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1 **River ecosystem metabolism and carbon biogeochemistry in a changing world**

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56

57 **River networks represent the largest biogeochemical nexus between the continents,**
58 **ocean and atmosphere. Our current understanding of the role of rivers in the global**
59 **carbon cycle remains limited, which makes it difficult to predict how global change may**
60 **alter the timing and spatial distribution of riverine carbon sequestration and**
61 **greenhouse gas emissions. Here we review the state of river ecosystem metabolism**
62 **research and synthesise current best available estimates of river ecosystem metabolism.**
63 **We quantify the organic and inorganic carbon flux from land to global rivers, and show**
64 **that their net ecosystem production and carbon dioxide emissions shift the organic to**
65 **inorganic carbon balance en route from land to the coastal ocean. Furthermore, we**
66 **discuss how global change may affect river ecosystem metabolism and related carbon**
67 **fluxes and identify research directions that can help develop better predictions of**
68 **global-change impacts on riverine ecosystem processes. We argue that a global river**
69 **observing system will play a key role in understanding river networks and their future**
70 **evolution in the context of the global carbon budget.**

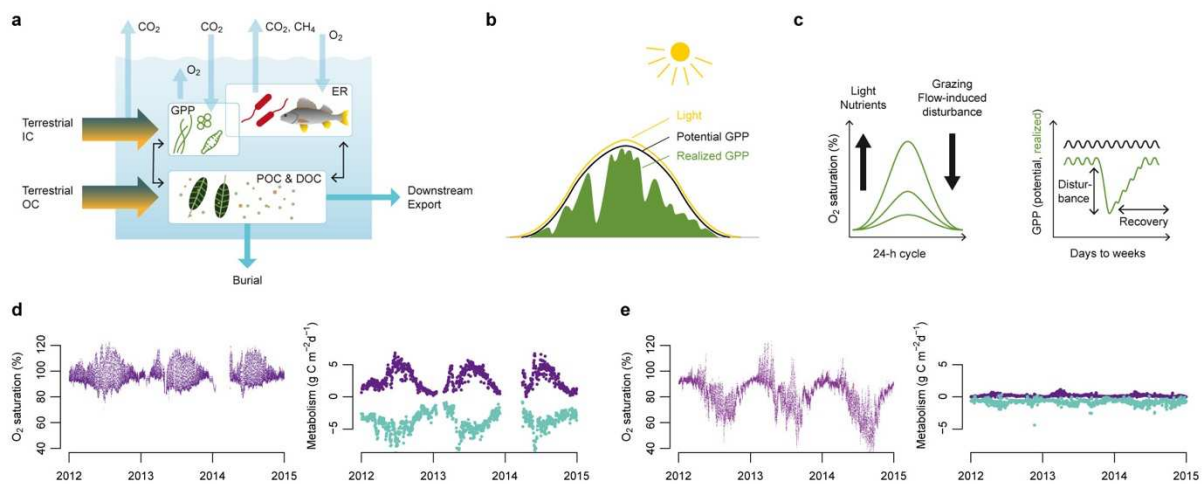
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74 Rivers (here understood as all flowing waters from the smallest headwater streams to large
75 rivers) are organized into fractal networks draining the continents and linking terrestrial and
76 marine ecosystems through lateral transfers of water, energy, and matter. Having long been
77 considered ‘pipes’ conservatively transferring carbon (C) from land to the ocean, today we
78 understand rivers are ‘biogeochemical reactors’ that metabolise organic C (OC) with net
79 emission of CO₂ and CH₄ to the atmosphere, and also OC burial in aquatic sediments,
80 floodplains, and deltas (e.g., refs.¹⁻³). This notion was adopted by the Intergovernmental

81 Panel on Climate Change (IPCC)⁴ and the Global Carbon Project⁵ in their global C budget
 82 assessments. Our current understanding of the role of rivers in the global C cycle remains
 83 limited to simple budget analyses (e.g. refs.^{6,7}), where rivers are still often treated collectively
 84 as a black box without quantifiable internal processes. This approach does not allow for
 85 predicting how global change will alter the timing and spatial distribution of riverine C
 86 sequestration and greenhouse gas (GHG) emissions. The notion of rivers as ‘biogeochemical
 87 reactors’ implies their nature as ecosystems with energy flows related to metabolism, defined
 88 as the fixation and dissipation of energy by all organisms⁸ (Fig. 1a). To date, a global scale
 89 assessment of river ecosystem metabolism has not yet been attempted, which is a critical gap
 90 in our understanding of the role of rivers in global C biogeochemistry. River ecosystem
 91 metabolism is the main control of C and nutrient cycling^{8,9}, food web energetics and
 92 biodiversity¹⁰, so it directly affects ecosystem health¹¹.



94

95 **Figure 1. River ecosystem metabolism.** (a) River ecosystem metabolism is the sum of the
 96 metabolism of all producers and consumers. Ecosystem gross primary production (GPP) and
 97 ecosystem respiration (ER) meld terrestrial subsidies of organic (OC) and inorganic (IC)
 98 carbon with gas fluxes and the oxygen balance in rivers. (b) and (c) The seasonal dynamics of
 99 light availability (yellow) imposes an upper boundary on the potential GPP, whereas flow
 100 disturbance and recovery, nutrients and grazing by consumers control GPP at shorter time
 101 scales, thereby shaping the realized GPP regime over a year. (d) and (e) Multi-annual regimes
 102 of oxygen saturation and metabolism (GPP: blue symbols; ER: yellow symbols) regimes of a
 103 productive (Au Sable River, Michigan) river with a summer peak and a non-productive river
 104 (Fanno Creek, Oregon). (b) and (c) are modified from ref.⁹.

105

106

107 Global change has altered the global C cycle and its feedback to Earth's climate. River
108 networks are not exempt from global change. Climate change perturbs the natural flow^{12,13},
109 temperature and icing¹⁴ of rivers, while damming and water abstraction further disrupt river
110 networks^{15,16}. Collectively, these disturbances have altered the global surface area of rivers¹⁷,
111 and freshwater distribution and availability^{18,19}. Concomitantly, land use and management
112 changes promote eutrophication through increased delivery of dissolved and particulate
113 nutrients and C to rivers^{20,21}. Global change has also perturbed global C fluxes between
114 terrestrial and river ecosystems²². These impacts on river ecosystem metabolism and ensuing
115 consequences for large-scale C biogeochemistry are increasingly well understood for river
116 segments. However, we currently lack the necessary data and models to scale this
117 understanding to entire river networks that sometimes span several terrestrial biomes.

118

119 Here we review the state of river ecosystem metabolism research and synthesise current best
120 available estimates of river ecosystem metabolism. Our review focuses on rivers, rather than
121 on all inland waters (including lakes, for instance), because of their organisation into
122 networks tightly connected to the landscape as well as their unique ecosystem properties and
123 susceptibilities to global change. We apply a mass-balance approach to assess the
124 contribution of ecosystem metabolism to the global river C budget, including C fluxes from
125 land to rivers, the atmosphere, and the coastal ocean. We discuss how global change (e.g.,
126 climate and land-use changes, flow regulation) may affect river ecosystem metabolism and
127 related C fluxes, and we identify research directions to improve our mechanistic
128 understanding needed to support better predictions of global-change impacts on these
129 ecosystem processes. Finally, we highlight the necessity of a global River Observing System
130 (RIOS) for river networks to be able to reach this goal.

