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**Article:**

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

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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 $CO_2$ and $CH_4$ 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

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81    Panel on Climate Change (IPCC)[4] and the Global Carbon Project[5] 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 organisms[8] (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    biodiversity[10], so it directly affects ecosystem health[11].

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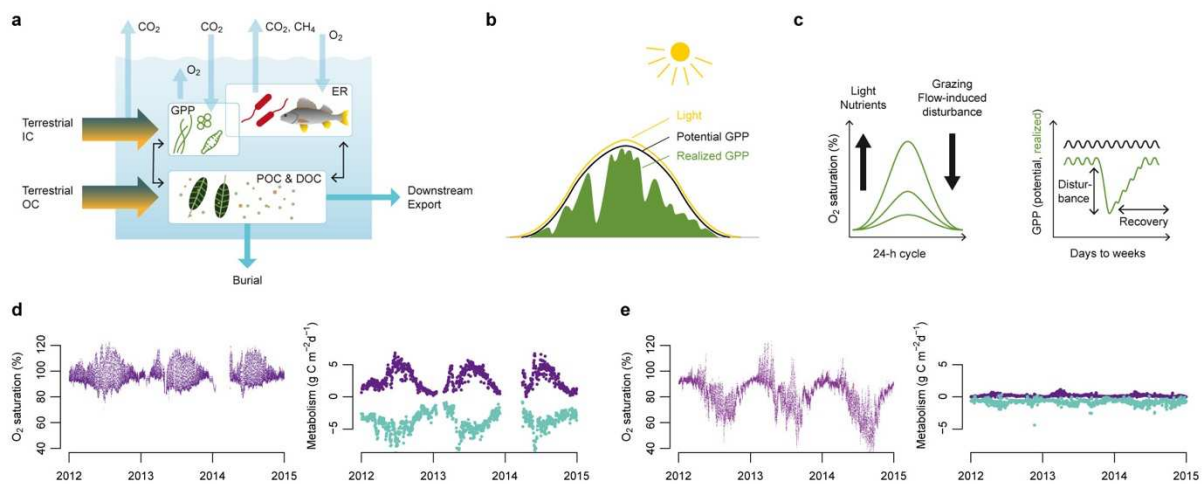


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95    **Figure 1. River ecosystem metabolism. (a)** River ecosystem metabolism is the sum of the
96    metabolism of all producers and consumers. Ecosystem gross primary production (GPP) and
97    ecosystem respiration (ER) meld terrestrial subsidies 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 icing[14] of rivers, while damming and water abstraction further disrupt river

110    networks[15,16]. Collectively, these disturbances have altered the global surface area of rivers[17],

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 ecosystems[22]. 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 $CO_2$ and, to a

144   lesser extent, of $CH_4$ 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 organisms[23].

149

150   ***Environmental drivers of ecosystem metabolism***. The drivers of ecosystem metabolism are

151   relatively well understood, increasingly facilitated by remote sensing, for terrestrial[24],

152   marine[25], and lake[26] 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 ER[37]. 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

5

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 difficult[41].

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   theory[42]. For example, studies along a thermal gradient[43] and across biomes[44] 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 theory[45].
188   Variables such as light and flow can also covary with temperature, which can make the
189   isolation of a temperature effect difficult[41]. 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 reservoirs[46]. 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 inputs[47]. In contrast, nutrient enrichment in a heavily shaded
199   Appalachian stream had no effect on GPP but enhanced ER fueled by terrestrial C inputs[48].
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 inputs[49].

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-latitudinal

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 Earth[53]. 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 turnover[56], 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 colleagues[57] 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 impacts[58]. Segatto and colleagues[59] 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-ecosystem[60] 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 $CO_2$ 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 guidelines[61] 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 $CH_4$

259  emissions (besides $CO_2$) from rivers, as well as OC burial and $CO_2$ and $CH_4$ from reservoirs.

260  **Box 1: $CO_2$ and $CH_4$ 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

8

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

*Carbon dioxide.* Summing up $CO_2$ emissions from tropical, temperate and high-latitude rivers, we estimate the mean global river $CO_2$ emissions at 1.9 Pg C $yr^{-1}$ and 2.3 Pg C $yr^{-1}$ according to Liu and colleagues[62] and Raymond and colleagues[2], respectively (*Supplementary Information*). Slight deviations from the originally reported values derive from upscaling approaches. Latitudinal gradients underline the tropical dominance (> 70%) of the global $CO_2$ emission. Low-order and high-slope rivers disproportionately contribute to the global river $CO_2$ emissions[2,63], likely because of high gas transfer velocities[64] and $CO_2$ supply by groundwater[3,65].

