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Article:

Battin, TJ, Lauerwald, R, Bernhardt, ES et al. (2023) River ecosystem metabolism and carbon biogeochemistry in a changing world. Nature, 613 (7944). pp. 449-459. ISSN: 0028-0836

https://doi.org/10.1038/s41586-022-05500-8

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River ecosystem metabolism and carbon biogeochemistry in a changing world

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

Rivers (here understood as all flowing waters from the smallest headwater streams to large rivers) are organized into fractal networks draining the continents and linking terrestrial and marine ecosystems through lateral transfers of water, energy, and matter. Having long been considered ‘pipes’ conservatively transferring carbon (C) from land to the ocean, today we understand rivers are ‘biogeochemical reactors’ that metabolise organic C (OC) with net emission of CO_2 and CH_4 to the atmosphere, and also OC burial in aquatic sediments, floodplains, and deltas (e.g., refs.[1–3]). This notion was adopted by the Intergovernmental

Panel on Climate Change (IPCC)[4] and the Global Carbon Project[5] in their global C budget assessments. Our current understanding of the role of rivers in the global C cycle remains limited to simple budget analyses (e.g. refs.[6,7]), where rivers are still often treated collectively as a black box without quantifiable internal processes. This approach does not allow for predicting how global change will alter the timing and spatial distribution of riverine C sequestration and greenhouse gas (GHG) emissions. The notion of rivers as 'biogeochemical reactors' implies their nature as ecosystems with energy flows related to metabolism, defined as the fixation and dissipation of energy by all organisms[8] (Fig. 1a). To date, a global scale assessment of river ecosystem metabolism has not yet been attempted, which is a critical gap in our understanding of the role of rivers in global C biogeochemistry. River ecosystem metabolism is the main control of C and nutrient cycling[8,9], food web energetics and biodiversity[10], so it directly affects ecosystem health[11].

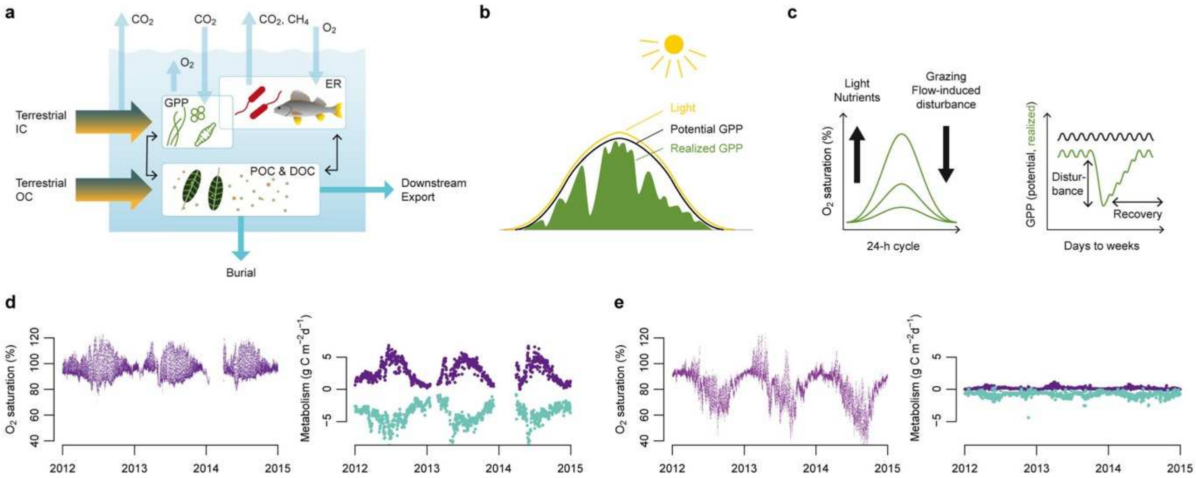


Figure 1. River ecosystem metabolism. (a) River ecosystem metabolism is the sum of the metabolism of all producers and consumers. Ecosystem gross primary production (GPP) and ecosystem respiration (ER) meld terrestrial subsidies of organic (OC) and inorganic (IC) carbon with gas fluxes and the oxygen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