131

132

133 **River ecosystem metabolism**

134 The energetics of river ecosystems is based on autochthonous energy from aquatic primary
135 production and allochthonous energy from the terrestrial environment (Fig. 1a). The balance
136 of the metabolic fluxes, gross primary production (GPP) and ecosystem respiration (ER;
137 autotrophic and heterotrophic), is net ecosystem production ($NEP = GPP - ER$). Positive NEP
138 means GPP exceeds ER (that is, the ecosystem is autotrophic), which can occur when the

139 excess of fixed energy is exported downstream, transiently stored in the food web, or buried
140 in sediments. Negative NEP denotes that ER exceeds GPP (that is, the ecosystem is
141 heterotrophic). Network-scale ER in excess of GPP must be subsidized by terrestrial organic
142 C (OC) or OC produced in upstream freshwater ecosystems. The excess ER that characterizes
143 most river segments, sustains widespread supersaturation and emission of CO₂ and, to a
144 lesser extent, of CH₄ from river networks. Those OC subsidies that escape riverine
145 consumption may be buried in river, floodplain or reservoir sediments or transported to
146 downstream terminal lakes or coastal oceans. Ecosystem metabolism is also pivotal for other
147 ecological processes in rivers; its seasonal timing drives ecosystem phenology by linking
148 energy and elemental fluxes with the ecology of aquatic organisms²³.

149
150 ***Environmental drivers of ecosystem metabolism.*** The drivers of ecosystem metabolism are
151 relatively well understood, increasingly facilitated by remote sensing, for terrestrial²⁴,
152 marine²⁵, and lake²⁶ ecosystems, but less so for rivers. Light, discharge, land use and
153 nutrients were identified as drivers of GPP and ER by early studies comparing metabolism
154 measured over a few days among multiple rivers^{27–29}. Following initial studies at multi-
155 annual scales^{27,30}, improvements to dissolved oxygen sensors and updates in process-based
156 modelling^{9,31,32} now enable resolving river GPP, ER and NEP on a daily basis over multiple
157 years and sites. The metabolic regimes detected by these time series can be classified based
158 on their temporal patterns of recurrent GPP peaks in spring or summer, shoulder peaks in
159 spring and fall, or with no seasonal patterns at all^{9,33–35}. Annual regimes allow assessing
160 environmental drivers of river ecosystem metabolism across temporal scales (from days to
161 multiple years). For instance, while the potential annual GPP regime is set by a “maximum
162 envelope” shaped by solar energy as a primary environmental driver, various secondary
163 environmental drivers constrain the potential GPP to realized regimes within this envelope^{9,36}
164 (Fig. 1b). This framework is in line with a recent study across 222 US rivers that revealed
165 total annual light availability and hydrologic disturbance as the primary drivers of variation in
166 annual GPP and ER³⁷. The drivers themselves result from the modulation of climate (chiefly
167 mean annual precipitation and temperature) by catchment geomorphology and vegetation.
168
169 Growing evidence suggests common sets of environmental drivers underlying metabolic
170 regimes. However, untangling the network of causal relationships is difficult. Unlike

171 terrestrial ecosystems, annual variations in temperature and light are often uncorrelated in
172 rivers because light availability is attenuated by external and internal factors. For instance,
173 riparian vegetation in part controls light that reaches small rivers^{36,38,39}, so the phenology of
174 terrestrial (particularly riparian) vegetation imparts distinct seasonal and geographic patterns
175 on GPP and NEP. In temperate regions, windows of elevated light availability prior to leaf
176 out of deciduous trees can stimulate peak GPP during spring, transiently shifting metabolism
177 towards autotrophy (e.g., ref.³⁰). Additionally, high concentrations of dissolved OC and
178 turbidity attenuate light, thereby lowering river GPP^{36,40}. Turbidity is often linked to elevated
179 flow, which can also constrain metabolism from reaching its theoretical maximum in most
180 rivers^{37,35}. Finally, the metabolic response to the same driver can differ across stream order,
181 making predictions at the network scale difficult⁴¹.

182 The relationship between river metabolism and temperature also remains unclear. Both GPP
183 and ER are temperature sensitive, but the effect of warming on river metabolism is still
184 equivocal because it is more variable and less predictable than estimates based on metabolic
185 theory⁴². For example, studies along a thermal gradient⁴³ and across biomes⁴⁴ have revealed
186 similar activation energies for both GPP and ER. An experimental warming of an open-
187 canopy stream by 3.3 °C tripled GPP, a much higher increase than predicted by theory⁴⁵.
188 Variables such as light and flow can also covary with temperature, which can make the
189 isolation of a temperature effect difficult⁴¹. Thus, scaling from species-specific responses will
190 not provide accurate predictions of ecosystem-level responses to increased temperature, and
191 warming will have idiosyncratic, and as yet unpredictable effects on river metabolism.

192 While clearly nutrient pollution leads to the eutrophication of streams and rivers globally, the
193 direct relationship between nutrient concentrations and loadings and GPP is not as clear as in
194 lakes and reservoirs⁴⁶. The few existing studies show diverging evidence. A long-term
195 experimental phosphorus enrichment in Alaska's Kuparuk River, draining arctic tundra and
196 thus lacking tree cover, and dominated by benthic mosses, shifted metabolism from
197 heterotrophy to autotrophy and increased the growth of moss, thereby reducing reliance of
198 consumers on terrestrial C inputs⁴⁷. In contrast, nutrient enrichment in a heavily shaded
199 Appalachian stream had no effect on GPP but enhanced ER fueled by terrestrial C inputs⁴⁸.
200 Metabolic responses to changing nutrients may also be more gradual than short-term data
201 collection efforts can capture: an analysis of two decades of monitoring data revealed

202 reductions in both GPP and ER in the Oria River, Spain, after sewage abatement and
203 concomitant reductions of nutrient and OC inputs⁴⁹.

204

205 **Global river heterotrophy.** As budgets of river metabolism become more common^{32,37,50–52}),
206 we can better constrain global estimates of river GPP, ER and NEP. Based on best currently
207 available budget studies, we summarize the mean annual estimates of areal metabolic fluxes
208 for tropical (GPP: 153 g C m⁻² yr⁻¹, ER: -760 g C m⁻² yr⁻¹, NEP: -606 g C m⁻² yr⁻¹), temperate
209 (GPP: 331 g C m⁻² yr⁻¹, ER: -591 g C m⁻² yr⁻¹, NEP: -260 g C m⁻² yr⁻¹), and high-latitude
210 (GPP: 279 g C m⁻² yr⁻¹, ER: -827 g C m⁻² yr⁻¹, NEP: -438 g C m⁻² yr⁻¹) rivers (*Supplementary*
211 *Information; Table SI 1*). While these fluxes show apparent differences by latitude, we note
212 limitations in their comparability. Existing time series from tropical and high-latitude rivers
213 rarely encompass a full annual cycle, are still few in numbers, and are skewed towards
214 smaller rivers. Nevertheless, the NEP estimates underline the pronounced heterotrophy of
215 river ecosystems. Our mean global NEP estimate (~ 426 g C m⁻² yr⁻¹) suggests that rivers
216 figure among the most heterotrophic ecosystems on Earth⁵³. Their heterotrophy is supported
217 by OC exported from autotrophic terrestrial ecosystems (global average terrestrial NEP of 74
218 g C m⁻² yr⁻¹, based on ref.⁵⁴). Ultimately, many rivers terminate into estuaries, which are
219 overall less heterotrophic (global average NEP: -189 g C m⁻² yr⁻¹; ref.⁵⁵). The continental
220 shelves are also under the influence of riverine inputs; their global NEP remains poorly
221 constrained and ranges between -6 and 2 g C m⁻² yr⁻¹ (ref.⁵⁵). This pattern of NEP across
222 ecosystems reveals rivers as ‘bioreactors’ that rapidly metabolise terrestrial OC subsidies and
223 highlights their relevance for C cycling at the global scale.