*Methane.* The global $CH_4$ emissions from rivers are estimated at ~0.005 (mean) and 0.008 (median) Pg C $yr^{-1}$, as the sum of the emissions from the three latitudes[66]. Given the currently available data, $CH_4$ emissions from tropical and temperate streams and rivers seem comparable. $CH_4$ emissions from small but abundant high-altitude streams may become more important in certain regions with the thawing of permafrost[67].

|  | $CO_2$ Emissions (Pg C $yr^{-1}$) | $CH_4$ 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 |

[1]according to Raymond and colleagues[2]
[2]according to Liu and colleagues[62]
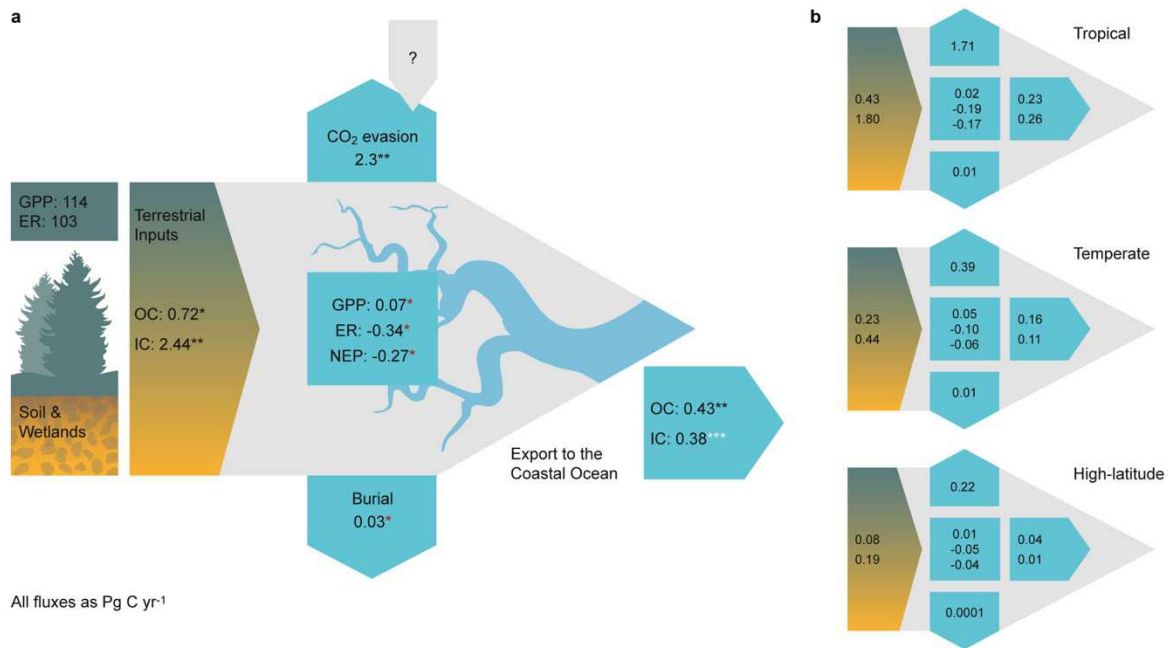
**Figure 2. Carbon fluxes from land through river networks to the atmosphere and the coastal ocean. (a)** Global fluxes of terrestrial inputs of organic (OC) and inorganic (IC) carbon from land to rivers, and export from rivers to the coastal ocean, river gross primary production (GPP), respiration (ER) and net ecosystem production (NEP), burial and $CO_2$ emission. The grey arrow denotes the possibility of $CO_2$ sequestration from the atmosphere during peak riverine GPP. **(b)** Decomposition of carbon fluxes into latitudinal bands (tropical: $< 25°$, 331,364 km$^2$ temperate: $25°- 60°$, 219,638 km$^2$; high-latitudinal: $> 60°$, 75,421 km$^2$ — water surface area from ref. [68]). Included in the C mass balance are also river $CH_4$ emissions, $CH_4$ and $CO_2$ emissions from reservoirs and C burial in reservoirs. However, owing to their very low values (Tables SI3, SI4, Box 1), these fluxes are not depicted as such. The number of stars associated with the global fluxes denotes the level of agreement (low, medium, and high) while the color of the stars denotes the robustness of the evidence (limited, medium, or robust as red, black and white, respectively) (*Supplementary Information*).