Global change has altered the global C cycle and its feedback to Earth's climate. River networks are not exempt from global change. Climate change perturbs the natural flow[12,13], temperature and icing[14] of rivers, while damming and water abstraction further disrupt river networks[15,16]. Collectively, these disturbances have altered the global surface area of rivers[17], and freshwater distribution and availability[18,19]. Concomitantly, land use and management changes promote eutrophication through increased delivery of dissolved and particulate nutrients and C to rivers[20,21]. Global change has also perturbed global C fluxes between terrestrial and river ecosystems[22]. These impacts on river ecosystem metabolism and ensuing consequences for large-scale C biogeochemistry are increasingly well understood for river segments. However, we currently lack the necessary data and models to scale this understanding to entire river networks that sometimes span several terrestrial biomes.

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

River ecosystem metabolism

The energetics of river ecosystems is based on autochthonous energy from aquatic primary production and allochthonous energy from the terrestrial environment (Fig. 1a). The balance of the metabolic fluxes, gross primary production (GPP) and ecosystem respiration (ER; autotrophic and heterotrophic), is net ecosystem production (NEP = GPP - ER). Positive NEP means GPP exceeds ER (that is, the ecosystem is autotrophic), which can occur when the excess of fixed energy is exported downstream, transiently stored in the food web, or buried in sediments. Negative NEP denotes that ER exceeds GPP (that is, the ecosystem is heterotrophic). Network-scale ER in excess of GPP must be subsidized by terrestrial organic C (OC) or OC produced in upstream freshwater ecosystems. The excess ER that characterizes most river segments, sustains widespread supersaturation and emission of CO_2 and, to a lesser extent, of CH_4 from river networks. Those OC subsidies that escape riverine consumption may be buried in river, floodplain or reservoir sediments or transported to downstream terminal lakes or coastal oceans. Ecosystem metabolism is also pivotal for other ecological processes in rivers; its seasonal timing drives ecosystem phenology by linking energy and elemental fluxes with the ecology of aquatic organisms[23].

Environmental drivers of ecosystem metabolism. The drivers of ecosystem metabolism are relatively well understood, increasingly facilitated by remote sensing, for terrestrial[24], marine[25], and lake[26] ecosystems, but less so for rivers. Light, discharge, land use and nutrients were identified as drivers of GPP and ER by early studies comparing metabolism measured over a few days among multiple rivers[27–29]. Following initial studies at multi-annual scales[27,30], improvements to dissolved oxygen sensors and updates in process-based modelling[9,31,32] now enable resolving river GPP, ER and NEP on a daily basis over multiple years and sites. The metabolic regimes detected by these time series can be classified based on their temporal patterns of recurrent GPP peaks in spring or summer, shoulder peaks in spring and fall, or with no seasonal patterns at all[9,33–35]. Annual regimes allow assessing environmental drivers of river ecosystem metabolism across temporal scales (from days to multiple years). For instance, while the potential annual GPP regime is set by a “maximum envelope” shaped by solar energy as a primary environmental driver, various secondary environmental drivers constrain the potential GPP to realized regimes within this envelope[9,36] (Fig. 1b). This framework is in line with a recent study across 222 US rivers that revealed total annual light availability and hydrologic disturbance as the primary drivers of variation in annual GPP and ER[37]. The drivers themselves result from the modulation of climate (chiefly mean annual precipitation and temperature) by catchment geomorphology and vegetation.

Growing evidence suggests common sets of environmental drivers underlying metabolic regimes. However, untangling the network of causal relationships is difficult. Unlike terrestrial ecosystems, annual variations in temperature and light are often uncorrelated in rivers because light availability is attenuated by external and internal factors. For instance, riparian vegetation in part controls light that reaches small rivers[36,38,39], so the phenology of terrestrial (particularly riparian) vegetation imparts distinct seasonal and geographic patterns on GPP and NEP. In temperate regions, windows of elevated light availability prior to leaf out of deciduous trees can stimulate peak GPP during spring, transiently shifting metabolism towards autotrophy (e.g., ref.[30]). Additionally, high concentrations of dissolved OC and turbidity attenuate light, thereby lowering river GPP[36,40]. Turbidity is often linked to elevated flow, which can also constrain metabolism from reaching its theoretical maximum in most rivers[37,35]. Finally, the metabolic response to the same driver can differ across stream order, making predictions at the network scale difficult[41].