224

225 **River network metabolism.** Measuring ecosystem metabolism at the scale of individual
226 rivers, ranging from tens of meters to several kilometres as determined by the distance of
227 oxygen turnover⁵⁶, does not reveal spatiotemporal patterns of metabolism that may emerge
228 from properties (e.g., dendritic structure) inherent to river networks. Furthermore, metabolic
229 regimes resolved over multiple years at the scale of entire river networks are required to
230 integrate regional and global river and terrestrial C cycling. Therefore, it is essential to
231 expand river C research from individual rivers to the network level.

232

233 Only a few recent studies have used modelling approaches to predict river metabolism at
234 network scales. Coupling optimal channel networks with empirical GPP time series, Koenig
235 and colleagues⁵⁷ revealed emergent productivity regimes of theoretical river networks. They
236 found larger rivers are important for network-scale productivity as catchment size increases,
237 but small rivers with relatively low GPP disproportionately influence network-scale
238 productivity because of their large collective surface area. Furthermore, spatial network
239 modelling revealed patterns of GPP and ER through the networks of the Deva and Cares
240 rivers in Spain, and how metabolism (particularly NEP) is shaped by the combined effects of
241 catchment and river properties, and human impacts⁵⁸. Segatto and colleagues⁵⁹ combined
242 GPP, ER and NEP regimes from several river segments with machine learning to predict
243 annual metabolic regimes throughout the Ybbs River network in Austria. Their approach
244 revealed that headwaters drive annual network heterotrophy, despite a distinct autotrophy
245 peak in spring. It also unveiled the river network as a metabolic meta-ecosystem⁶⁰ where
246 local NEP is supported by both upstream (autochthonous and allochthonous) and lateral
247 (allochthonous) OC. More such studies are required to gain mechanistic understanding of
248 network metabolism and to integrate it with terrestrial C budgets.

249

250 **Integrating large-scale carbon fluxes**

251 High global river heterotrophy and CO₂ emissions (Box 1) prompted us to integrate river
252 metabolism with C fluxes from land to rivers, and further to the coastal ocean (Fig. 2). Using
253 a mass-balance approach, we quantified relevant fluxes both at the global scale and
254 decomposed into latitudinal bands. We assess uncertainties following IPCC guidelines⁶¹ and
255 indicate lower and upper boundaries (LB and UB) from sensitivity analyses for the budget
256 closure (*Supplementary Information*). Where only UB is indicated, our estimate is
257 conservative and equal to LB. Where appropriate, we also report bootstrapped errors for
258 selected C fluxes (*Supplementary Information*). Our mass balance also includes global CH₄
259 emissions (besides CO₂) from rivers, as well as OC burial and CO₂ and CH₄ from reservoirs.

260 **Box 1: CO₂ and CH₄ emissions from the world's rivers**




261 Rivers are major sources of GHG to the atmosphere. The spatial and temporal heterogeneity
262 of river networks and the multidimensional controls on GHG production make it difficult to

263 properly estimate their GHG emissions. New bottom-up and modelling approaches are
 264 revising global and regional flux estimates at rapid pace.

265
 266 *Carbon dioxide.* Summing up CO₂ emissions from tropical, temperate and high-latitude
 267 rivers, we estimate the mean global river CO₂ emissions at 1.9 Pg C yr⁻¹ and 2.3 Pg C yr⁻¹
 268 according to Liu and colleagues⁶² and Raymond and colleagues², respectively (*Supplementary*
 269 *Information*). Slight deviations from the originally reported values derive from upscaling
 270 approaches. Latitudinal gradients underline the tropical dominance (> 70%) of the global CO₂
 271 emission. Low-order and high-slope rivers disproportionately contribute to the global river
 272 CO₂ emissions^{2,63}, likely because of high gas transfer velocities⁶⁴ and CO₂ supply by
 273 groundwater^{3,65}.

274
 275 *Methane.* The global CH₄ emissions from rivers are estimated at ~0.005 (mean) and 0.008
 276 (median) Pg C yr⁻¹, as the sum of the emissions from the three latitudes⁶⁶. Given the currently
 277 available data, CH₄ emissions from tropical and temperate streams and rivers seem
 278 comparable. CH₄ emissions from small but abundant high-altitude streams may become more
 279 important in certain regions with the thawing of permafrost⁶⁷.

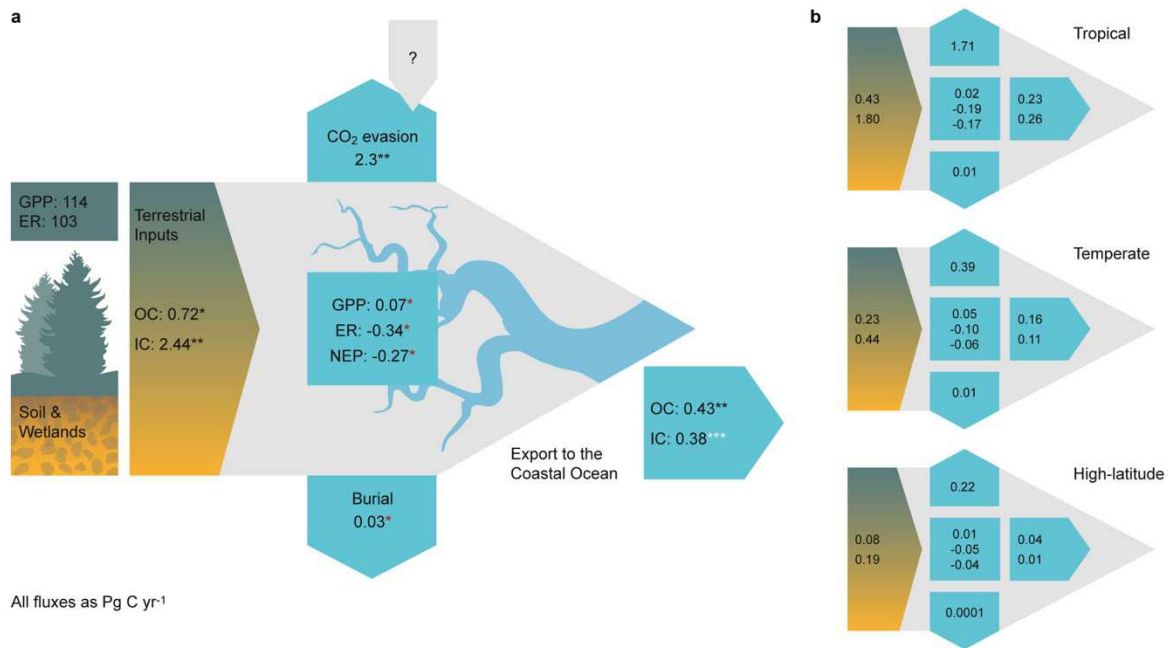
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	CO ₂	CH ₄
	Emissions (Pg C yr ⁻¹)	Emissions (Pg C yr ⁻¹)
 Tropical	Mean:1.68 ¹ Mean:1.10 ²	Mean:0.002 Median:0.001
 Temperate	Mean:0.36 ¹ Mean:0.57 ²	Mean:0.002 Median:0.005
 High-latitude	Mean:0.22 ¹ Mean:0.25 ²	Mean: 0.0008 Median: 0.002