The terrestrial biosphere releases dissolved and particulate organic C (DOC and POC, respectively), as well as nutrients (N, P) and inorganic C (IC) to rivers[69]. The similarity of the C:N ratios of river and soil organic matter has corroborated the relevance of terrestrial sources for C and nutrients in several northeastern US rivers systems[70]. Our mass-balance approach estimated the global lateral OC flux from land to rivers at 0.72 Pg C yr$^{-1}$ (LB: 0.58 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 Pg C yr$^{-1}$) (Fig. 2) (*Supplementary Information*). This total C flux of 3.2 Pg C yr$^{-1}$ (UB: 4.2 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 $CO_2$ 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 $CO_2$ emissions from the Amazon River network as the $CO_2$ from soil and aquatic

315      heterotrophic respiration combined[74]. 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., $CH_4$, 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 $CO_2$. 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 emissions[79]. Although recent estimates of OC burial[77,78] and $CO_2$

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 $CO_2$ evasion seem higher in small Artic (> 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 $CO_2$ to the emissions from small headwaters[3], not included, for instance, in the study on the

350 Mississippi River[82]. The broad range of river NEP contributions to $CO_2$ emissions further

351 highlights current difficulties in closing the terrestrial-aquatic continuum C budget.

352 Despite systematic heterotrophy, there can be episodic $CO_2$ under-saturation in rivers during

353 periods of high autotrophic productivity (i.e., positive NEP) and its associated drawdown of

354 atmospheric $CO_2$. During such periods, riverine autotrophs may use bicarbonate in addition to

355 $CO_2$ to compensate for the low diffusivity and potential depletion of $CO_2$ in water[85] 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 $CO_2$ 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 $CO_2$ 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 assessment[86]. 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 $CO_2$ air-ocean flux. The

370    delivery of riverine C subsidies likely caused the ocean to be a net source of $CO_2$ under pre-

371    industrial conditions[87]. This pre-industrial $CO_2$ 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 added[22]. However, this export flux might still be

374    underestimated[90]. 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 $CO_2$ and $CH_4$ 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 $CO_2$ and $CH_4$ emissions based on

389    selected examples covering different spatial and temporal scales.
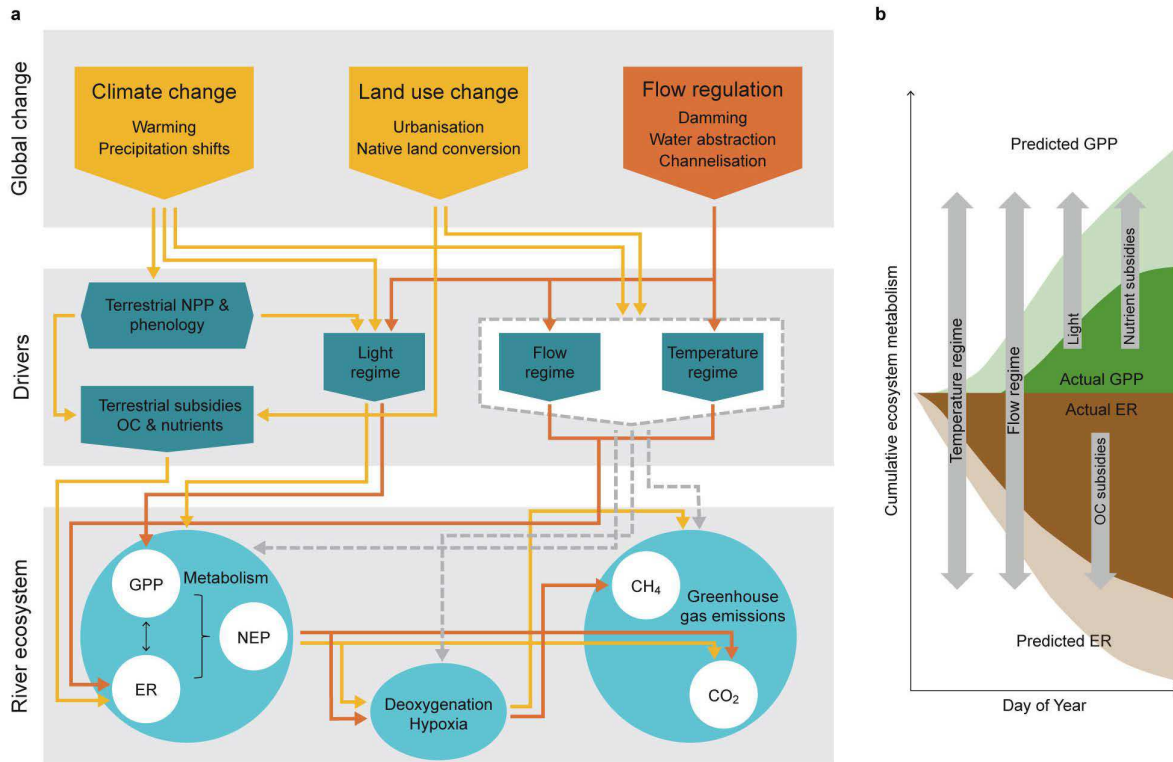
**Figure 3. Complexity of global-change impacts on river ecosystem metabolism and $CO_2$ and $CH_4$ emissions. (a)** Trajectories showing how climate change, land use change and flow regulation potentially impact river ecosystem metabolism, deoxygenation, and both $CO_2$ and $CH_4$ emissions. Yellow trajectories refer to climate and land use changes, brown trajectories to flow regulation; dashed grey trajectories refer to flow (turbulence-induced gas exchange) and temperature (gas solubility) impacts. **(b)** Potential effects of global-change drivers on river ecosystem gross primary production (GPP) and respiration (ER). Shown are cumulative actual and predicted GPP and ER. The effects of changing flow and temperature regimes either increase or decrease both GPP and ER, while light and nutrients stimulate GPP, and OC stimulates ER.