The relationship between river metabolism and temperature also remains unclear. Both GPP and ER are temperature sensitive, but the effect of warming on river metabolism is still equivocal because it is more variable and less predictable than estimates based on metabolic theory[42]. For example, studies along a thermal gradient[43] and across biomes[44] have revealed similar activation energies for both GPP and ER. An experimental warming of an open-canopy stream by 3.3 °C tripled GPP, a much higher increase than predicted by theory[45]. Variables such as light and flow can also covary with temperature, which can make the isolation of a temperature effect difficult[41]. Thus, scaling from species-specific responses will not provide accurate predictions of ecosystem-level responses to increased temperature, and warming will have idiosyncratic, and as yet unpredictable effects on river metabolism.

While clearly nutrient pollution leads to the eutrophication of streams and rivers globally, the direct relationship between nutrient concentrations and loadings and GPP is not as clear as in lakes and reservoirs[46]. The few existing studies show diverging evidence. A long-term experimental phosphorus enrichment in Alaska’s Kuparuk River, draining arctic tundra and thus lacking tree cover, and dominated by benthic mosses, shifted metabolism from heterotrophy to autotrophy and increased the growth of moss, thereby reducing reliance of consumers on terrestrial C inputs[47]. In contrast, nutrient enrichment in a heavily shaded Appalachian stream had no effect on GPP but enhanced ER fueled by terrestrial C inputs[48]. Metabolic responses to changing nutrients may also be more gradual than short-term data collection efforts can capture: an analysis of two decades of monitoring data revealed reductions in both GPP and ER in the Oria River, Spain, after sewage abatement and concomitant reductions of nutrient and OC inputs[49].

Global river heterotrophy. As budgets of river metabolism become more common[32,37,50–52]), we can better constrain global estimates of river GPP, ER and NEP. Based on best currently available budget studies, we summarize the mean annual estimates of areal metabolic fluxes 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 (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 (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 Information;* **Table SI 1**). While these fluxes show apparent differences by latitude, we note limitations in their comparability. Existing time series from tropical and high-latitude rivers rarely encompass a full annual cycle, are still few in numbers, and are skewed towards smaller rivers. Nevertheless, the NEP estimates underline the pronounced heterotrophy of river ecosystems. Our mean global NEP estimate (~ 426 g C m^{-2} yr^{-1}) suggests that rivers figure among the most heterotrophic ecosystems on Earth[53]. Their heterotrophy is supported by OC exported from autotrophic terrestrial ecosystems (global average terrestrial NEP of 74 g C m^{-2} yr^{-1}, based on ref.[54]). Ultimately, many rivers terminate into estuaries, which are overall less heterotrophic (global average NEP: -189 g C m^{-2} yr^{-1}; ref.[55]). The continental shelves are also under the influence of riverine inputs; their global NEP remains poorly constrained and ranges between -6 and 2 g C m^{-2} yr^{-1} (ref.[55]). This pattern of NEP across ecosystems reveals rivers as ‘bioreactors’ that rapidly metabolise terrestrial OC subsidies and highlights their relevance for C cycling at the global scale.

River network metabolism. Measuring ecosystem metabolism at the scale of individual rivers, ranging from tens of meters to several kilometres as determined by the distance of oxygen turnover[56], does not reveal spatiotemporal patterns of metabolism that may emerge from properties (e.g., dendritic structure) inherent to river networks. Furthermore, metabolic regimes resolved over multiple years at the scale of entire river networks are required to integrate regional and global river and terrestrial C cycling. Therefore, it is essential to expand river C research from individual rivers to the network level.

