can be used to assess biotic controls on organic matter  
438 decomposition – even between stream habitats and across biomes.

439 Metabolic rates of ectotherms increase with organism body size and  
440 environmental temperature (Brown et al., 2004). For instance, metabolic rates of  
441 metazoans often scale with body mass as a power law with an exponent of  $\frac{3}{4}$ , which is  
442 predicted by optimal resource supply networks (Brown et al., 2004). Because an

443 individual's performance reflects its mass-dependent metabolic requirements, an  
444 assemblage's capacity to process metabolic substrates therefore depends on both its total  
445 biomass, and how biomass is apportioned among small or large individuals.  
446 Consequently, total biomass and the size structure of ecological communities are  
447 important predictors of ecosystem processes governed by consumers, such as the  
448 decomposition of particulate organic matter, dissolved OM, including organic pollutants.

449 Body mass–abundance (M-N) scaling relationships provide a potential bridge  
450 between an assemblage's metabolic capacity and the bioreactor capacity of a system.  
451 When individual organisms are grouped into body-mass classes, irrespective of  
452 taxonomic identity, the negative slope of the resultant frequency distributions on double-  
453 log axes (i.e. size- spectra; White et al., 2007) provides a measure of community size  
454 structure, and the area under the slope (and intercept) provides a measure of total  
455 biomass (Fig. 2g). This relationship is defined by the equation Eq. (1):

456

$$457 \text{Abundance } (N) \sim \beta_0 + \text{body mass } (M) + \varepsilon,$$

458

459 where  $\beta_0$  is the intercept and  $\varepsilon$  an error term.

460 Freshwater communities are structured by body size, which is inversely  
461 proportional to population densities (Schmid et al., 2000). Also, the body size of different  
462 groups can provide an indication of trophic level in hyporheic food web (Kerr and Dickie,  
463 2001), despite some exceptions should be considered (e.g. parasites; Leaper and Huxham,  
464 2002). This allows the size-spectrum slope act as a proxy for a community's metabolic  
465 efficiency (i.e. its capacity to transfer energy and biomass through trophic levels).  
466 Metabolic scaling coefficients (slope and intercept of size-spectra) could be used to  
467 predict bioreactor capacity, based primarily on universal body-mass constraints on  
468 individual metabolism and information on food web (Brown et al., 2004; Petchey and  
469 Belgrano, 2010). The size-spectrum slope (M-N slope) scales with the efficiency of energy  
470 transfer across trophic levels (Brown and Gillooly, 2003), and typically becomes steeper  
471 as metabolic efficiency decreases (e.g. abundance decreases dramatically from low to high  
472 trophic levels; Kerr and Dickie 2001; Perkins et al., 2018). Consequently, a strong positive  
473 relationship is predicted between a system's size-spectrum slope and its decomposition  
474 capacity, allowing slopes to predict and quantify decomposition rates (Fig. 2h).

475 Metabolic scaling theory, therefore, provides a potentially powerful approach to  
476 reconcile differences in organic matter decomposition among riverine habitats and across

477 latitudinal gradients, within the analytical rationale that established measurements of  
478 decomposition rates (Woodward et al., 2012) can be used to determine the exponential  
479 decay coefficient ( $k$ ) using Eq. (2):

480

$$481 \text{Decomposition rate } (k) = -(\log(X_t) - \log(X_0))/t$$

482

483 where  $X_0$  represents the initial quantity of an organic matter substrate, and  $X_t$  represents  
484 the quantity of substrate remaining at time  $t$ . The exponential coefficient  $t$  should be  
485 expressed in terms of thermal sums (degree days) to correct for potential temperature  
486 effects and/or differences in sampling duration. Based on our premises, Eq. (2) can be  
487 combined with Eq. (1) to build a predictive model of the decomposition rate as:

488

$$489 \text{Decomposition rate } (k) \sim \beta_0 + \text{habitat} \times M\text{-}N \text{ slope} + \text{latitude} \times M\text{-}N \text{ slope} + \varepsilon$$

490

491 Where predictor *M-N slope* have both an additive and interactive effect on the response  
492 decomposition rate due to its strong sensitivity to temperature (e.g. Dossena et al., 2012;  
493 O’Gorman et al., 2017) and its habitat-dependency in riverine systems (Peralta-Maraver  
494 et al., 2019b). Note that *habitat* and *latitude* do not drive abundance themselves, but  
495 integrate the variability in abiotic factors such as dissolved oxygen concentrations and  
496 temperature.

497

498 To test our analytical framework, we used data from Peralta-Maraver et al. (2019a)  
499 describing POM breakdown across 30 UK rivers (Fig. 3a). This study used measurements  
500 of organic matter decomposition rates ( $k$ ) using a standardized bioassay. Peralta-Maraver  
501 et al. (2019a) measured decomposition rates and provide fine-resolution data describing  
502 the body size and abundance of prokaryotes, protists, meiofauna and macroinvertebrates.  
503 In addition, the authors distinguished communities inhabiting benthic (0–5 cm depth)  
504 and hyporheic (15 cm depth) habitats. We applied Eq. (1) to build 60 M-N scaling curves  
505 (30 rivers by two habitats), showing a considerably steeper M-N relationship in hyporheic  
506 compared to benthic habitats (Fig. 3b). Other measured abiotic variables (e.g. pH) were  
507 excluded to facilitate model performance. The M-N slope is a powerful predictor of  
508 decomposition rates ( $R^2 = 0.60$ , Fig. 3c). Details of the model selection approach, model  
509 fitting, and model coefficients are provided in the Appendix.

510

510 Our analysis did not include latitude or temperature due to insufficient variability  
at the regional scale, and thus the validation of our framework is still limited to temperate

511 systems. In warmer subtropical and tropical regions, organism size tends to decline with  
512 increasing temperature due to greater energetic costs (James, 1970; Atkinson, 1994;  
513 Evans et al., 2020). Furthermore, greater energetic demands should reduce population  
514 carrying capacity with increasing temperature (Bernhardt et al., 2018, but see O’Gorman  
515 et al., 2017), assuming a fixed supply of resources (Brown et al., 2004). Thus, relative  
516 consumer abundance may be lower at low latitudes compared to temperate and boreal  
517 systems (Heino et al., 2018), but low-latitude consumers may be more productive,  
518 because higher temperatures limit body sizes and smaller species have higher biomass  
519 turnover rates. Such potential differences in productivity, as well as differences in the  
520 thermal conditions, mean that the capacity of assemblages to drive metabolic processes  
521 that underpin organic matter decomposition likely varies with latitude, with  
522 consequences for delivery of related ecosystem services

523 Metabolic scaling theory is based on a few key variables (body size and  
524 temperature) and deviations from expected scaling patterns can indicate the influence of  
525 additional factors (Perkins et al., 2018). For example, in many contexts, both biotic  
526 interactions and abiotic constraints likely modify the expression of body size as well as  
527 temperature scaling patterns. It could enable prediction of bioreactor capacity in riverine  
528 ecosystems across latitudes at which the nature and strength of biotic interactions differ  
529 (Schemske et al., 2009; González-Bergonzoni et al., 2012). The use of M-N scaling  
530 coefficients as predictors of decomposition rates also integrate the effects of  
531 environmental constraints, such as dry and wet phases in aquatic–terrestrial ecotones.  
532 Although multiple interacting mechanisms affect the bioreactor capacity of riverine  
533 ecosystems along global latitudinal gradients, metabolic scaling offers a valuable  
534 framework to understand and predict differences in the decomposition of OM at large  
535 spatial scales.

536

## 537 **6. Conclusions**

538 Organic matter decomposition pathways are highly interconnected and extend through  
539 and beyond multiple river habitats. Thus, to better understand and, predict riverine  
540 bioreactor functioning, integrative analytical approaches are required, such as those  
541 provided by the metabolic scaling theory (Brown et al., 2004). This understanding could  
542 be advanced by quantitative meta-analysis of data documenting processes such as leaf  
543 litter and dissolved OM decomposition, supplemented by data describing community  
544 size-spectra coefficients, as in our models. New data are needed to document and predict



545 OM decomposition rates on: (1) interactions between climate and riparian inputs at  
546 global scales; (2) latitudinal variability in dry-wet transitions as a driver of  
547 decomposition processes in aquatic-terrestrial ecotones; (3) the contributions of  
548 terrestrial and aquatic organisms to decomposition in aquatic-terrestrial systems; (4) the  
549 indirect effects of different biotic groups on decomposition processes (e.g. through  
550 bioturbation, decomposer grazing); (5) the contribution of meiofauna and microfauna;  
551 (6) the contribution of groundwater invertebrates across latitudes; (6) vertical changes  
552 in decomposition processes between surface water and aquifers; (7) the M-N scaling  
553 coefficients that enable prediction of decomposition in different regions; and (8) the  
554 response of decomposition processes to specific anthropogenic stressors.

555 The higher temperatures and/or higher productivity of relatively small-bodied  
556 consumers at lower latitudes (Heino et al. 2018) warrant comparative global-scale  
557 studies of bioreactor capacity. Global efforts should quantify and evaluate the regulating  
558 ecosystem services provided by the riverine bioreactor. Then, suitable management  
559 strategies could be developed to maintain, or even enhance the delivery of ecosystem  
560 services by riverine ecosystems locally. Building partnerships between international  
561 teams will enable transfer of world-leading knowledge, expertise and cutting-edge  
562 methodologies on freshwater research and management. This is especially important  
563 considering the time pressures that ongoing global change impose on decision-making.