*Changing terrestrial carbon subsidies.* A first example relates to the large-scale impacts of climate change on terrestrial subsidies to rivers (Fig. 3a,b). Atmospheric $CO_2$ fertilization, increased nitrogen deposition, or longer growth periods due to climate warming have augmented terrestrial NPP and changed its phenology (i.e., timing) in many parts of the world[93]. Empirical evidence and model results suggest that these increases in terrestrial NPP not only enhance anthropogenic OC storage on land[94] but also amplify OC subsidies into inland waters in high-latitude and tropical regions[74,95–97]. Recent evidence shows that these

14

409 augmented terrestrial OC subsidies are mostly recycled within river networks, sustaining

410 increased ER and $CO_2$ emissions[71]. Earth system models (ESM) further predict that the

411 delivery of terrestrial C and river $CO_2$ emissions will accelerate due to climate change during

412 the 21$^{st}$ century[74,98,99]. In addition, increasing precipitation at high latitudes decreases

413 terrestrial net ecosystem exchange but increases C leaching from terrestrial ecosystems[100]. In

414 contrast, an observed long-term decline of $CO_2$ supersaturation in rivers has been attributed to

415 reduced soil production and leaching of $CO_2$, 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 $CO_2$ from river networks in wetter regions, thereby

423 emphasizing the importance of catchment hydrology for plumbing terrestrial and river C

424 fluxes at global scale[62]. Furthermore, increasing DOC concentrations in Swedish rivers over

425 the last decades were linked to elevated precipitation and higher runoff[105], and DIC fluxes are

426 also typically higher during wetter years[106]. 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 network[107]. 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 autotrophic[107].

434 As winters become milder and precipitation increasingly changes from snow to rain[108] in

435 alpine regions, such metabolic shifts may increase $CO_2$ 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 $CO_2$ (refs.[109–111]).

440  Agricultural soils themselves are a major source of OC and nutrients to the world's rivers[20].

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 $CO_2$ and $CH_4$ (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 emissions[119].

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  rivers[120]. 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  rivers[14].

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 alterations[123]. 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 disconnect[124]. With ongoing drying, GPP collapses but ER proceeds,

465  which promotes heterotrophy of non-perennial rivers[125]. These metabolic processes, along

466  with increasing water residence time, induced hypoxia and promoted $CH_4$ production during

467  an experimentally induced drought in a boreal river[126]. A similar metabolic shift occurred

468  throughout a boreal river network during the 2018 heatwave in Europe[126]. While such

469  droughts are rather uncommon in cold and humid high-latitudinal regions, non-perennial

16

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 latter[37]. 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 OC[37]. 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    colleagues[37], 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 GPP[131].