Only a few recent studies have used modelling approaches to predict river metabolism at network scales. Coupling optimal channel networks with empirical GPP time series, Koenig and colleagues[57] revealed emergent productivity regimes of theoretical river networks. They found larger rivers are important for network-scale productivity as catchment size increases, but small rivers with relatively low GPP disproportionately influence network-scale productivity because of their large collective surface area. Furthermore, spatial network modelling revealed patterns of GPP and ER through the networks of the Deva and Cares rivers in Spain, and how metabolism (particularly NEP) is shaped by the combined effects of catchment and river properties, and human impacts[58]. Segatto and colleagues[59] combined GPP, ER and NEP regimes from several river segments with machine learning to predict annual metabolic regimes throughout the Ybbs River network in Austria. Their approach revealed that headwaters drive annual network heterotrophy, despite a distinct autotrophy peak in spring. It also unveiled the river network as a metabolic meta-ecosystem[60] where local NEP is supported by both upstream (autochthonous and allochthonous) and lateral (allochthonous) OC. More such studies are required to gain mechanistic understanding of network metabolism and to integrate it with terrestrial C budgets.

Integrating large-scale carbon fluxes

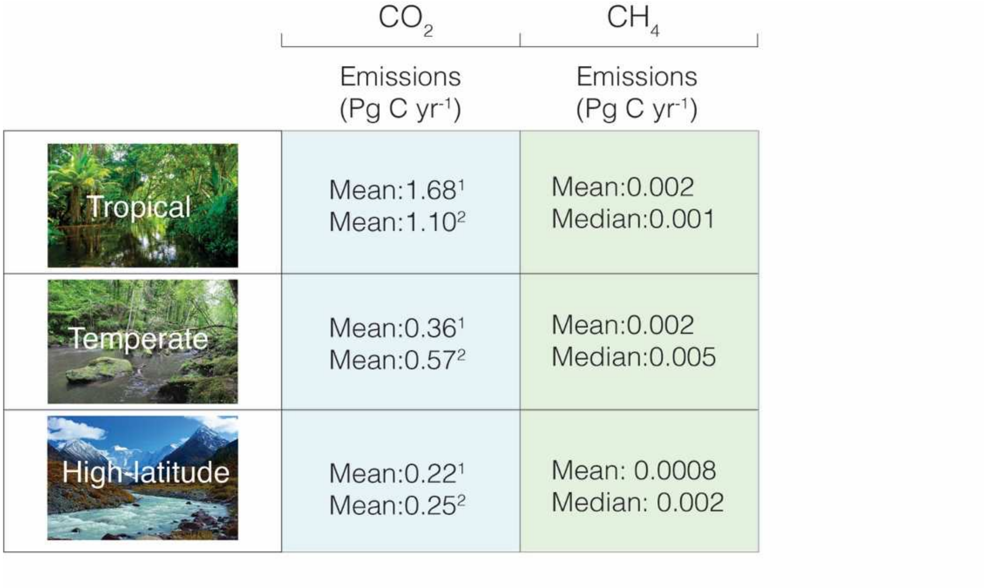
High global river heterotrophy and CO_2 emissions (Box 1) prompted us to integrate river metabolism with C fluxes from land to rivers, and further to the coastal ocean (Fig. 2). Using a mass-balance approach, we quantified relevant fluxes both at the global scale and decomposed into latitudinal bands. We assess uncertainties following IPCC guidelines[61] and indicate lower and upper boundaries (LB and UB) from sensitivity analyses for the budget closure (*Supplementary Information*). Where only UB is indicated, our estimate is conservative and equal to LB. Where appropriate, we also report bootstrapped errors for selected C fluxes (*Supplementary Information*). Our mass balance also includes global CH_4 emissions (besides CO_2) from rivers, as well as OC burial and CO_2 and CH_4 from reservoirs.