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## 579 **Appendix**

580 We analysed data from a large regional scale survey (Peralta-Maraver et al., 2019a). Data  
581 were collected at 30 study sites covering 10 catchments across England and Wales.  
582 Systems varied from small upland, acidic headwater streams, to large lowland, base-rich  
583 chalk streams. Raw data include measurements of multiple environmental variables  
584 representing each sampling site such as pH, water depth, canopy cover, and others (see  
585 Peralta-Maraver et al., 2019a). Streambed communities were sampled using colonization  
586 traps (mesh = 0.5 cm, volume = 38–45 mL) containing an organic bioassay (cotton-strips  
587 assay), as a standardized measure of leaf litter decomposition (Tiegs et al., 2019). Three  
588 traps per sampling site were deployed in the original study, and we averaged  
589 decomposition and community measurements by stream and habitat to maximize  
590 representation of the streambed community per sampling unit.

591 Decomposition rate was calculated applying equation 2 (Woodward et al., 2012).  
592 Sampled organisms were identified and counted ( $N$ ) and their body dimensions (width  
593 and length) measured then transformed into dry body-mass ( $M$ ) with established  
594 allometric relationships (Peralta-Maraver et al. 2019a).

595 We constructed the M-N scaling relationships for each site and habitat using the  
596 logarithmic size-binning method (Edwards et al., 2017) and applying equation 1. Size bins  
597 were determined from the ( $\log_{10}$ ) body mass ( $M$ ) range for each sampled community and  
598 the abundances of organisms were then summed within each size bin (White et al., 2007).  
599 Six bins were used to maximize the number of size bins while minimizing the number of  
600 empty size bins (Perkins et al., 2018).

601 Finally, a model selection approach based on the Akaike information criterion  
602 (AIC) was applied to determine whether habitat and M-N scaling coefficients predict the  
603 decomposition rate. Latitude was not included in the analysis due to the low variability  
604 across study sites. Model selection routines identified the model including an interaction  
605 between M-N slope and habitat (Eq. 3) on decomposition rate ( $k$ ) as the best candidate  
606 (Table A1). Model assumptions of normality and homoscedasticity of the residuals and  
607 the presence of influential observations were validated visually following (Zuur et al.,  
608 2019). Results from the model evidenced a strong positive effect of the M-N slope on the  
609 decomposition rate of leaf litter (Table A2).

613 **Table A1.** AIC rankings and weights of models describing the relationship between the  
614 M-N scaling coefficients (intercept and slope) and habitat (benthic and hyporheic zones)  
615 on decomposition rates of leaf litter ( $k$ ). The model with best fit is shown in bold. We show  
616 the number of estimated parameters (N), the difference in AIC between models ( $\Delta$ AIC),  
617 their relative log-likelihood and weights ( $w_i$ ).

Model	N	AIC	$\Delta$ AIC	Log-lik	$w_i$
$k \sim \text{habitat}$	3	-517.60	16.50	$0.03 \times 10^{-2}$	$0.02 \times 10^{-2}$
$k \sim \text{habitat} + M\text{-}N \text{ intercept}$	4	-520.70	13.40	$0.12 \times 10^{-2}$	$0.07 \times 10^{-2}$
$k \sim \text{habitat} + M\text{-}N \text{ slope}$	4	-521.60	12.50	$0.19 \times 10^{-2}$	$0.12 \times 10^{-2}$
$k \sim \text{habitat} + M\text{-}N \text{ intercept} + M\text{-}N \text{ slope}$	5	-519.70	14.40	$0.07 \times 10^{-2}$	$0.05 \times 10^{-2}$
$k \sim \text{habitat} + M\text{-}N \text{ intercept} + \text{habitat} \times M\text{-}N \text{ intercept}$	5	-525.80	8.30	$1.54 \times 10^{-2}$	$0.93 \times 10^{-2}$
<b><math>k \sim \text{habitat} + M\text{-}N \text{ slope} + \text{habitat} \times M\text{-}N \text{ slope}</math></b>	<b>5</b>	<b>-534.10</b>	<b>0.00</b>	<b>1.00</b>	<b>0.60</b>
$k \sim \text{habitat} + M\text{-}N \text{ intercept} + M\text{-}N \text{ slope} + \text{habitat} \times M\text{-}N \text{ intercept}$	6	-526.80	7.30	$2.53 \times 10^{-2}$	0.01
$k \sim \text{habitat} + M\text{-}N \text{ intercept} + M\text{-}N \text{ slope} + \text{habitat} \times M\text{-}N \text{ slope}$	6	-532.50	1.60	0.45	0.27
$k \sim \text{habitat} + M\text{-}N \text{ intercept} + M\text{-}N \text{ slope} + \text{habitat} \times M\text{-}N \text{ intercept}$ + $\text{habitat} \times M\text{-}N \text{ slope}$	7	-530.54	3.57	0.16	0.10

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619

620 **Table A2.** Summary statistics of the best fitting model ( $R^2 = 0.60$ , see Table A.1).

	Coefficient	SE	t-value	p-value
<i>Intercept</i>	0.02	$0.22 \times 10^{-2}$	7.42	
<i>Habitat</i>	-0.01	$0.29 \times 10^{-2}$	-4.73	$< 0.01 \times 10^{-2}$
<i>M-N slope</i>	0.02	$0.52 \times 10^{-2}$	4.75	$< 0.01 \times 10^{-2}$
<i>Habitat <math>\times</math> M-N slope</i>	-0.02	$0.60 \times 10^{-2}$	-3.91	$< 0.01 \times 10^{-2}$

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## References

- 638  
639 Arce, M. I., Mendoza-Lera, C., Almagro, M., Catalán, N., Romani, A. M., Martí, E., ... & Marcé,  
640 R. 2019. A conceptual framework for understanding the biogeochemistry of dry  
641 riverbeds through the lens of soil science. *Earth-Sci. Rev.* 188, 441-453.  
642 <https://doi.org/10.1016/j.earscirev.2018.12.001>
- 643 Adis, J., & Junk, W. J. 2002. Terrestrial invertebrates inhabiting lowland river floodplains  
644 of Central Amazonia and Central Europe: a review. *Freshw. Biol.* 47(4), 711-731.  
645 <https://doi.org/10.1046/j.1365-2427.2002.00892.x>
- 646 Adyasari, D., Oehler, T., Afiati, N., & Moosdorf, N. 2018. Groundwater nutrient inputs into  
647 an urbanized tropical estuary system in Indonesia. *Sci. Total Environ.* 627, 1066-  
648 1079. <https://doi.org/10.1016/j.scitotenv.2018.01.281>
- 649 Albertson, L. K., Sklar, L. S., Cooper, S. D., & Cardinale, B. J. 2019. Aquatic  
650 macroinvertebrates stabilize gravel bed sediment: A test using silk net-spinning  
651 caddisflies in semi-natural river channels. *PloS One*, 14(1), e0209087.  
652 <https://doi.org/10.1371/journal.pone.0209087>
- 653 Alexander, R. B., Smith, R. A., & Schwarz, G. E. 2000. Effect of stream channel size on the  
654 delivery of nitrogen to the Gulf of Mexico. *Nature*, 403(6771), 758-761.  
655 <https://doi.org/10.1038/35001562>
- 656 Amy, G., & Drewes, J. 2007. Soil aquifer treatment (SAT) as a natural and sustainable  
657 wastewater reclamation/reuse technology: fate of wastewater effluent organic  
658 matter (EfOM) and trace organic compounds. *Environ. Monit. Assess.* 129(1-3), 19-  
659 26. <https://doi.org/10.1007/s10661-006-9421-4>
- 660 Arye, G., Dror, I., & Berkowitz, B. 2011. Fate and transport of carbamazepine in soil aquifer  
661 treatment (SAT) infiltration basin soils. *Chemosphere*, 82(2), 244-252.  
662 <https://doi.org/10.1016/j.chemosphere.2010.09.062>
- 663 Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms?. *Adv.*  
664 *Ecol. Res.* 25(3), 1-58. [https://doi.org/10.1016/S0065-2504\(08\)60212-3](https://doi.org/10.1016/S0065-2504(08)60212-3)
- 665 Aufdenkampe, A. K., Mayorga, E., Raymond, P. A., Melack, J. M., Doney, S. C., Alin, S. R., ...  
666 Yoo, K. 2011. Riverine coupling of biogeochemical cycles between land, oceans,  
667 and atmosphere. *Front. Ecol. Environ.* 9(1), 53-60.  
668 <https://doi.org/10.1890/100014>
- 669 Austin, A. T., & Vivanco, L. 2006. Plant litter decomposition in a semi-arid ecosystem  
670 controlled by photodegradation. *Nature*, 442(7102), 555-558.  
671 <https://doi.org/10.1038/nature05038>

672 Baigún, C. R. M., Puig, A., Minotti, P. G., Kandus, P., Quintana, R., Vicari, R., ... Nestler, J.A.,  
673 2008. Resource use in the Parana River Delta (Argentina): moving away from an  
674 ecohydrological approach? *Ecohydrol. Hydrobiol.* 8(2-4), 245-262.  
675 <https://doi.org/10.2478/v10104-009-0019-7>.