281

282 ¹according to Raymond and colleagues²

283 ²according to Liu and colleagues⁶²



284

285 **Figure 2. Carbon fluxes from land through river networks to the atmosphere and the**
 286 **coastal ocean. (a)** Global fluxes of terrestrial inputs of organic (OC) and inorganic (IC) carbon
 287 from land to rivers, and export from rivers to the coastal ocean, river gross primary production
 288 (GPP), respiration (ER) and net ecosystem production (NEP), burial and CO₂ emission. The
 289 grey arrow denotes the possibility of CO₂ sequestration from the atmosphere during peak
 290 riverine GPP. **(b)** Decomposition of carbon fluxes into latitudinal bands (tropical: < 25°,
 291 331,364 km² temperate: 25°- 60°, 219,638 km²; high-latitude: > 60°, 75,421 km² — water
 292 surface area from ref. ⁶⁸). Included in the C mass balance are also river CH₄ emissions, CH₄
 293 and CO₂ emissions from reservoirs and C burial in reservoirs. However, owing to their very
 294 low values (Tables SI3, SI4, Box 1), these fluxes are not depicted as such. The number of stars
 295 associated with the global fluxes denotes the level of agreement (low, medium, and high) while
 296 the color of the stars denotes the robustness of the evidence (limited, medium, or robust as red,
 297 black and white, respectively) (*Supplementary Information*).

298

299 The terrestrial biosphere releases dissolved and particulate organic C (DOC and POC,
 300 respectively), as well as nutrients (N, P) and inorganic C (IC) to rivers⁶⁹. The similarity of the
 301 C:N ratios of river and soil organic matter has corroborated the relevance of terrestrial
 302 sources for C and nutrients in several northeastern US rivers systems⁷⁰. Our mass-balance
 303 approach estimated the global lateral OC flux from land to rivers at 0.72 Pg C yr⁻¹ (LB: 0.58
 304 Pg C yr⁻¹; UB: 1.23 Pg C yr⁻¹) and the IC flux at 2.44 Pg C yr⁻¹ (LB: 2.37 Pg C yr⁻¹; UB: 3.17
 305 Pg C yr⁻¹) (Fig. 2) (*Supplementary Information*). This total C flux of 3.2 Pg C yr⁻¹ (UB: 4.2
 306 Pg C yr⁻¹), admittedly poorly constrained, is close to earlier estimates of lateral C transfer

307 from land to rivers^{71,72}. Our mass balance is among the first to partition the total C flux to
308 river networks into organic and inorganic fractions, thereby highlighting the large size of the
309 IC flux.

310 The low OC:IC ratio (0.3; LB: 0.20, UB: 0.47) of the terrestrial-to-river C flux highlights the
311 importance of terrestrial CO₂ inputs, both from upland and wetland soils^{73,74}, as a dominant
312 C source, deriving not only from chemical weathering and heterotrophic soil respiration, but
313 also from autotrophic root respiration. For instance, root respiration contributes about as
314 much to CO₂ emissions from the Amazon River network as the CO₂ from soil and aquatic
315 heterotrophic respiration combined⁷⁴. Therefore, while OC inputs to rivers can be considered
316 as a fraction of terrestrial net primary production (NPP; GPP - autotrophic R), the biospheric
317 IC and OC inputs to rivers should rather be considered as a fraction of terrestrial GPP with
318 small additions from carbonate minerals. The total global lateral C transfer of 3.2 Pg C yr⁻¹ to
319 rivers is equivalent to roughly one quarter of the global terrestrial NEP of 11 Pg C yr⁻¹
320 according to ref.⁵⁴ and calculated as river NEP (i.e., GPP-ER). The amount of C currently
321 accumulating in the terrestrial biosphere represents another quarter of terrestrial NEP, the
322 remainder being attributable to land use change, harvested biomass, natural fires, and
323 emission of reduced forms of compounds (e.g., CH₄, volatile organic C)⁵⁴. While the global
324 estimates of terrestrial NEP, and its components NPP (GPP-autotrophic respiration) and
325 heterotrophic soil respiration, are associated with uncertainties which are larger than our
326 estimate of land-to-river C transfers (see ref. ⁵⁴), our comparison still highlights the
327 importance of river C cycling for C budgets of the continents.

328 As inferred from our global estimate of fluvial NEP (-0.27 Pg C yr⁻¹; LB: -0.13 Pg C yr⁻¹,
329 UB: -0.33 Pg C yr⁻¹), rivers transform roughly 37% (LB: 12%, UB: 42%) of the terrestrial
330 OC flux to respiratory CO₂. We tentatively attribute the low processing efficiency for OC in
331 rivers to the short residence times within most river networks and the relatively low
332 bioavailability of terrestrial OC^{75,76}. A further fraction of the terrestrial OC can also be
333 transiently buried (as POC) within river floodplains and reservoirs, which may promote its
334 degradation through increased residence times. However, constraining the magnitude of POC
335 burial within the global river networks is inherently difficult. For instance, global inventories
336 of reservoirs typically exclude small impoundments^{77,78}, despite their apparent contribution to
337 OC burial and GHG emissions⁷⁹. Although recent estimates of OC burial^{77,78} and CO₂

338 emissions from reservoirs (e.g.,^{2,80}) converge, these fluxes could actually be up to one order
339 of magnitude larger (Table SI 3, SI 4). We therefore use conservative and upperbound
340 estimates for emissions (0.037 Pg C yr⁻¹; UB: 0.3 Pg C yr⁻¹) and burial (0.027 Pg C yr⁻¹; UB:
341 0.18 Pg C yr⁻¹) for our C budget.