Box 1: CO_2 and CH_4 emissions from the world's rivers

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

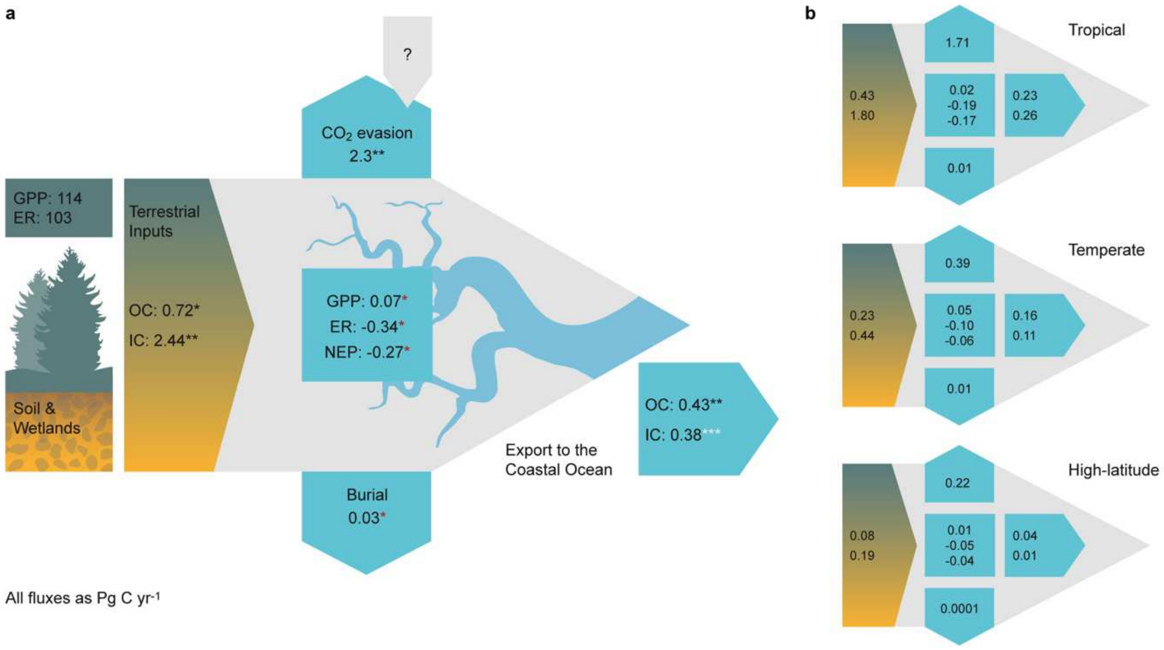


Figure 2. Carbon fluxes from land through river networks to the atmosphere and the coastal ocean. (a) Global fluxes of terrestrial inputs of organic (OC) and inorganic (IC) carbon from land to rivers, and export from rivers to the coastal ocean, river gross primary production (GPP), respiration (ER) 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 from land to rivers[71,72]. Our mass balance is among the first to partition the total C flux to river networks into organic and inorganic fractions, thereby highlighting the large size of the IC flux.

The low OC:IC ratio (0.3; LB: 0.20, UB: 0.47) of the terrestrial-to-river C flux highlights the importance of terrestrial CO_2 inputs, both from upland and wetland soils[73,74], as a dominant C source, deriving not only from chemical weathering and heterotrophic soil respiration, but also from autotrophic root respiration. For instance, root respiration contributes about as much to CO_2 emissions from the Amazon River network as the CO_2 from soil and aquatic heterotrophic respiration combined[74]. Therefore, while OC inputs to rivers can be considered as a fraction of terrestrial net primary production (NPP; GPP - autotrophic R), the biospheric IC and OC inputs to rivers should rather be considered as a fraction of terrestrial GPP with small additions from carbonate minerals. The total global lateral C transfer of 3.2 Pg C yr^{-1} to rivers is equivalent to roughly one quarter of the global terrestrial NEP of 11 Pg C yr^{-1} according to ref.[54] and calculated as river NEP (i.e., GPP-ER). The amount of C currently accumulating in the terrestrial biosphere represents another quarter of terrestrial NEP, the remainder being attributable to land use change, harvested biomass, natural fires, and emission of reduced forms of compounds (e.g., CH_4, volatile organic C)[54]. While the global estimates of terrestrial NEP, and its components NPP (GPP-autotrophic respiration) and heterotrophic soil respiration, are associated with uncertainties which are larger than our estimate of land-to-river C transfers (see ref. [54]), our comparison still highlights the importance of river C cycling for C budgets of the continents.