676 Baranov, V., Lewandowski, J., & Krause, S. 2016a. Bioturbation enhances the aerobic  
677 respiration of lake sediments in warming lakes. *Biol. Lett.* 12(8), 20160448.  
678 <https://doi.org/10.1098/rsbl.2016.0448>

679 Baranov, V., Lewandowski, J., Romeijn, P., Singer, G., & Krause, S. 2016b. Effects of  
680 bioirrigation of non-biting midges (Diptera: Chironomidae) on lake sediment  
681 respiration. *Sci. Rep.* 6, 27329. <https://doi.org/10.1038/srep27329>

682 Barbosa, J. E. D. L., Medeiros, E. S. F., Brasil, J., Cordeiro, R. D. S., Crispim, M. C. B., & Silva,  
683 G. H. G. D. 2012. Aquatic systems in semi-arid Brazil: limnology and management.  
684 *Acta Limnol. Bras.* 24(1), 103-118. [https://doi.org/10.1590/S2179-  
685 975X2012005000030](https://doi.org/10.1590/S2179-975X2012005000030)

686 Bastian, M., Boyero, L., Jackes, B. R., & Pearson, R. G. 2007. Leaf litter diversity and  
687 shredder preferences in an Australian tropical rain-forest stream. *J. Trop. Ecol.*  
688 23(2), 219-229. <https://doi.org/10.1017/S0266467406003920>

689 Battin, T. J., Besemer, K., Bengtsson, M. M., Romani, A. M., & Packmann, A. I. 2016. The  
690 ecology and biogeochemistry of stream biofilms. *Nat. Rev. Microbiol.* 14(4), 251.  
691 <https://doi.org/10.1038/nrmicro.2016.15>

692 Battin, T. J., Kaplan, L. A., Findlay, S., Hopkinson, C. S., Marti, E., Packman, A. I., Newbold, A.  
693 I., Sabater, F. 2008. Biophysical controls on organic carbon fluxes in fluvial  
694 networks. *Nat. Geosci.* 1, 95. <https://doi.org/10.1038/ngeo101>

695 Benson, L. J., & Pearson, R. G. 1993. Litter inputs to a tropical Australian rainforest stream.  
696 *Aust. J. Ecol.* 18(4), 377-383. [https://doi.org/10.1111/j.1442-  
697 9993.1993.tb00465.x](https://doi.org/10.1111/j.1442-9993.1993.tb00465.x)

698 Benstead, J. P., & Leigh, D. S. 2012. An expanded role for river networks. *Nat. Geosci.* 5 (10):  
699 678-679. <https://doi.org/10.1038/ngeo1593>

700 Berggren, M., & del Giorgio, P. A. 2015. Distinct patterns of microbial metabolism  
701 associated to riverine dissolved organic carbon of different source and quality. *J.*  
702 *Geophys. Res-Bioge.* 120, 989-999. <https://doi.org/10.1002/2015JG002963>

703 Bernhardt, J. R., Sunday, J. M., & O'Connor, M. I. 2018. Metabolic theory and the  
704 temperature-size rule explain the temperature dependence of population  
705 carrying capacity. *Am. Nat.* 192(6), 687-697. <https://doi.org/10.1086/700114>

- 706 Bonada, N., & Resh, V. H. 2013. Mediterranean-climate streams and rivers: geographically  
707 separated but ecologically comparable freshwater systems. *Hydrobiologia*,  
708 719(1), 1-29. <https://doi.org/10.1007/s10750-013-1634-2>
- 709 Boulton A.J., Boyero L., Covich A.P., Dobson M., Lake P.S. & Pearson R.G. 2008. Are tropical  
710 streams ecologically different from temperate streams? In D. Dudgeon (Ed),  
711 *Tropical Stream Ecology* (pp. 257– 284). London, UK: Elsevier.  
712 <https://doi.org/10.1016/B978-012088449-0.50011-X>
- 713 Boyero, L., Pearson, R. G., Dudgeon, D., Graça, M. A. S., Gessner, M. O., Albariño, R. J., ...  
714 Callisto, M. 2011a. Global distribution of a key trophic guild contrasts with  
715 common latitudinal diversity patterns. *Ecology*, 92(9), 1839-1848.  
716 <https://doi.org/10.1890/10-2244.1>
- 717 Boyero, L., Pearson, R. G., Gessner, M. O., Barmuta, L. A., Ferreira, V., Graça, M. A., ... Helson,  
718 J. E. 2011b. A global experiment suggests climate warming will not accelerate  
719 litter decomposition in streams but might reduce carbon sequestration. *Ecol. Lett.*  
720 14(3), 289-294. <https://doi.org/10.1111/j.1461-0248.2010.01578.x>
- 721 Boyero, L., Ramirez, A., Dudgeon, D., Pearson, R. G. 2009. Are tropical streams really  
722 different? *J. North. Am. Benthol.* 28(2), 397–403. <https://doi.org/10.1899/08-146.1>
- 723
- 724 Brandt, L. A., King, J. Y., & Milchunas, D. G. 2007. Effects of ultraviolet radiation on litter  
725 decomposition depend on precipitation and litter chemistry in a shortgrass  
726 steppe ecosystem. *Global Change Biol.* 13(10), 2193-2205.  
727 <https://doi.org/10.1111/j.1365-2486.2007.01428.x>
- 728 Brown, J. H., & Gillooly, J. F. 2003. Ecological food webs: high-quality data facilitate  
729 theoretical unification. *Proceedings of the National Academy of Sciences*, 100(4),  
730 1467-1468. <https://doi.org/10.1073/pnas.0630310100>
- 731 Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., West, G. B. 2004. Toward a metabolic  
732 theory of ecology. *Ecology* 85(7), 1771 – 1789. <https://doi.org/10.1890/03-9000>
- 733 Burrows, R. M., Beesley, L., Douglas, M. M., Pusey, B. J., & Kennard, M. J. 2020. Water  
734 velocity and groundwater upwelling influence benthic algal biomass in a sandy  
735 tropical river: implications for water-resource development. *Hydrobiologia*,  
736 847(5), 1207–1219. <https://doi.org/10.1007/s10750-020-04176-3>
- 737 Bush, B. M., Ulyshen, M. D., Fair, C. G., & Batzer, D. P. 2019. Assessing the effects of mesh  
738 enclosures on invertebrates and litter breakdown in a floodplain forest of the

739 Southeastern USA. *Wetl. Ecol. Manag.* 27(1), 149-156.  
740 <https://doi.org/10.1007/s11273-018-9648-1>

741 Cherry, D. S., Guthrie, R. K., & Harvey, R. S. 1974. Temperature influence on bacterial  
742 populations in three aquatic systems. *Water Res.*, 8(3), 149-155.  
743 [https://doi.org/10.1016/0043-1354\(74\)90037-2](https://doi.org/10.1016/0043-1354(74)90037-2)

744 Cioneck, V. M., Alves, G. H. Z., Tófoli, R. M., Rodrigues-Filho, J. L., & Dias, R. M. 2019. Brazil  
745 in the mud again: lessons not learned from Mariana dam collapse. *Biodivers .*  
746 *Conserv.*, 28(7), 1935-1938. <https://doi.org/10.1007/s10531-019-01762-3>

747 Cleven, E. J., & Meyer, E. I. 2003. A sandy hyporheic zone limited vertically by a solid  
748 boundary. *Arch. Hydrobiol.* 157(2), 267-288. <https://doi.org/10.1127/0003-9136/2003/0157-0267>

749

750 Cole, J. J., Prairie, Y. T., Caraco, N. F., Mcdowell, W. H., Tranvik, L. J., Striegl, R. G., ... Melack,  
751 J. 2007. Plumbing the global carbon cycle: integrating inland waters into the  
752 terrestrial carbon budget. *Ecosystems*, 10(1), 171-184.  
753 <https://doi.org/10.1007/s10021-006-9013-8>

754 Colls, M., Timoner, X., Font, C., Sabater, S., & Acuña, V. 2019. Effects of duration, frequency,  
755 and severity of the non-flow period on stream biofilm metabolism. *Ecosystems*,  
756 22(6), 1393-1405. <https://doi.org/10.1007/s10021-019-00345-1>

757 Corti, R., Datry, T., Drummond, L., & Larned, S. T. 2011. Natural variation in immersion and  
758 emersion affects breakdown and invertebrate colonization of leaf litter in a  
759 temporary river. *Aquat. Sci.* 73(4), 537-550. <https://doi.org/10.1007/s00027-011-0216-5>

760

761 Cunha, A., Almeida, A., Coelho, F. J. R. C., Gomes, N. C. M., Oliveira, V., & Santos, A. L. 2010.  
762 Bacterial extracellular enzymatic activity in globally changing aquatic  
763 ecosystems. *Curr. Res. Tech. Edu. Topics Applied Microbiol. Microbial Biotech.* 1,  
764 124-135.