342 Our budget further suggests that river NEP is the source of approximately 12% (LB: 4%, UB:
343 14%) of the global river C emissions (2.3 Pg C yr⁻¹, including reservoir emissions; UB: 2.9
344 Pg C yr⁻¹). This estimate is lower than the contributions reported from US rivers (19 to
345 39%)³, the Amazon River and its floodplains (20%)⁸¹ and Mississippi River (22%)⁸². NEP
346 contributions to CO₂ evasion seem higher in small Arctic (> 80%)⁸³ and boreal (75%)⁸⁴ rivers
347 draining catchments with OC rich soils. This apparent “mismatch” between our global budget
348 approach and local field studies may be attributable to the high contributions of terrestrial
349 CO₂ to the emissions from small headwaters³, not included, for instance, in the study on the
350 Mississippi River⁸². The broad range of river NEP contributions to CO₂ emissions further
351 highlights current difficulties in closing the terrestrial-aquatic continuum C budget.

352 Despite systematic heterotrophy, there can be episodic CO₂ under-saturation in rivers during
353 periods of high autotrophic productivity (i.e., positive NEP) and its associated drawdown of
354 atmospheric CO₂. During such periods, riverine autotrophs may use bicarbonate in addition to
355 CO₂ to compensate for the low diffusivity and potential depletion of CO₂ in water⁸⁵ further
356 complicating carbon budgets. Thus, although it is intuitive to assume that autotrophs in rivers
357 primarily satisfy their C demand from terrestrial IC subsidies that contribute to the storage of
358 terrestrial IC within river networks, extended periods of atmospheric CO₂ drawdown may
359 alter the carbon budget presented here.

360 Our mass balance allowed us to assess the partitioning of the IC/OC flux from land into
361 global rivers and its evolution en route to the coastal ocean. River NEP and CO₂ evasion
362 profoundly alters the OC to IC ratio from 0.3 at the terrestrial-inland water interface to 1.1 at
363 the inland-coastal water interface (Fig. 2). At the point most rivers meet the coastal ocean,
364 bicarbonate is derived almost entirely from chemical weathering of soil minerals. Excluding
365 this weathering-derived contribution, our budget estimates that only about 26% (LB: 21%,
366 UB: 32%) of terrestrial C delivered to rivers makes it to the coastal ocean, which agrees with
367 a previous assessment⁸⁶. While river networks are remarkably proficient at retaining,

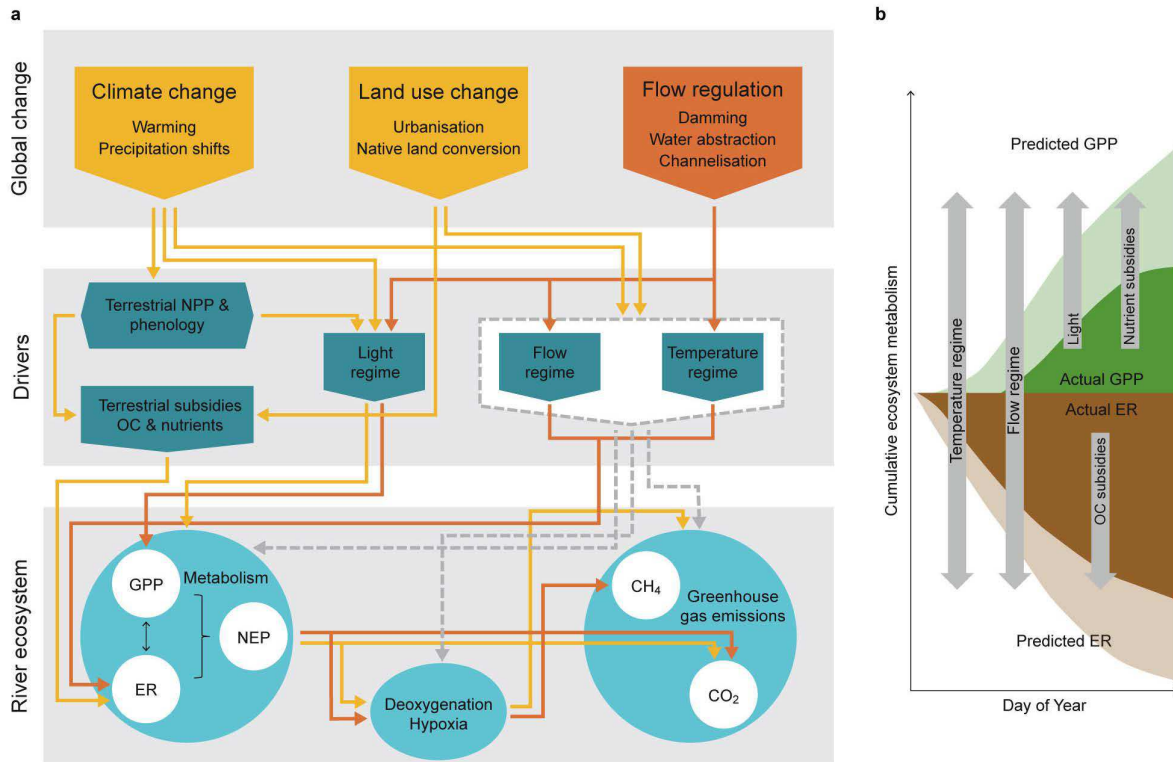
368 metabolising and emitting terrestrial C, the remnant OC at river mouths fuels coastal
369 heterotrophic metabolism and has important consequences for the CO₂ air-ocean flux. The
370 delivery of riverine C subsidies likely caused the ocean to be a net source of CO₂ under pre-
371 industrial conditions⁸⁷. This pre-industrial CO₂ outgassing fuelled by river OC has been
372 estimated at about 0.3 Pg C yr⁻¹ (refs.^{88,89}) to which an anthropogenically enhanced delivery
373 (0.1 Pg C yr⁻¹) may need to be added²². However, this export flux might still be
374 underestimated⁹⁰. This is because high flows disproportionately contribute to river C exports
375 but are systematically undersampled, and also because of direct C exports from small but
376 abundant mountainous rivers into coastal waters^{91,92}. For our C budget, we used the rather
377 conservative estimate of riverine OC export fluxes of 0.38 Pg C yr⁻¹ as compromise between
378 published estimates with a high degree of agreement, but also applied an UB (0.7 Pg C yr⁻¹)
379 as suggested by ref.⁵⁵.

380

381 **Global change impacts on river metabolism and greenhouse gas emissions**

382

383 Global change impacts on river ecosystem metabolism are complex (Fig. 3); even more so
384 are the related consequences for CO₂ and CH₄ production, transport, and emissions. As
385 discussed above, this complexity partially emanates from the different drivers of GPP and
386 ER, which act at different spatial (e.g., from catchment to channel processes) and temporal
387 (e.g., from storm events to seasonality) scales. Below we illustrate the complexity of global-
388 change impacts on river ecosystem metabolism and related CO₂ and CH₄ emissions based on
389 selected examples covering different spatial and temporal scales.



390

391 **Figure 3. Complexity of global-change impacts on river ecosystem metabolism and CO₂**
 392 **and CH₄ emissions. (a)** Trajectories showing how climate change, land use change and
 393 flow regulation potentially impact river ecosystem metabolism, deoxygenation, and both CO₂ and
 394 CH₄ emissions. Yellow trajectories refer to climate and land use changes, brown trajectories to
 395 flow regulation; dashed grey trajectories refer to flow (turbulence-induced gas exchange) and
 396 temperature (gas solubility) impacts. **(b)** Potential effects of global-change drivers on river
 397 ecosystem gross primary production (GPP) and respiration (ER). Shown are cumulative actual
 398 and predicted GPP and ER. The effects of changing flow and temperature regimes either
 399 increase or decrease both GPP and ER, while light and nutrients stimulate GPP, and OC
 400 stimulates ER.

