

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

Running title: Organic matter decomposition by the riverine bioreactor

Ignacio Peralta–Maraver^{1,2*} (0000-0002-3467-7664),

Rachel Stubbington³ (0000-0001-8475-5109), Shai Arnon⁴ (0000-0002-7109-8979),

Pavel Kratina⁵ (0000-0002-9144-7937), Stefan Krause⁶ (0000-0003-2521-2248), Vivian

de Mello Cionek⁷ (0000-0002-0879-690X), Nei Kavaguichi Leite⁸ (0000-0002-7732-

8122), Aurea Luiza Lemes da Silva⁸ (0000-0001-8176-8983), Sidinei Magela Thomaz⁹

(0000-0002-5236-1364), Malte Posselt¹⁰ (0000-0001-8979-8044), Victoria Susan

Milner¹¹ (0000-0001-8027-3647), Andrea Momblanch¹² (0000-0003-3165-4691),

Marcelo S. Moretti¹³ (0000-0003-1994-2105), Rodolfo L. B. Nóbrega¹⁴ (0000-0002-9858-

8222), Daniel M. Perkins² (0000-0003-0866-4816), Mauricio M. Petrucio⁸ (0000-0002-

7242-9426), Isabel Reche¹ (0000-0003-2908-1724), Victor Saito¹⁵ (0000-0001-6112-

7249), Hugo Sarmiento¹⁶ (0000-0001-5220-7992), Emily Strange¹⁷ (0000-0001-8491-

3912), Ricardo Hideo Taniwaki¹⁸ (0000-0002-2186-8998), James White¹⁹ (0000-0003-

2280-1442), Gustavo Henrique Zaia Alves²⁰ (0000-0002-9233-2824), Anne L. Robertson²

(0000-0001-8398-3556).

Affiliations:

¹Departamento de Ecología, Universidad de Granada, Granada, España.

²Department of Life Sciences, Roehampton University, London, UK.

³School of Science and Technology, Nottingham Trent University, Nottingham, UK.

⁴Zuckerberg Institute for Water Research, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Beersheba, Israel.

⁵School of Biological and Chemical Sciences, Queen Mary University of London, London, UK.

⁶School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, UK.

⁷Programa de Pós-Graduação em Ciência e Tecnologia Ambiental, Universidade do Vale do Itajaí, Itajaí, Santa Catarina, Brazil.

⁸Department of Ecology and Zoology, Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil.

⁹Universidade Estadual de Maringá, Department of Biology, Maringá, Paraná, Brazil.

35 ¹⁰Department of Environmental Science, Stockholm University, Stockholm, Sweden.

36 ¹¹School of Applied Sciences, University of Huddersfield, Huddersfield, UK.

37 ¹²Cranfield Water Science Institute, Cranfield University, Cranfield, UK.

38 ¹³Laboratory of Aquatic Insect Ecology, Universidade Vila Velha, Vila Velha, Espírito
39 Santo, Brazil.

40 ¹⁴Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst
41 Road, Ascot, SL5 7PY UK.

42 ¹⁵Departamento de Ciências Ambientais, Universidade Federal de São Carlos, São Carlos,
43 São Paulo, Brazil.

44 ¹⁶Department of Hydrobiology, Universidade Federal de São Carlos, São Carlos, São Paulo,
45 Brazil.

46 ¹⁷Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands.

47 ¹⁸Centro de Engenharia, Modelagem e Ciências Sociais Aplicadas, Universidade Federal do
48 ABC, Santo André, São Paulo, Brazil.

49 ¹⁹River Restoration Centre, Cranfield University, Cranfield, Bedfordshire, UK.

50 ²⁰Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.

51
52 ***Corresponding author:** peraltamaraver@ugr.es

53
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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⁻¹ 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⁻¹ 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 (CO₂),
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 (Stubington 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; Stubington 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 β_0 is the intercept and ε 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 (Δ AIC),
617 their relative log-likelihood and weights (w_i).

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

618

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	0.22×10^{-2}	7.42	
<i>Habitat</i>	-0.01	0.29×10^{-2}	-4.73	$< 0.01 \times 10^{-2}$
<i>M-N slope</i>	0.02	0.52×10^{-2}	4.75	$< 0.01 \times 10^{-2}$
<i>Habitat \times M-N slope</i>	-0.02	0.60×10^{-2}	-3.91	$< 0.01 \times 10^{-2}$

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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.