765 Dallmann, J., Phillips, C. B., Teitelbaum, Y., Sund, N., Schumer, R., Arnon, S., & Packman, A.  
766 I. 2020. Impacts of suspended clay particle deposition on sand-bed  
767 morphodynamics. *Water Resour. Res.* 56(8), e2019WR027010.  
768 <https://doi.org/10.1029/2019WR027010>

769 Danielopol, D. L., Pospisil, P., Dreher, J., Mösslacher, F., Torreiter, P., Geiger-Kaiser, M., &  
770 Gunatilaka, A. 2000. A groundwater ecosystem in the wetlands of the Danube at  
771 Vienna (Austria). In Wilkens, H., Culvers, D. C., & Humphreys, W. F. (Eds), *Caves*

- 772           *and Other Subterranean Ecosystems. Ecosystems of the World* (vol. 30, pp. 481–  
773           513). Amsterdam: Elsevier.
- 774   Datry, T., Bonada, N., & Boulton, A. J. 2017a. Conclusions: Recent advances and future  
775           prospects in the ecology and management of intermittent rivers and ephemeral  
776           streams. In T. Datry, N., Bonada, & A. J. Boulton (Eds.), *Intermittent rivers and*  
777           *ephemeral streams: Ecology and management* (pp. 563–584). Amsterdam, The  
778           Netherlands: Academic Press. [https://doi.org/10.1016/B978-0-12-803835-](https://doi.org/10.1016/B978-0-12-803835-2.00031-0)  
779           [2.00031-0](https://doi.org/10.1016/B978-0-12-803835-2.00031-0)
- 780   Datry, T., Boulton, A. J., Bonada, N., Fritz, K., Leigh, C., Sauquet, ... Dahm, C.N. 2018. Flow  
781           intermittence and ecosystem services in rivers of the Anthropocene. *J. App. Ecol.*  
782           55(1), 353–364. <https://doi.org/10.1111/1365-2664.12941>
- 783   Datry, T., Foulquier, A., Corti, R., von Schiller, D., Tockner, K., Mendoza-Lera, ... Zoppini, A.,  
784           2018. A global analysis of terrestrial plant litter dynamics in non-perennial  
785           waterways. *Nat. Geosci.* 11, 497–503. [https://doi.org/10.1038/s41561-018-](https://doi.org/10.1038/s41561-018-0134-4)  
786           [0134-4](https://doi.org/10.1038/s41561-018-0134-4)
- 787   Datry, T., Larned, S. T., & Tockner, K. 2014. Intermittent rivers: a challenge for freshwater  
788           ecology. *BioScience*, 64(3), 229-235. <https://doi.org/10.1093/biosci/bit027>
- 789   Datry, T., Vander Vorste, R., Goitia, E., Moya, N., Campero, M., Rodriguez, F., ... & Oberdorff,  
790           T. 2017b. Context-dependent resistance of freshwater invertebrate communities  
791           to drying. *Ecol. Evol.* 7(9), 3201-3211. <https://doi.org/10.1002/ece3.2870>
- 792   Deng, L., Krauss, S., Feichtmayer, J., Hofmann, R., Arndt, H., Griebler, C. 2014. Grazing of  
793           heterotrophic flagellates on viruses is driven by feeding behavior. *Environ.*  
794           *Microbiol. Rep.* 6(4), 325-330. <https://doi.org/10.1111/1758-2229.12119>
- 795   Di Castri F., Hansen, A., & Holland, M. M. 1988. A new look at eco-tones: emerging  
796           international projects on landscape boundaries. *Biol. Int. (Speccial Issuse)*, 17,1–  
797           163.
- 798   Drake, T. W., Raymond, P. A., & Spencer, R. G. 2018. Terrestrial carbon inputs to inland  
799           waters: A current synthesis of estimates and uncertainty. *Limnol. Oceanogr. Lett.*  
800           3(3), 132-142. <https://doi.org/10.1002/lol2.10055>
- 801   Domisch, S., Araújo, M. B., Bonada, N., Pauls, S. U., Jähnig, S. C., & Haase, P. 2013. Modelling  
802           distribution in European stream macroinvertebrates under future climates.  
803           *Global Change Biol.* 19(3), 752-762. <https://doi.org/10.1111/gcb.12107>
- 804   Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M., &  
805           Woodward, G. 2012. Warming alters community size structure and ecosystem



806 functioning. *Proc. Biol. Sci.* 279(1740), 3011-3019.  
807 <https://doi.org/10.1098/rspb.2012.0394>

808 Edwards, A. M., Robinson, J. P., Plank, M. J., Baum, J. K., Blanchard, J. L. 2017. Testing and  
809 recommending methods for fitting size spectra to data. *Methods Ecol. Evol.* 8, 57–  
810 67. <https://doi.org/10.1111/2041-210X.12641>

811 Evans, L.E., Hirst, A.G., Kratina, P., & Beaugrand, G. 2020. Temperature-mediated changes  
812 in zooplankton body size: large scale temporal and spatial analysis. *Ecography*,  
813 43(4): 581-590. <https://doi.org/10.1111/ecog.04631>

814 Escobar, H. 2015. Mud tsunami wreaks ecological havoc in Brazil. *Science*, 350 (6265),  
815 1138–1139. <https://doi.org/10.1126/science.350.6265.1138>

816 Findlay, S., Quinn, J. M., Hickey, C. W., Burrell, G., & Downes, M. 2001. Effects of land use  
817 and riparian flowpath on delivery of dissolved organic carbon to streams. *Limnol.*  
818 *Oceanogr.* 46(2), 345-355. <https://doi.org/10.4319/lo.2001.46.2.0345>

819 Friedlingstein, P., Jones, M., O'sullivan, M., Andrew, R., Hauck, J., Peters, G., ... Zaehle, S.  
820 2019. Global carbon budget 2019. *Earth System Science Data*, 11(4), 1783-1838.  
821 <https://doi.org/10.5194/essd-11-1783-2019>

822 Foght, J. 2008. Anaerobic biodegradation of aromatic hydrocarbons: pathways and  
823 prospects. *J. Mol. Microbiol. Biotechnol.* 15(2-3), 93-120.  
824 <https://doi.org/10.1159/000121324>

825 Follstad Shah, J. J., Kominoski, J. S., Ardón, M., Dodds, W. K., Gessner, M. O., Griffiths, N. A.,  
826 ... Manning, D. W. 2017. Global synthesis of the temperature sensitivity of leaf  
827 litter breakdown in streams and rivers. *Global Change Biol.* 23(8), 3064-3075.  
828 <https://doi.org/10.1111/gcb.13609>

829 Gasith, A., & Resh, V. H. 1999. Streams in Mediterranean climate regions: abiotic influences  
830 and biotic responses to predictable seasonal events. *Annu. Rev. Ecol. Evol. Syst.*  
831 30(1), 51-81. <https://doi.org/10.1146/annurev.ecolsys.30.1.51>

832 Gessner, M. O., Chauvet, E., Dobson, M., 1999. A perspective on leaf litter breakdown in  
833 streams. *Oikos*, 85(2), 377–384. <https://doi.org/10.2307/3546505>

834 Gleeson, T., Befus, K. M., Jasechko, S., Luijendijk, E., & Cardenas, M. B. 2016. The global  
835 volume and distribution of modern groundwater. *Nat. Geosci.* 9(2), 161-167.  
836 <https://doi.org/10.1038/ngeo2590>

837 Gibert, J., Culver, D. C., Dole-Olivier, M. J., Malard, F., Christman, M. C., & Deharveng, L. 2009.  
838 Assessing and conserving groundwater biodiversity: synthesis and perspectives.

839 *Freshw. Biol.* 54(4), 930-941. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2427.2009.02201.x)  
840 [2427.2009.02201.x](https://doi.org/10.1111/j.1365-2427.2009.02201.x)

841 Gonçalves, J. F., Graça, M. A. S., Callisto, M., 2007. Litter decomposition in a Cerrado  
842 savannah stream is retarded by leaf toughness, low dissolved nutrients and a low  
843 density of shredders. *Freshw. Biol.* 52(8), 1440–1451.  
844 <https://doi.org/10.1111/j.1365-2427.2007.01769.x>

845 González-Bergonzoni, I., Meerhoff, M., Davidson, T. A., Teixeira-de Mello, F., Baattrup-  
846 Pedersen, A., & Jeppesen, E. 2012. Meta-analysis shows a consistent and strong  
847 latitudinal pattern in fish omnivory across ecosystems. *Ecosystems*, 15(3), 492-  
848 503. <https://doi.org/10.1007/s10021-012-9524-4>

849 Graça, M. A. S., 2001. The role of invertebrates on leaf litter decomposition in streams: a  
850 review. *Nt. Rev. Hydrobiol.* 86(4-5), 383–394. [https://doi.org/10.1002/1522-](https://doi.org/10.1002/1522-2632(200107)86:4/5<383::AID-IROH383>3.0.CO;2-D)  
851 [2632\(200107\)86:4/5<383::AID-IROH383>3.0.CO;2-D](https://doi.org/10.1002/1522-2632(200107)86:4/5<383::AID-IROH383>3.0.CO;2-D)

852 Graça, M. A. S., Hyde, K., Chauvet, E. 2016. Aquatic hyphomycetes and litter decomposition  
853 in tropical: subtropical low order streams. *Fungal Ecol.* 19, 182–189.  
854 <https://doi.org/10.1016/j.funeco.2015.08.001>

855 Griebler, C., Avramov, M. 2015. Groundwater ecosystem services: A review. *Freshw. Sci.*  
856 34(1), 355-367. <https://doi.org/10.1086/679903>