401

402 **Changing terrestrial carbon subsidies.** A first example relates to the large-scale impacts of
 403 climate change on terrestrial subsidies to rivers (Fig. 3a,b). Atmospheric CO₂ fertilization,
 404 increased nitrogen deposition, or longer growth periods due to climate warming have
 405 augmented terrestrial NPP and changed its phenology (i.e., timing) in many parts of the
 406 world⁹³. Empirical evidence and model results suggest that these increases in terrestrial NPP
 407 not only enhance anthropogenic OC storage on land⁹⁴ but also amplify OC subsidies into
 408 inland waters in high-latitude and tropical regions^{74,95–97}. Recent evidence shows that these

409 augmented terrestrial OC subsidies are mostly recycled within river networks, sustaining
410 increased ER and CO₂ emissions⁷¹. Earth system models (ESM) further predict that the
411 delivery of terrestrial C and river CO₂ emissions will accelerate due to climate change during
412 the 21st century^{74,98,99}. In addition, increasing precipitation at high latitudes decreases
413 terrestrial net ecosystem exchange but increases C leaching from terrestrial ecosystems¹⁰⁰. In
414 contrast, an observed long-term decline of CO₂ supersaturation in rivers has been attributed to
415 reduced soil production and leaching of CO₂, reservoir building, land use change, and
416 recovery from acidification^{101–103}. Overall, trends in the magnitude of terrestrial C leaching
417 into temperate rivers remain uncertain.

418 Climate change also affects the timing and extent of water routing through catchments and
419 consequently the transport of terrestrial C into rivers. In fact, C fluxes from catchments to
420 rivers are often limited by hydrologic transport and therefore increase during high
421 precipitation^{69,75,104}. Recent work has demonstrated that indeed a greater percentage of
422 terrestrial GPP is routed to and evaded as CO₂ from river networks in wetter regions, thereby
423 emphasizing the importance of catchment hydrology for plumbing terrestrial and river C
424 fluxes at global scale⁶². Furthermore, increasing DOC concentrations in Swedish rivers over
425 the last decades were linked to elevated precipitation and higher runoff¹⁰⁵, and DIC fluxes are
426 also typically higher during wetter years¹⁰⁶. Therefore, it is intuitive to assume that climate-
427 induced alterations of catchment hydrology will increase leakage of terrestrial C in some
428 regions (wetter climate) but decrease it in others (drier climate).

429 Pulsed terrestrial OC subsidies can also influence river ecosystem metabolism at an annual
430 scale. For instance, low snowpack and early snowmelt during a mild winter shifted
431 metabolism toward increased heterotrophy in an alpine river network¹⁰⁷. Such a shift is
432 unusual and attributable to pulsed terrestrial OC deliveries, transiently fuelling ER and
433 reducing the magnitude of the spring window when these rivers are typically autotrophic¹⁰⁷.
434 As winters become milder and precipitation increasingly changes from snow to rain¹⁰⁸ in
435 alpine regions, such metabolic shifts may increase CO₂ emissions from alpine rivers.

436 A second example illustrates the effects of agricultural land conversion on river ecosystem
437 metabolism and GHG (Fig. 3a,b). Land-use change, including deforestation in the Congo
438 basin and conversion of peatlands into oil palm plantations in Southeast Asia, mobilises

439 ancient but bioreactive OM, which, upon arrival in rivers, is respired to CO₂ (refs.^{109–111}).
440 Agricultural soils themselves are a major source of OC and nutrients to the world's rivers²⁰.
441 These subsidies alter the magnitude and seasonality of GPP and ER of agricultural rivers^{112–}
442 ¹¹⁴. Besides increasing subsidies to rivers, agriculture can also cause riparian deforestation
443 and channel geomorphology alterations, which further impair river ecosystem
444 metabolism^{115,116}. While several studies have pointed to agricultural rivers as significant
445 sources of CO₂ and CH₄ (refs.^{117,118}), the apportioning of these sources (i.e., allochthonous
446 *versus* autochthonous) remains poorly studied to date. Disentangling the relationships
447 between agricultural river metabolism and GHG emissions is important given the large
448 contributions from agriculture to global GHG emissions¹¹⁹.

449 ***Changing river flow regimes.*** While the above examples relate to changes in catchment land-
450 use and hydrology, changing river flow regimes are also important (Fig. 3a,b). Because the
451 atmospheric holding capacity of water is highly sensitive to temperature, precipitation
452 extremes will become more intense and frequent, with impacts on the natural flow regimes of
453 rivers¹²⁰. Droughts will shape the flow regime in some regions, flash floods attributed to
454 storm runoff in others, and many areas will experience longer periods of drought between
455 more extreme flooding^{121,122}. Furthermore, river ice extent and duration are declining
456 globally, further transforming the natural flow, light, and gas-exchange regimes of numerous
457 rivers¹⁴.

458

459 Globally, a large fraction of rivers are non-perennial, and both the distribution and magnitude
460 of flow intermittency will change with climate and other anthropogenic alterations¹²³. These
461 changes will affect river metabolism, but the nature and magnitude of these changes remain
462 uncertain, as do the implications for regional and global C cycling (Fig. 3a,b). As the flow
463 recedes, particularly headwaters, accounting for the bulk of stream length in global river
464 networks, contract and disconnect¹²⁴. With ongoing drying, GPP collapses but ER proceeds,
465 which promotes heterotrophy of non-perennial rivers¹²⁵. These metabolic processes, along
466 with increasing water residence time, induced hypoxia and promoted CH₄ production during
467 an experimentally induced drought in a boreal river¹²⁶. A similar metabolic shift occurred
468 throughout a boreal river network during the 2018 heatwave in Europe¹²⁶. While such
469 droughts are rather uncommon in cold and humid high-latitude regions, non-perennial

470 rivers are a common feature of arid and semi-arid regions^{123,127}. The paucity of data on
471 ecosystem metabolism and related GHG emissions from non-perennial rivers contrast with
472 their worldwide prevalence^{123,127}.

473

474 Increasing flood frequency, associated with climate change, will also have important yet
475 poorly understood effects on river metabolism. A recent study covering 222 US rivers
476 showed that more variable flow regimes (i.e., higher ‘flashiness’) reduced both annual GPP
477 and ER, with an even stronger effect on the latter³⁷. High flood-related flows regularly
478 perturb benthic primary producers and can ultimately erode them, thereby reducing annual
479 GPP in shallower rivers. The pronounced effect of flow disturbance on annual ER was
480 attributed to short mean OC residence times, potentially decoupling river ER from the supply
481 rate of terrestrial OC³⁷. Such disturbances of ecosystem metabolism appear particularly
482 pronounced in urban rivers, which experience frequent ‘flashy’ flows during heavy rain
483 because of the imperviousness of their catchments^{128–130}. As suggested by Bernhardt and
484 colleagues³⁷, increasingly perturbed flow regimes may limit the accumulation and storage of
485 primary producer biomass and terrestrial OC, which would have implications for river food
486 webs.