As inferred from our global estimate of fluvial NEP (-0.27 Pg C yr^{-1}; LB: -0.13 Pg C yr^{-1}, UB: -0.33 Pg C yr^{-1}), rivers transform roughly 37% (LB: 12%, UB: 42%) of the terrestrial OC flux to respiratory CO_2. We tentatively attribute the low processing efficiency for OC in rivers to the short residence times within most river networks and the relatively low bioavailability of terrestrial OC[75,76]. A further fraction of the terrestrial OC can also be transiently buried (as POC) within river floodplains and reservoirs, which may promote its degradation through increased residence times. However, constraining the magnitude of POC burial within the global river networks is inherently difficult. For instance, global inventories of reservoirs typically exclude small impoundments[77,78], despite their apparent contribution to OC burial and GHG emissions[79]. Although recent estimates of OC burial[77,78] and CO_2

emissions from reservoirs (e.g.,[2,80]) converge, these fluxes could actually be up to one order of magnitude larger (Table SI 3, SI 4). We therefore use conservative and upperbound 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: 0.18 Pg C yr^{-1}) for our C budget.

Our budget further suggests that river NEP is the source of approximately 12% (LB: 4%, UB: 14%) of the global river C emissions (2.3 Pg C yr^{-1}, including reservoir emissions; UB: 2.9 Pg C yr^{-1}). This estimate is lower than the contributions reported from US rivers (19 to 39%)[3], the Amazon River and its floodplains (20%)[81] and Mississippi River (22%)[82]. NEP contributions to CO_2 evasion seem higher in small Artic (> 80%)[83] and boreal (75%)[84] rivers draining catchments with OC rich soils. This apparent "mismatch" between our global budget approach and local field studies may be attributable to the high contributions of terrestrial CO_2 to the emissions from small headwaters[3], not included, for instance, in the study on the Mississippi River[82]. The broad range of river NEP contributions to CO_2 emissions further highlights current difficulties in closing the terrestrial-aquatic continuum C budget.

Despite systematic heterotrophy, there can be episodic CO_2 under-saturation in rivers during periods of high autotrophic productivity (i.e., positive NEP) and its associated drawdown of atmospheric CO_2. During such periods, riverine autotrophs may use bicarbonate in addition to CO_2 to compensate for the low diffusivity and potential depletion of CO_2 in water[85] further complicating carbon budgets. Thus, although it is intuitive to assume that autotrophs in rivers primarily satisfy their C demand from terrestrial IC subsidies that contribute to the storage of terrestrial IC within river networks, extended periods of atmospheric CO_2 drawdown may alter the carbon budget presented here.

Our mass balance allowed us to assess the partitioning of the IC/OC flux from land into global rivers and its evolution en route to the coastal ocean. River NEP and CO_2 evasion profoundly alters the OC to IC ratio from 0.3 at the terrestrial-inland water interface to 1.1 at the inland-coastal water interface (Fig. 2). At the point most rivers meet the coastal ocean, bicarbonate is derived almost entirely from chemical weathering of soil minerals. Excluding this weathering-derived contribution, our budget estimates that only about 26% (LB: 21%, UB: 32%) of terrestrial C delivered to rivers makes it to the coastal ocean, which agrees with a previous assessment[86]. While river networks are remarkably proficient at retaining, metabolising and emitting terrestrial C, the remnant OC at river mouths fuels coastal heterotrophic metabolism and has important consequences for the CO_2 air-ocean flux. The delivery of riverine C subsidies likely caused the ocean to be a net source of CO_2 under pre-industrial conditions[87]. This pre-industrial CO_2 outgassing fuelled by river OC has been estimated at about 0.3 Pg C yr^{-1} (refs.[88,89]) to which an anthropogenically enhanced delivery (0.1 Pg C yr^{-1}) may need to be added[22]. However, this export flux might still be underestimated[90]. This is because high flows disproportionately contribute to river C exports but are systematically undersampled, and also because of direct C exports from small but abundant mountainous rivers into coastal waters[91,92]. For our C budget, we used the rather conservative estimate of riverine OC export fluxes of 0.38 Pg C yr^{-1} as compromise between published estimates with a high degree of agreement, but also applied an UB (0.7 Pg C yr^{-1}) as suggested by ref.[55].

Global change impacts on river metabolism and greenhouse gas emissions

Global change impacts on river ecosystem metabolism are complex (Fig. 3); even more so are the related consequences for CO_2 and CH_4 production, transport, and emissions. As discussed above, this complexity partially emanates from the different drivers of GPP and ER, which act at different spatial (e.g., from catchment to channel processes) and temporal (e.g., from storm events to seasonality) scales. Below we illustrate the complexity of global-change impacts on river ecosystem metabolism and related CO_2 and CH_4 emissions based on selected examples covering different spatial and temporal scales.