857 Heino, J., Melo, A. S., Jyrkänkallio-Mikkola, J., Petsch, D. K., Saito, V. S., Tolonen, K. T., ...  
858 Soininen, J. 2018. Subtropical streams harbour higher genus richness and lower  
859 abundance of insects compared to boreal streams, but scale matters. *J. Biogeogr.*  
860 45(9), 1983-1993. <https://doi.org/10.1111/jbi.13400>

861 Hill, B. H., Kolka, R. K., McCormick, F. H., Starry, M. A. 2014. A synoptic survey of ecosystem  
862 services from headwater catchments in the United States. *Ecosyst. Serv.* 7, 106-  
863 115. <https://doi.org/10.1016/j.ecoser.2013.12.004>

864 House, W. A. 2003. Geochemical cycling of phosphorus in rivers. *Appl. Geochem.* 18(5),  
865 739-748. [https://doi.org/10.1016/S0883-2927\(02\)00158-0](https://doi.org/10.1016/S0883-2927(02)00158-0)

866 Hose, G., & Stumpp, C. 2019. Architects of the underworld: bioturbation by groundwater  
867 invertebrates influences aquatic hydraulic properties. *Aquat. Sci.*, 81(20), 20.  
868 <https://doi.org/10.1007/s00027-018-0613-0>

869 Hotchkiss, E. R., Hall Jr, R. O., Sponseller, R. A., Butman, D., Klaminder, J., Laudon, H.,  
870 Rosvall, M., Karlsson, J. 2015. Sources of and processes controlling CO<sub>2</sub> emissions  
871 change with the size of streams and rivers. *Nat. Geosci.* 8, 696.  
872 <https://doi.org/10.1038/ngeo2507>

- 873 Howarth, R. G., Billen, G., Swaney, D., Townsend, A., Jaworski, N., Lajtha, K., ... Zhao-Liang,  
874 Z. 1996. In Howarth R.W. (eds), *Nitrogen Cycling in the North Atlantic Ocean and*  
875 *its Watersheds* (pp. 75-139). Dordrecht: Springer. [https://doi.org/10.1007/978-](https://doi.org/10.1007/978-94-009-1776-7_3)  
876 [94-009-1776-7\\_3](https://doi.org/10.1007/978-94-009-1776-7_3)
- 877 Jackson, R. B., Carpenter, S. R., Dahm, C. N., McKnight, D. M., Naiman, R.J., Postel, S. L., &  
878 Running, S. W. 2001. Water in a changing world. *Ecol. Appl.* 11, 1027–1045.  
879 [https://doi.org/10.1890/1051-0761\(2001\)011\[1027:WIACW\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1027:WIACW]2.0.CO;2)
- 880 Jaeger, A., Coll, C., Posselt, M., Mechelke, J., Rutere, C., Betterle, A., ... Singh, T. 2019. Using  
881 recirculating flumes and a response surface model to investigate the role of  
882 hyporheic exchange and bacterial diversity on micropollutant half-lives. *Environ.*  
883 *Sci-Proc. Imp.* 21(12), 2093-2108. <https://doi.org/10.1039/C9EM00327D>
- 884 James, F. C. 1970. Geographic size variation in birds and its relationship to climate.  
885 *Ecology*, 51(3), 365-390. <https://doi.org/10.2307/1935374>
- 886 Johnson, S. L., & Jones, J. A. 2000. Stream temperature responses to forest harvest and  
887 debris flows in western Cascades, Oregon. *Can. J. Fish. Aquat. Sci.* 57(S2), 30-39.
- 888 Junk, W.J., Bayley P.B., Sparks R.E., 1989. The flood pulse concept in river-floodplain  
889 systems. *Can. J. Fish. Aquat. Sci.* 106, 110-127. [https://doi.org/10.1007/978-94-](https://doi.org/10.1007/978-94-015-8212-4_14)  
890 [015-8212-4\\_14](https://doi.org/10.1007/978-94-015-8212-4_14)
- 891 Jurado, A., Vázquez-Suñé, E., Carrera, J., de Alda, M. L., Pujades, E., & Barceló, D. 2012.  
892 Emerging organic contaminants in groundwater in Spain: a review of sources,  
893 recent occurrence and fate in a European context. *Sci. Total Environ.* 440, 82-94.  
894 <https://doi.org/10.1016/j.scitotenv.2012.08.029>
- 895 Kelly, D. W., Dick, J. T., & Montgomery, W. I. 2002. The functional role of Gammarus  
896 (Crustacea, Amphipoda): shredders, predators, or both?. *Hydrobiologia*, 485(1-3),  
897 199-203. <https://doi.org/10.1023/A:1021370405349>
- 898 Kelly, D. J., Bothwell, M. L., & Schindler, D. W. 2003. Effects of solar ultraviolet radiation on  
899 stream benthic communities: an intersite comparison. *Ecology*, 84(10), 2724-  
900 2740. <https://doi.org/10.1890/02-0658>
- 901 Kerr, S. R., & Dickie, L. M. 2001. *The biomass spectrum: a predator-prey theory of aquatic*  
902 *production*. New York, USA: Columbia University Press.  
903 <https://doi.org/10.2307/3071789>
- 904 Krause, S., Hannah, D. M., & Fleckenstein, J. H. 2009. Hyporheic hydrology: interactions at  
905 the groundwater-surface water interface. *Hydrol. Process.* 23(15), 2103-2263.  
906 <https://doi.org/10.1002/hyp.7366>

907 Krause, S., Hannah, D. M., Fleckenstein, J. H., Heppell, C. M., Kaeser, D., Pickup, R., Pinay, G.,  
908 Wood, P. J., 2011a. Inter-disciplinary perspectives on processes in the hyporheic  
909 zone. *Ecohydrology*, 4(4), 481-499. <https://doi.org/10.1002/eco.176>

910 Krause, S., Hannah, D. M., Sadler, J. P., Wood, P. J. 2011b. Ecohydrology on the edge:  
911 interactions across the interfaces of wetland, riparian and groundwater-based  
912 ecosystems. *Ecohydrology*, 4(4), 477-480. <https://doi.org/10.1002/eco.240>

913 Krause, S., Lewandowski, J., Grimm, N.B., Hannah, D.M., Pinay, G., ... Turk, V. 2017.  
914 Ecohydrological interfaces as hot spots of ecosystem processes. *Water Resour.*  
915 *Res.* 53(8), 6359–6376. <https://doi.org/10.1002/2016WR019516>

916 Kolvenbach, B. A., Helbling, D. E., Kohler, H. -P. E., Corvini, P. F. X. 2014. Emerging  
917 chemicals and the evolution of biodegradation capacities and pathways in  
918 bacteria. *Curr. Opin. Biotechnol.* 27, 8–14.  
919 <https://doi.org/10.1016/j.copbio.2013.08.017>

920 Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. 2010. Emerging concepts in temporary-  
921 river ecology. *Freshw. Biol.* 55(4), 717-738. <https://doi.org/10.1111/j.1365-2427.2009.02322.x>

922

923 Leaper, R., & Huxham, M. (2002). Size constraints in a real food web: predator, parasite  
924 and prey body-size relationships. *Oikos*, 99(3), 443-456.  
925 <https://doi.org/10.1034/j.1600-0706.2002.10888.x>

926 Leite-Rossi, L. A., Saito, V. S., Cunha-Santino, M. B., & Trivinho-Strixino, S. 2016. How does  
927 leaf litter chemistry influence its decomposition and colonization by shredder  
928 Chironomidae (Diptera) larvae in a tropical stream?. *Hydrobiologia*, 771(1), 119-  
929 130. <https://doi.org/10.1007/s10750-015-2626-1>

930 Lennon, J. T., & Cottingham, K. L. 2008. Microbial productivity in variable resource  
931 environments. *Ecology*, 89(4), 1001-1014. <https://doi.org/10.1890/07-1380.1>

932 Lepers, E., Lambin, E. F., Janetos, A. C., DeFries, R., Achard, F., Ramankutty, N., & Scholes,  
933 R. J. 2005. A synthesis of information on rapid land-cover change for the period  
934 1981–2000. *BioScience*, 55(2), 115-124. [https://doi.org/10.1641/0006-3568\(2005\)055\[0115:ASOIOR\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0115:ASOIOR]2.0.CO;2)

935

936 Lewandowski, J., Arnon, S., Banks, E., Batelaan, O., Betterle, A., 2019. Is the hyporheic zone  
937 relevant beyond the scientific community? *Water* 11, 1–33.  
938 <https://doi.org/10.3390/w11112230>

939 Lewandowski, J., Putschew, A., Schwesig, D., Neumann, C., Radke, M. 2011. Fate of organic  
940 micropollutants in the hyporheic zone of a eutrophic lowland stream: results of a

941 preliminary field study. *Sci. Total Environ.* 409(10), 1824-1835.  
942 <https://doi.org/10.1016/j.scitotenv.2011.01.028>

943 Liao, K., Bai, Y., Huo, Y., Jian, Z., Hu, W., Zhao, C., & Qu, J. 2018. Integrating microbial  
944 biomass, composition and function to discern the level of anthropogenic activity  
945 in a river ecosystem. *Environ. Int.*, 116, 147-155.  
946 <https://doi.org/10.1016/j.envint.2018.04.003>