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 $CO_2$ and $CH_4$ 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 $CO_2$ and $CH_4$

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 $CO_2$ production in the oxygenated waters of reservoirs, while methanogenesis and $CH_4$

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 damming[137] as has the decrease in $CO_2$ evasion (32%) from Chinese

511    rivers over the last three decades[103]. 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 oxide[138] and $CH_4$ (ref.[139]),

521    respectively. Deoxygenation is increasingly well documented in tidal zones, coastal waters[140]

522    and lakes[141]. 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 the these challenges, we propose a global River

534 Observing System (RIOS) (Fig. 4), similar to those existing for terrestrial (e.g., ICOS[144]),

535 lake (e.g., GLEON[145]) and marine (e.g., ARGO floats[146]) domains.

536
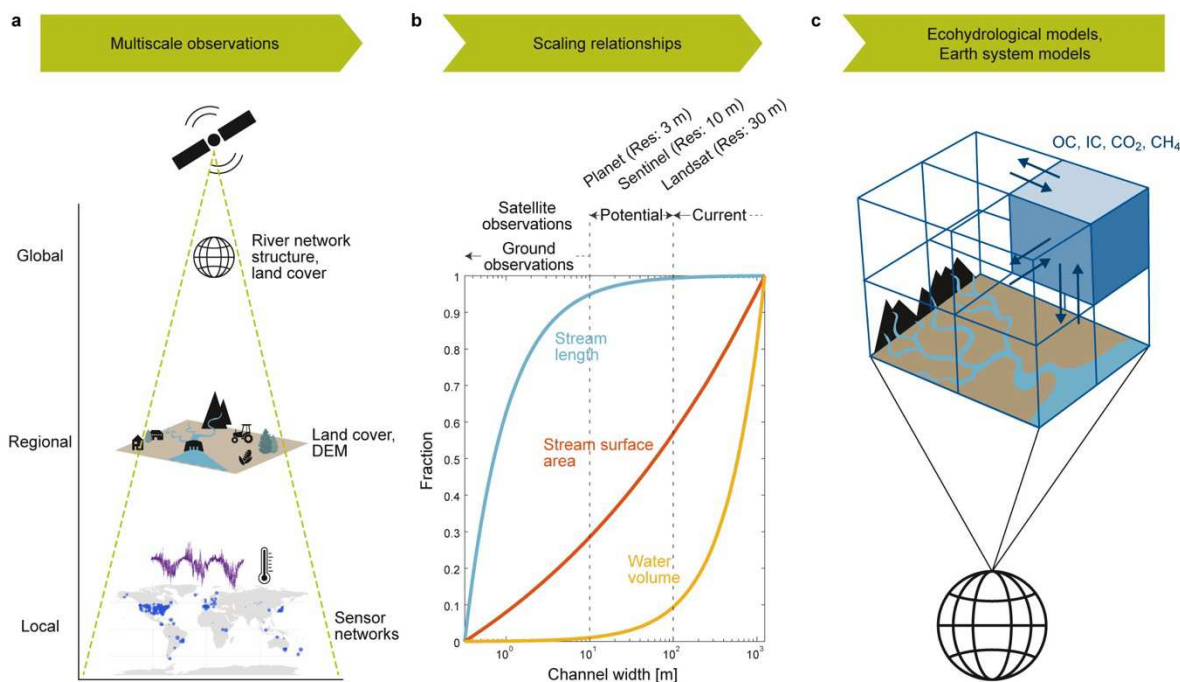
537



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-latitudinal and high-altitudinal 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 $O_2$ 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], surface[68] and inundation area[17], water storage[18], discharge[153,154], suspended

583    sediments[155], and ice cover[14]. Advances in remote sensing are promising and shall soon

584    provide data that are also relevant to ecosystem processes and C biogeochemistry[156] (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 networks[158], they are also used to

596    integrate river GPP[57], DOC transport and uptake[75,159], as well as GHG emissions (e.g., $N_2O$,

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], modelling[162] and

601    conceptual frameworks[163] will facilitate predictions of the spatiotemporal dynamics of river

602    networks, which seems particularly important for headwaters that are often non-perennial[164].

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    small[165]. 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-DGNM[72], Tethys-Chloris[166]) 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 $CO_2$ 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

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.

652

653
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655

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