487

488 The effects of shrinking ice cover on river flow regimes may be even more pronounced than
489 those of droughts and floods. However, it is currently difficult to predict how changes in ice
490 cover influence river ecosystem metabolism beyond the mere assumption that increased light
491 availability may increase annual GPP¹³¹.

492

493 River impoundment and associated water management can also affect river metabolism and
494 GHG emission. Dams retain sediments, OC and nutrients with profound impacts on the
495 biogeochemistry of rivers and the coastal ocean^{77,78,80,132}. Depending on their age, geography
496 and operation, reservoirs can emit large amounts of CO₂ and CH₄ to the atmosphere^{66,133,134}.
497 The influence of reservoirs on river ecosystem metabolism and GHG emissions does not stop
498 at the dam. Rather it can extend downriver. For instance, water clarity and hydropeaking can
499 affect GPP downriver of the Glen Canyon Dam (Colorado River)¹³⁵, while CO₂ and CH₄
500 leaking from a reservoir through the tailwaters can lead to a ‘carbopeaking’ downriver of
501 major dams (e.g., ref.¹³⁶).

502

503 Underlying the GHG production and emissions from reservoirs are the combined effects of
504 increased water residence time, temperature, nutrient and OC accumulation, and related
505 ecosystem metabolism. For instance, accumulated OC and elevated temperature foster ER
506 and CO₂ production in the oxygenated waters of reservoirs, while methanogenesis and CH₄
507 production dominate metabolism in the deeper anoxic waters and sediments (e.g., ref.¹³²).
508 Furthermore, reservoirs facilitate algal blooms, thereby transiently shifting the metabolism
509 towards autotrophy. Such a shift towards autotrophy in large and nutrient-rich rivers in Asia
510 has been attributed to damming¹³⁷ as has the decrease in CO₂ evasion (32%) from Chinese
511 rivers over the last three decades¹⁰³. These observations would benefit from better
512 mechanistic insights. Dam removal after decommissioning offers useful opportunities to gain
513 these insights.

514

515 ***River ecosystem deoxygenation and health.*** Many of the global-change impacts on river
516 ecosystem metabolism illustrated above can ultimately lead to eutrophication and further to
517 deoxygenation when ER outweighs oxygen resupply from GPP or atmospheric exchange. As
518 a consequence, river metabolism switches from an aerobic to an anaerobic state. Such a state
519 shift triggers alternative metabolic pathways, foremost denitrification and methanogenesis
520 with the production of the potent greenhouse gases nitrous oxide¹³⁸ and CH₄ (ref.¹³⁹),
521 respectively. Deoxygenation is increasingly well documented in tidal zones, coastal waters¹⁴⁰
522 and lakes¹⁴¹. While hypoxia has been well known from the hyporheic zone in rivers (e.g., ref.
523 ¹⁴²), it is only recently that we are becoming aware of its spatiotemporal extent at the
524 ecosystem scale in rivers^{128,143}. In rivers, large-scale deoxygenation can imperil biodiversity,
525 impose barriers to fish migration, kill fish, and compromise water quality, thereby
526 jeopardizing ecosystem health and services.

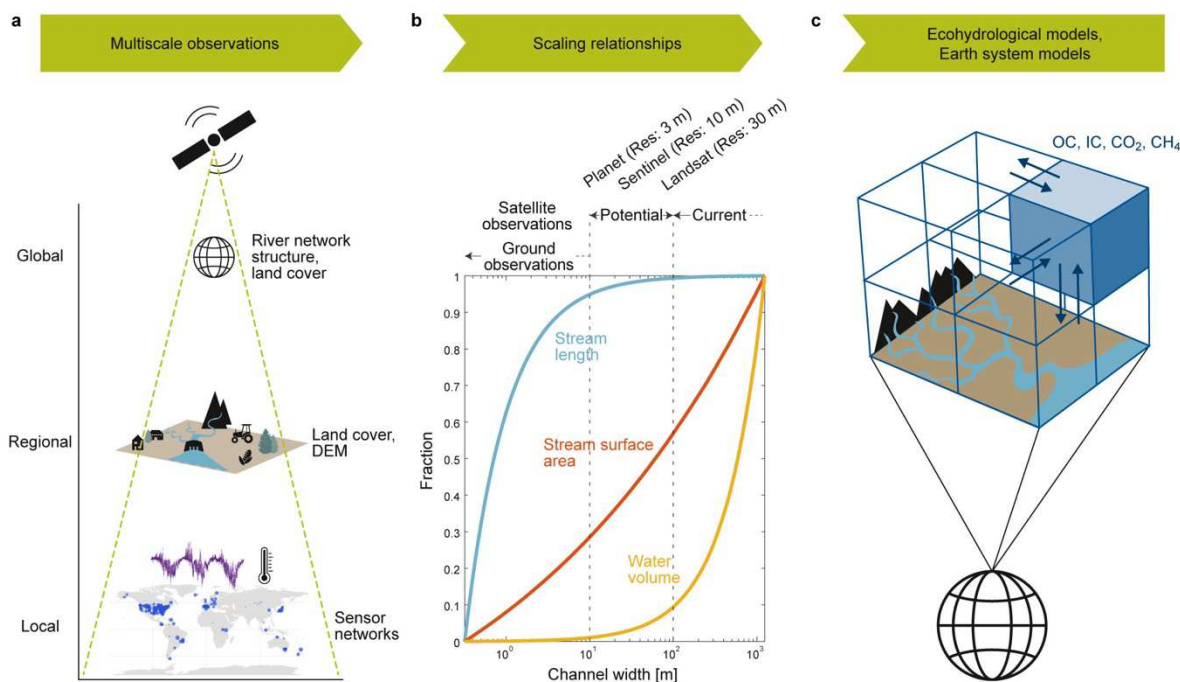
527

528 **Priorities for river network research**

529 The awareness of rivers as important components of the global C cycle offers new and
530 exciting research opportunities. The recognition of global change impacts on river
531 ecosystems also emphasizes the need to better understand and predict the role of rivers for
532 large-scale C fluxes from land to the atmosphere and the oceans. Both opportunities and
533 needs come with challenges. Responding to these challenges, we propose a global River

534 Observing System (RIOS) (Fig. 4), similar to those existing for terrestrial (e.g., ICOS¹⁴⁴),
 535 lake (e.g., GLEON¹⁴⁵) and marine (e.g., ARGO floats¹⁴⁶) domains.