947 Majdi, N., Boiché, A., Traunspurger, W., & Lecerf, A. 2014. Predator effects on a detritus-  
948 based food web are primarily mediated by non-trophic interactions. *J. Anim. Ecol.*  
949 83(4), 953-962. <https://doi.org/10.1111/1365-2656.12189>

950 Majdi, N., Colls, M., Weiss, L., Acuña, V., Sabater, S., & Traunspurger, W. 2020) Duration  
951 and frequency of non-flow periods affect the abundance and diversity of stream  
952 meiofauna. *Freshw. Biol.* 65(11), 1906–1922.  
953 <https://doi.org/10.1111/fwb.13587>

954 Majdi, N., & Traunspurger, W. 2017. Leaf fall affects the isotopic niches of meiofauna and  
955 macrofauna in a stream food web. *Food Webs*, 10, 5-14.  
956 <https://doi.org/10.1016/j.fooweb.2017.01.002>

957 Maurice, L., & Bloomfield, J. 2012. Stygobitic invertebrates in groundwater—a review  
958 from a hydrogeological perspective. *Freshwater Reviews*, 5(1), 51-71.  
959 <https://doi.org/10.1608/FRJ-5.1.443>

960 McArthur, J. V., Barnes, J. R., Hansen, B. J., & Leff, L. G. 1988. Seasonal dynamics of leaf litter  
961 breakdown in a Utah alpine stream. *J. North. Am. Benthol.* 7(1), 44-50.  
962 <https://doi.org/10.2307/1467830>

963 McClain, M. E. & Elsenbeer, H. 2001) Terrestrial inputs to Amazon streams and internal  
964 biogeochemical processing, in: McClain, M. E., Victoria, R. L., Richey, J. E. (Eds),  
965 *The biogeochemistry of the Amazon basin*. Oxford University Press, New York, pp.  
966 185–208

967 Mechelke, J., Longrée, P., Singer, H., & Hollender, J. 2019. Vacuum-assisted evaporative  
968 concentration combined with LC-HRMS/MS for ultra-trace-level screening of  
969 organic micropollutants in environmental water samples. *Anal. Bioanal. Chem.*  
970 411(12), 2555-2567. <https://doi.org/10.1007/s00216-019-01696-3>

971 Meckenstock, R. U., Elsner, M., Griebler, C., Lueders, T., Stumpp, C., Dejonghe, W., ... van  
972 Breukelen, B. 2015. Biodegradation: Updating the concepts of control for  
973 microbial clean-up in contaminated aquifers. *Environ. Sci. Technol.* 49(12), 7073-  
974 7081. <https://doi.org/10.1021/acs.est.5b00715>

- 975 Mendes, F., Kiffer, W. P. Jr, Moretti, M. S. 2017. Structural and functional composition of  
976 invertebrate communities associated with leaf patches in forest streams: a  
977 comparison between mesohabitats and catchments. *Hydrobiologia*, 800, 115–  
978 127. <https://doi.org/10.1007/s10750-017-3249-5>
- 979 Morellato, L. P. C., Talora, D. C., Takahasi, A., Bencke, C. C., Romera, E. C., & Zipparro, V. B.  
980 2000. Phenology of Atlantic rain forest trees: a comparative study <sup>1</sup>. *Biotropica*,  
981 32(4b), 811-823. <https://doi.org/10.1111/j.1744-7429.2000.tb00620.x>
- 982 Moosdorf, N., Stieglitz, T., Waska, H., Dürr, H. H., & Hartmann, J. 2015. Submarine  
983 groundwater discharge from tropical islands: a review. *Grundwasser*, 20(1), 53-  
984 67. <https://doi.org/10.1007/s00767-014-0275-3>
- 985 Mulholland, P. J., Helton, A. M., Poole, G. C., Hall, R. O., Hamilton, S. K., Peterson, B. J., ...  
986 Thomas, S.M. 2008. Stream denitrification across biomes and its response to  
987 anthropogenic nitrate loading. *Nature*, 452, 202–205.  
988 <https://doi.org/10.1038/nature06686>
- 989 Nilsson, C., Lepori, F., Malmqvist, B., Törnlund, E., Hjerdt, N., Helfield, J. M., ... & Lundqvist,  
990 H. 2005. Forecasting environmental responses to restoration of rivers used as log  
991 floatways: an interdisciplinary challenge. *Ecosystems*, 8(7), 779-800.  
992 <https://doi.org/10.1007/s10021-005-0030-9>
- 993 Nessimian, J. L., Dorvillé, L. F. M., Sanseverino, A. M., & Baptista, D. F. 1998. Relation  
994 between flood pulse and functional composition of the macroinvertebrate  
995 benthic fauna in the lower Rio Negro, Amazonas, Brazil. *Amazoniana*, 15(1/2), 35-  
996 50.
- 997 O'Connell, M., Baldwin, D. S., Robertson, A. I., & Rees, G. 2000. Release and bioavailability  
998 of dissolved organic matter from floodplain litter: influence of origin and oxygen  
999 levels. *Freshw. Biol.* 45(3), 333-342. [https://doi.org/10.1111/j.1365-  
1000 2427.2000.00627.x](https://doi.org/10.1111/j.1365-2427.2000.00627.x)
- 1001 O'Gorman, E. J., Zhao, L., Pichler, D. E., Adams, G., Friberg, N., Rall, B.C., Seeney, A., Zhang,  
1002 H., Reuman, D. C. and Woodward, G. 2017. Unexpected changes in community size  
1003 structure in a natural warming experiment. *Nat. Clim. Change*, 7(9), 659-663.  
1004 <https://doi.org/10.1038/nclimate3368>
- 1005 Olsson, T., & Söderström, O. 1978. Springtime migration and growth of *Parameletus*  
1006 chelifer (Ephemeroptera) in a temporary stream in northern Sweden. *Oikos*, 31,  
1007 284-289. <https://doi.org/10.2307/3543652>

- 1008 Padial, A. A., & Thomaz, S. M. 2006. Effects of flooding regime upon the decomposition of  
1009 *Eichhornia azurea* (Sw.) Kunth measured on a tropical, flow-regulated floodplain  
1010 (Paraná River, Brazil). *River Res. Appl.* 22(7), 791-801.  
1011 <https://doi.org/10.1002/rra.936>
- 1012 Perkins, D. M., Durance, I., Edwards, F. K., Grey, J., Hildrew, A. G., Jackson, M., ... Woodward,  
1013 G. 2018. Bending the rules: exploitation of allochthonous resources by a top-  
1014 predator modifies size-abundance scaling in stream food webs. *Ecol. Lett.* 21(12),  
1015 1771-1780. <https://doi.org/10.1111/ele.13147>
- 1016 Peralta-Maraver, I., Perkins, D. M., Thompson, M. S., Fussmann, K., Reiss, J., Robertson, A.  
1017 L. 2019a. Comparing biotic drivers of litter breakdown across stream  
1018 compartments. *J. Anim. Ecol.* 88(8), 1146-1157. [https://doi.org/10.1111/1365-  
1019 2656.13000](https://doi.org/10.1111/1365-2656.13000)
- 1020 Peralta-Maraver, I., Reiss, J., Robertson, A. L. 2018. Interplay of hydrology, community  
1021 ecology and pollutant attenuation in the hyporheic zone. *Sci. Total Environ.* 610,  
1022 267-275. <https://doi.org/10.1016/j.scitotenv.2017.08.036>
- 1023 Peralta-Maraver, I., Robertson, A. L., & Perkins, D. M. 2019b. Depth and vertical  
1024 hydrodynamics constrain the size structure of a lowland streambed community.  
1025 *Biol. Lett.* 15(7), 20190317. <https://doi.org/10.1098/rsbl.2019.0317>
- 1026 Petchey, O. L., & Belgrano, A. 2010. Body-size distributions and size-spectra: universal  
1027 indicators of ecological status? *Biol. Lett.* 6, 434-  
1028 437. <https://doi.org/10.1098/rsbl.2010.0240>
- 1029 Peterson, B. J., Wollheim, W. M., Mulholland, P. J., Webster, J. R., Meyer, J. L., Tank, J. L., ... &  
1030 McDowell, W. H. 2001. Control of nitrogen export from watersheds by headwater  
1031 streams. *Science*, 292(5514), 86-90. <https://doi.org/10.1126/science.1056874>
- 1032 Posselt, M., Mechelke, J., Rutere, C., Coll, C., Jaeger, A., Raza, M., ... & Horn, M. A. 2020.  
1033 Bacterial diversity controls transformation of wastewater-derived organic  
1034 contaminants in River-Simulating Flumes. *Environ. Sci. Technol.* 54(9), 5467-  
1035 5479. <https://doi.org/10.1021/acs.est.0c00767>
- 1036 Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., ... Joern, A. 2013.  
1037 Invertebrates, ecosystem services and climate change. *Biol. Rev.* 88(2), 327-348.  
1038 <https://doi.org/10.1111/brv.12002>
- 1039 Pringle C. M., Paaby-Hansen P., Vaux P. D., & Goldman C. R. 1986) In situ nutrient assays  
1040 of periphyton growth in a lowland Costa Rican stream. *Hydrobiologia*, 134, 207-  
1041 213. <https://doi.org/10.1007/BF00008489>