536



537

538 **Figure 4. A global River Observation System (RIOS).** (a) Multiscale observations integrate
 539 data from distributed sensor networks, field surveys and satellite imagery. Sensor networks
 540 provide time series of ecosystem metabolism, GHGs and environmental drivers, taking into
 541 account the nested organisation of river networks and their spatiotemporal heterogeneity.
 542 World map of sensor-based estimates (from days to multiple years) of daily river ecosystem
 543 metabolism (updated from ref.¹⁴⁷) highlights the bias towards temperate rivers, with poor
 544 coverage of tropical, high-latitude and high-altitude rivers. Field surveys serve sensor
 545 calibration and the determination of gas exchange velocities. Remote sensing maps regional
 546 and global-scale river network properties, as well as land cover and anthropogenic
 547 disturbances. (b) Scaling laws help extrapolate quantities from individual river segments to
 548 entire river networks and fill gaps left by satellite imagery. Changes of channel length, flow
 549 depth, velocity and width through river networks can be predicted using scaling laws. Vertical
 550 dashed lines denote the fraction (y-axis) of the total stream length, surface area and water
 551 volume at network scale in channels narrower than a certain width (x-axis) (see *Supplementary*
 552 *Information*). (c) Mechanistic and statistical models are required to integrate the multiscale
 553 observational data of river ecosystem processes and C fluxes, and link these with catchment-
 554 level processes and C fluxes. Such modeling frameworks will integrate river network C
 555 biogeochemistry with Earth system models.

556

557 The first key challenge is to better constrain the uncertainty associated with river network

558 metabolism and how it influences our conceptualization of various C fluxes at both local and

559 large spatial scales (Fig. 2). To achieve this major endeavour, a key research priority is to
560 dramatically increase the number of multiannual time series of ecosystem metabolism, GHG
561 emissions and related metadata, covering a broad spectrum of river ecosystems. Here the
562 focus should be to facilitate measurements at the network scale that helps fill geographic (i.e.,
563 tropics, high-latitude and high-altitude regions) and knowledge (e.g., network responses to
564 flow extremes and changing climate) gaps. Filling these gaps is greatly facilitated by the
565 recent improvements in O₂ and other sensors and statistical approaches^{31,32}, however a further
566 priority is the development of next-generation inexpensive GHG sensors and further support
567 and research on creating networks of “smart” sensors. This effort must be accompanied by
568 the proper training of staff to maintain sensors. Furthermore, water quality data from
569 governmental agencies should be better leveraged to complement time series from
570 sensors^{32,148}. Increasing the quantity and quality of river metabolism and GHG time series
571 requires coordinated approaches steered by working groups and facilitated by the use of
572 standardized protocols. Recent advances in information and communications technology, as
573 well as in the governance of complex sensor networks, including ensuring data availability,
574 will facilitate the implementation of this effort^{149,150}. Given the scale of the endeavour, the
575 research community will need to secure large-scale, collaborative and transnational funding
576 to also better include the Global South.

577

578 The second key challenge relates to the upscaling of measured C fluxes from individual river
579 segments to river networks. This requires the integration of multi-scale ground (i.e., sensor
580 networks) and satellite observations with scaling laws, and further with catchment-scale
581 mechanistic models. Today, satellites offer opportunities to quantify river network
582 topology^{151,152}, surface⁶⁸ and inundation area¹⁷, water storage¹⁸, discharge^{153,154}, suspended
583 sediments¹⁵⁵, and ice cover¹⁴. Advances in remote sensing are promising and shall soon
584 provide data that are also relevant to ecosystem processes and C biogeochemistry¹⁵⁶ (Table SI
585 6). However, satellite imagery still leaves substantial data gaps. Global satellite analysis of
586 river surface area currently excludes narrow rivers (< 90 m wide), thereby excluding the
587 majority of the world’s rivers^{68,157} (Fig. 4). Furthermore, riparian vegetation still poses an
588 unresolved problem in detecting and characterising these narrow rivers. Therefore, a key
589 research priority would be to unify new remote sensing methods related to riparian

590 vegetation, ice cover, and suspended sediment concentration to quantify channel width and
591 light availability (a main driver of GPP) in the world's smallest and largest rivers .
592

593 Simple scaling laws can be used to predict how channel length and flow geometry (i.e., water
594 depth, velocity and width) change through river networks (Fig. 4) (*Supplementary*
595 *Information*). Owing the to universal features of river networks¹⁵⁸, they are also used to
596 integrate river GPP⁵⁷, DOC transport and uptake^{75,159}, as well as GHG emissions (e.g., N₂O,
597 ref.^{160,161}) over entire networks and probe constraints on these processes. However, the
598 applicability of scaling laws for river ecosystem science has limitations. Scaling laws often
599 only resolve steady state conditions, thus not accounting for the dynamic nature of river
600 networks (e.g., expansion and contraction). New mapping^{68,123,151,152}, modelling¹⁶² and
601 conceptual frameworks¹⁶³ will facilitate predictions of the spatiotemporal dynamics of river
602 networks, which seems particularly important for headwaters that are often non-perennial¹⁶⁴.
603 Furthermore, scaling relationships require validation across the entire spectrum of river sizes,
604 particularly the smallest perennial rivers within networks that do not become infinitely
605 small¹⁶⁵. Therefore, a priority for the research community is the development of integrated
606 global field campaigns to resolve problems with scaling laws and unify the scales of ground
607 and satellite observations in small and large rivers. This entails recruiting scientists and
608 volunteers to make relatively simple measurements (e.g., stream width) using standardized
609 protocols across a broad range of rivers.
610

611 Finally, our ability to understand, and thus predict, large-scale river C dynamics and impacts
612 would benefit from improved iterative interactions between observations and simulations.
613 However, current biogeochemical modelling frameworks often still fail to properly represent
614 river ecosystem processes, particularly metabolism, and the fate of the various C forms at
615 relevant spatial and temporal scales. Furthermore, most modeling frameworks fall short of
616 integrating C cycling with nutrient cycling and deoxygenation, which appears critical though
617 given the global change impacts on these latter processes. Therefore, opportunities to adapt
618 and improve modeling frameworks (e.g., IMAGE-DGNM⁷², Tethys-Chloris¹⁶⁶) are
619 numerous. Given the dynamic nature of river networks, also these latest modeling
620 frameworks (e.g., ref. ⁷²) would need to resolve river ecosystem processes at daily scales
621 — still a computational challenge. A key research priority therefore is to integrate the global

622 rivers into ESMs used to project climate change in response to anthropogenic CO₂ emissions,
623 still ignoring the fraction of the terrestrial C sink leaking to river networks. In fact, the
624 exclusion of this leakage, despite its large uncertainty, biases estimates of the terrestrial net C
625 uptake (too low) and biospheric C stock increase (too high)⁶⁴.

626

627 Our call for a global RIOS is critical. By addressing the above key challenges, the global
628 RIOS will promote ambitious research and finally allow the proper accounting of regional
629 and global C fluxes at the interface between land, river, atmosphere, and the coastal ocean. It
630 will propel mechanistic understanding of these fluxes and underlying processes, help
631 disentangling the complexity of global-change impacts on river C biogeochemistry and
632 predict their future evolution. Ultimately, a global RIOS will also serve as a scaffold upon
633 which to build understanding of catchment-scale hydrology, geomorphology and ecology.

634

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644

645

646 **Contributions**

647 T.J.B conceptualized the review with inputs from all co-authors, R.L. and P.Re. provided the
648 carbon budget, T.M and J.A.R. provided the GHG data, R.O.H., E.S.B. and L.G.G. provided
649 ecosystem metabolism data, E.B., E.S.B. E.R.H, and R.O.H provided material for the figures,
650 J.A.R. designed the figures, T.J.B. wrote a first draft of the manuscript, which was revised
651 and edited by all co-authors.

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