1042 Rahm, B. G., Hill, N. B., Shaw, S. B., & Riha, S. J. 2016. Nitrate dynamics in two streams  
1043 impacted by wastewater treatment plant discharge: Point sources or sinks? *J. Am.*  
1044 *Water Resour. As.* 52(3), 592-604. <https://doi.org/10.1111/1752-1688.12410>

1045 Raymond, P. A., Hartmann, J., Lauerwald, R., Sobek, S., McDonald, C., Hoover, M., ... &  
1046 Kortelainen, P. 2013. Global carbon dioxide emissions from inland waters.  
1047 *Nature*, 503(7476), 355-359. <https://doi.org/10.1038/nature12760>

1048 Reche, I., Pace, M. L., & Cole, J. J. 1998. Interactions of photobleaching and inorganic  
1049 nutrients in determining bacterial growth on colored dissolved organic carbon.  
1050 *Microb. Ecol.* 36(3-4), 270-280. <https://doi.org/10.1007/s002489900114>

1051 Refsgaard, J. C., Auken, E., Bamberg, C. A., Christensen, B. S., Clausen, T., Dalgaard, E., ... He,  
1052 X. 2014. Nitrate reduction in geologically heterogeneous catchments—A  
1053 framework for assessing the scale of predictive capability of hydrological models.  
1054 *Sci. Total Environ.* 468, 1278-1288.  
1055 <https://doi.org/10.1016/j.scitotenv.2013.07.042>

1056 Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F. T., Gruber, N., Janssens, I. A., ... &  
1057 Arndt, S. 2013. Anthropogenic perturbation of the carbon fluxes from land to  
1058 ocean. *Nature geosci.* 6(8), 597-607. <https://doi.org/10.1038/ngeo1830>

1059 Reiss, J., Perkins, D. M., Fussmann, K. E., Krause, S., Canhoto, C., Romeijn, P., & Robertson,  
1060 A. L. 2019. Groundwater flooding: Ecosystem structure following an extreme  
1061 recharge event. *Sci. Total Environ.* 652, 1252-1260.  
1062 <https://doi.org/10.1016/j.scitotenv.2018.10.216>

1063 Robertson, A. L., Smith, J. W. N., Johns, T., & Proudlove, G. S. 2009. The distribution and  
1064 diversity of stygobites in Great Britain: an analysis to inform groundwater  
1065 management. *Q. J. Eng. Geol.* 42 (3), 359-368. [https://doi.org/10.1144/1470-](https://doi.org/10.1144/1470-9236/08-046)  
1066 [9236/08-046](https://doi.org/10.1144/1470-9236/08-046)

1067 Santos-Junior, C.D., Logares, R., & Henrique-Silva, F. 2020. Linking microbial genomes  
1068 with their potential to degrade terrestrial organic matter in the Amazon River.  
1069 *Microbiome* 8, 151. <https://doi.org/10.1186/s40168-020-00930-w>

1070 Schaper, J. L., Posselt, M., Bouchez, C., Jaeger, A., Nuetzmann, G., Putschew, A., ... &  
1071 Lewandowski, J. 2019. Fate of Trace Organic Compounds in the Hyporheic Zone:  
1072 Influence of Retardation, the Benthic Biolayer, and Organic Carbon. *Environ. Sci.*  
1073 *Technol.* 53(8), 4224-4234. <https://doi.org/10.1021/acs.est.8b06231>



- 1074 Schaper, J. L., Seher, W., Nützmann, G., Putschew, A., Jekel, M., Lewandowski, J. 2018. The  
1075 fate of polar trace organic compounds in the hyporheic zone. *Water Resour.* 140,  
1076 158-166. <https://doi.org/10.1016/j.watres.2018.04.040>
- 1077 Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. 2009. Is there a  
1078 latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol.*  
1079 *Syst.* 40, 245-269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>
- 1080 Schmid, P. E., Tokeshi, M., & Schmid-Araya, J. M. 2000. Relation between population  
1081 density and body size in stream communities. *Science*, 289(5484), 1557-1560.  
1082 <https://doi.org/10.1126/science.289.5484.1557>
- 1083 Schneider, I. & Topalova, Y. 2009. Structural and functional changes in river microbial  
1084 communities after dairy wastewater discharge. *Biotechnol. Biotechnol. Equip.*  
1085 23(2), 1210–1216. <https://doi.org/10.1080/13102818.2009.10818576>
- 1086 Seitzinger, S., Harrison, J. A., Böhlke, J. K., Bouwman, A. F., Lowrance, R., Peterson, B., ... &  
1087 Drecht, G. V. 2006. Denitrification across landscapes and waterscapes: a  
1088 synthesis. *Ecol. Appl.* 16(6), 2064-2090. [https://doi.org/10.1890/1051-  
1089 0761\(2006\)016\[2064:DALAWA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[2064:DALAWA]2.0.CO;2)
- 1090 Shumilova, O., Zak, D., Datry, T., von Schiller, D., Corti, R., Foulquier, A., ... & Arce, M. I.  
1091 (2019). Simulating rewetting events in intermittent rivers and ephemeral  
1092 streams: A global analysis of leached nutrients and organic matter. *Global Change*  
1093 *Biol.* 25(5), 1591-1611. <https://doi.org/10.1111/gcb.14537>
- 1094 Sibly, R. M., Brown, J. H., & Kodric-Brown, A. 2012. *Metabolic ecology: a scaling approach.*  
1095 New Jersey, USA: John Wiley & Sons.
- 1096 Silva-Araújo, M., Silva-Junior, E. F., Neres-Lima, V., Feijó-Lima, R., Tromboni, F., Lourenço-  
1097 Amorim, C., ... & Zandonà, E. 2020. Effects of riparian deforestation on benthic  
1098 invertebrate community and leaf processing in Atlantic forest streams. *Perspect.*  
1099 *Ecol. Conserv.* (in press. <https://doi.org/10.1016/j.pecon.2020.09.004>
- 1100 Sket, B. 1999. High biodiversity in hypogean waters and its endangerment—the situation  
1101 in Slovenia, the Dinaric karst, and Europe. *Crustaceana*, 72(8), 767-779.  
1102 <https://doi.org/10.1163/156854099503951>
- 1103 Sponseller, R.A. & Benfield, E.F. Influences of land use on leaf breakdown in southern  
1104 Appalachian headwater streams: a multi-scale analysis. 2001. *J. North. Am.*  
1105 *Benthol.* 20(1), 44-59. <https://doi.org/10.2307/1468187>
- 1106 Steward, A.L., Marshall, J.C., Sheldon, F., Harch, B., Choy, S., Bunn, S.E., Tockner, K. 2011.  
1107 Terrestrial invertebrates of dry river beds are not simply subsets of riparian

1108 assemblages. *Aquat. Sci.* 73, 551–566. <https://doi.org/10.1007/s00027-011->  
1109 [0217-4](https://doi.org/10.1007/s00027-011-0217-4)

1110 Stubbington, R., England, J., Wood, P. J., & Sefton, C. E. 2017. Temporary streams in  
1111 temperate zones: recognizing, monitoring and restoring transitional aquatic-  
1112 terrestrial ecosystems. *Wiley Interdiscip. Rev. Water.* 4(4), e1223.  
1113 <https://doi.org/10.1002/wat2.1223>

1114 Stubbington, R. Datry, T. 2013. The macroinvertebrate seedbank promotes community  
1115 persistence in temporary rivers across climate zones. *Freshw. Biol.* 58(6), 1202–  
1116 1220. <https://doi.org/10.1111/fwb.12121>

1117 Sweeney, B. W., Bott, T. L., Jackson, J. K., Kaplan, L. A., Newbold, J. D., Standley, L. J., ... &  
1118 Horwitz, R. J. 2004. Riparian deforestation, stream narrowing, and loss of stream  
1119 ecosystem services. *Proc. Natl. Acad. Sci. U.S.A.* 101(39), 14132-14137.  
1120 <https://doi.org/10.1073/pnas.0405895101>

1121 Taniwaki, R. H., Piggott, J. J., Ferraz, S. F., & Matthaei, C. D. 2017. Climate change and  
1122 multiple stressors in small tropical streams. *Hydrobiologia*, 793(1), 41-53.  
1123 <https://doi.org/10.1007/s10750-016-2907-3>

1124 Taniwaki, R. H., Matthaei, C. D., Cardoso, T. K., Ferraz, S. F., Martinelli, L. A., & Piggott, J. J.  
1125 2019. The effect of agriculture on the seasonal dynamics and functional diversity  
1126 of benthic biofilm in tropical headwater streams. *Biotropica*, 51(1), 18-27.  
1127 <https://doi.org/10.1111/btp.12617>

1128 Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entekin, S. A., & Stephen, M. L. 2010. A  
1129 review of allochthonous organic matter dynamics and metabolism in streams. *J.*  
1130 *North. Am. Benthol.* 29(1), 118-146. <https://doi.org/10.1899/08-170.1>

1131 Tank J. L. & Webster J. R. 1998) Interaction of substrate and nutrient availability on wood  
1132 biofilm processes in streams. *Ecology*, 79(6), 2168–2179.  
1133 [https://doi.org/10.1890/0012-9658\(1998\)079\[2168:IOSANA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2168:IOSANA]2.0.CO;2)

1134 Tiegs, S. D., Costello, D. M., Isken, M. W., Woodward, G., McIntyre, P. B., Gessner, M. O., ... &  
1135 Albariño, R. 2019. Global patterns and drivers of ecosystem functioning in rivers  
1136 and riparian zones. *Sci. Adv.* 5(1), eaav0486.  
1137 <https://doi.org/10.1126/sciadv.aav0486>

1138 Thompson, P. L., & Bärlocher, F. 1989. Effect of pH on leaf breakdown in streams and in  
1139 the laboratory. *J. North. Am. Benthol.* 8(3), 203-210.  
1140 <https://doi.org/10.2307/1467323>

- 1141 Tockner, K., & Stanford, J. A. 2002. Riverine flood plains: present state and future trends.  
1142 *Environ. Conserv.* 29(3), 308-330.  
1143 <https://doi.org/10.1017/S037689290200022X>
- 1144 Tooth, S., & Nanson, G. C. 2000. The role of vegetation in the formation of anabranching  
1145 channels in an ephemeral river, Northern plains, arid central Australia. *Hydrol.*  
1146 *Process.* 14(16-17), 3099-3117. [https://doi.org/10.1002/1099-  
1147 1085\(200011/12\)14:16/17<3099::AID-HYP136>3.0.CO;2-4](https://doi.org/10.1002/1099-1085(200011/12)14:16/17<3099::AID-HYP136>3.0.CO;2-4)
- 1148 Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. 1980. The river  
1149 continuum concept. *Can. J. Fish. Aquat. Sci.* 37 (1), 130-137.  
1150 <https://doi.org/10.1139/f80-017>
- 1151 Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., ... &  
1152 Tilman, D. G. 1997. Human alteration of the global nitrogen cycle: sources and  
1153 consequences. *Ecol. Appl.* 7(3), 737-750. [https://doi.org/10.1890/1051-  
1154 0761\(1997\)007\[0737:HAOTGN\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0737:HAOTGN]2.0.CO;2)
- 1155 Von Schiller, D., Datry, T., Corti, R., Foulquier, A., Tockner, K., Marcé, R., ... & Mendoza-Lera,  
1156 C. 2019. Sediment respiration pulses in intermittent rivers and ephemeral  
1157 streams. *Global Biogeochem. Cycles.* 33(10), 1251-1263.  
1158 <https://doi.org/10.1029/2019GB006276>
- 1159 Walalite, T., Dekker, S. C., Keizer, F. M., Kardel, I., Schot, P. P., deJong, S. M., Wassen, M. J.,  
1160 2016. Flood water hydrochemistry patterns suggest floodplain sink function for  
1161 dissolved solids from the Songkhram Monsoon River (Thailand). *Wetlands*, 36,  
1162 995-1008. <https://doi.org/10.1007/s13157-016-0814-z>
- 1163 Wang, F., Lin, D., Li, W., Dou, P., Han, L., Huang, M., ... & Yao, J. 2020. Meiofauna promotes  
1164 litter decomposition in stream ecosystems depending on leaf species. *Ecol. Evol.*  
1165 10(17), 9257-9270. <https://doi.org/10.1002/ece3.6610>
- 1166 Wang, S. Y., Sudduth, E. B., Wallenstein, M. D., Wright, J. P., & Bernhardt, E. S. 2011.  
1167 Watershed urbanization alters the composition and function of stream bacterial  
1168 communities. *PLoS One*, 6(8), e22972.  
1169 <https://doi.org/10.1371/journal.pone.0022972>
- 1170 Wantzen, K.M., Wagner, R., 2006. Detritus processing by invertebrate shredders: a  
1171 neotropical-temperate comparison. *J. North. Am. Benthol.* 25(1), 216-32.  
1172 [https://doi.org/10.1899/0887-3593\(2006\)25\[216:DPBISA\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2006)25[216:DPBISA]2.0.CO;2)
- 1173 Wantzen, K.M., Yule, C.M., Mathooko, J.M., Pringle, C.M., Dudgeon, D., 2008. Organic mat-  
1174 ter processing in tropical streams. In: Dudgeon, D. (Ed.), *Tropical Stream Ecology*.

1175 Elsevier, London, pp. 43–64. Webster, J.R., & Benfield, E.F. 1986. Vascular plant  
1176 breakdown in freshwater ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 17, 567–594.  
1177 <https://doi.org/10.1146/annurev.es.17.110186.003031>

1178 Weitere, M., Scherwass, A., Sieben, K. T., & Arndt, H. 2005. Planktonic food web structure  
1179 and potential carbon flow in the lower river Rhine with a focus on the role of  
1180 protozoans. *River Res. Appl.* 21(5), 535-549. <https://doi.org/10.1002/rra.825>

1181 Weitowitz, D., Robertson, A., Bloomfield, J., Maurice, L., Reiss, J. 2019. Obligate  
1182 groundwater crustaceans mediate biofilm interactions in a subsurface food web.  
1183 *Freshwater Science*, 38(3), 491-502. <https://doi.org/10.1086/704751>

1184 Wetzel, R. G. 2001. Limnology: lake and river ecosystems. San Diego: Academic Press.

1185 White, E. P., Ernest, S. M., Kerkhoff, A. J., Enquist, B. J. 2007. Relationships between body  
1186 size and abundance in ecology. *Trends Ecol. Evol.* 22(6), 323-330.  
1187 <https://doi.org/10.1016/j.tree.2007.03.007>

1188 Williams, C. J., Yamashita, Y., Wilson, H. F., Jaffé, R., & Xenopoulos, M. A. 2010. Unraveling  
1189 the role of land use and microbial activity in shaping dissolved organic matter  
1190 characteristics in stream ecosystems. *Limnol. Oceanogr.* 55(3), 1159-1171.  
1191 <https://doi.org/10.4319/lo.2010.55.3.1159>

1192 Withers, P. J. A., & Jarvie, H. P. 2008. Delivery and cycling of phosphorus in rivers: a review.  
1193 *Sci. Total Environ.* 400(1-3), 379-395.  
1194 <https://doi.org/10.1016/j.scitotenv.2008.08.002>

1195 Wold A.P. & Hershey A.E. 1999. Spatial and temporal variability of nutrient limitation in 6  
1196 North Shore tributaries to Lake Superior. *J. North. Am. Benthol.* 18(1), 2–14.  
1197 <https://doi.org/10.2307/1468005>

1198 Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., ... & Dobson, M.  
1199 2012. Continental-scale effects of nutrient pollution on stream ecosystem  
1200 functioning. *Science*, 336(6087), 1438-1440.  
1201 <https://doi.org/10.1126/science.1219534>

1202 Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species  
1203 coexistence. *Oecologia*, 130(1), 1-14. <https://doi.org/10.1007/s004420100809>

1204 Zhang, H., Yuan, W., Dong, W., Liu, S., 2014. Seasonal patterns of litterfall in forest  
1205 ecosystem worldwide. *Ecol. Complex.* 20, 240-247.  
1206 <https://doi.org/10.1016/j.ecocom.2014.01.003>

1207 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) Mixed effects models  
1208 and extensions in ecology with R. Springer, New York.

1209  
1210  
1211  
1212  
1213  
1214  
1215  
1216  
1217  
1218  
1219  
1220  
1221  
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1243 **FIGURE CAPTIONS**

1244  
1245 **Fig. 1** Flow chart illustrating the hierarchy of knowledge that this review will follow  
1246 through the different sections.

1247  
1248 **Fig. 2.** Conceptual diagram of riverine bioreactor functioning. Organic matter (OM)  
1249 decomposition processes are hierarchically interconnected through the different compartments  
1250 of the riverine bioreactor. **(a)** Litter fall production and temperature are higher and more  
1251 constant in tropical than in temperate streams and rivers. **(b)** Anthropogenic release represents  
1252 a major input source of dissolved organic matter (DOM) and dissolved pollutants in riverine  
1253 systems. Dissolved compounds penetrate in streambed and reach groundwater systems and  
1254 aquifers (main sources of drinking water for human consumption). Life activities of streambed  
1255 macroinvertebrates **(c)** and groundwater stygobites (subterranean invertebrates that live in  
1256 groundwater systems) **(d)** result in bioturbation and bioirrigation phenomena that promote  
1257 water exchange, water mixing, sediment aeration and boost microbial activity. **(e)** Protists  
1258 grazing on biofilms promote its absorption surface and growth. **(f)** Decomposition of particulate  
1259 and DOM expands on aquatic-terrestrial ecotones along floodplains, and intermittent streams  
1260 and rivers as a consequence of the flood-pulse. The metabolic theory of ecology predicts that  
1261 mean body size of the ectotherms declines as environmental temperature increases at low  
1262 latitudes to meet the higher energy demands **(g)**. The size spectra can be used as an integrative  
1263 index to predict and compare decomposition rate at global scales **(h)**.

1264  
1265 **Fig. 3.** Empirical support for the proposed analytical framework to predict  
1266 decomposition rates. Using the size spectra (M-N slope) from streambed communities  
1267 allows to predict the organic matter decomposition rate in riverine bioreactor within the  
1268 streambed habitats. **(a)** Locations of the 30 study rivers in the United Kingdom sampled by  
1269 Peralta-Maraver et al. (2019). **(b)** Fitted body-mass abundance relationship for each one of the  
1270 communities including those sampled in the benthic (solid grey line) and the hyporheic zones  
1271 (solid black line). **(c)** Predicted relationship between the M-N slope and the decomposition rate  
1272 measured in degree days (dd) for each habitat.