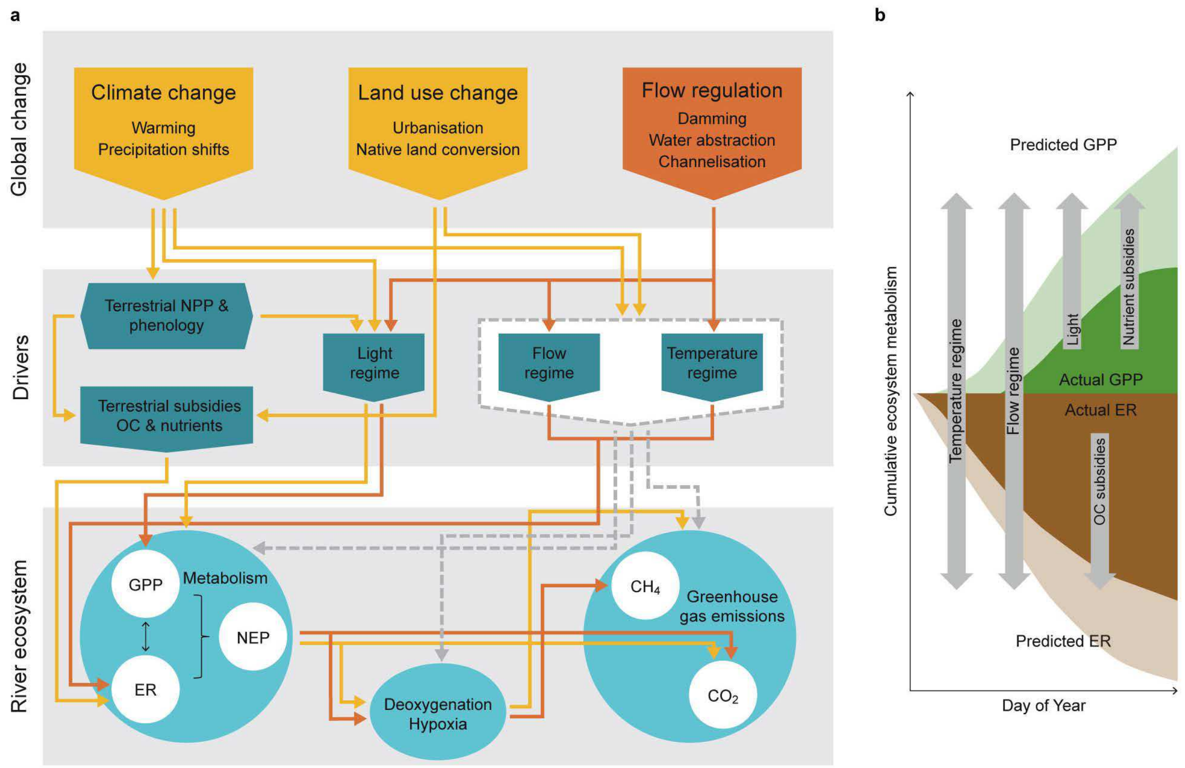


Figure 3. Complexity of global-change impacts on river ecosystem metabolism and CO_2 and CH_4 emissions. (a) Trajectories showing how climate change, land use change and flow regulation potentially impact river ecosystem metabolism, deoxygenation, and both CO_2 and CH_4 emissions. Yellow trajectories 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 augmented terrestrial OC subsidies are mostly recycled within river networks, sustaining increased ER and CO_2 emissions[71]. Earth system models (ESM) further predict that the delivery of terrestrial C and river CO_2 emissions will accelerate due to climate change during the 21st century[74,98,99]. In addition, increasing precipitation at high latitudes decreases terrestrial net ecosystem exchange but increases C leaching from terrestrial ecosystems[100]. In contrast, an observed long-term decline of CO_2 supersaturation in rivers has been attributed to reduced soil production and leaching of CO_2, reservoir building, land use change, and recovery from acidification[101–103]. Overall, trends in the magnitude of terrestrial C leaching into temperate rivers remain uncertain.

Climate change also affects the timing and extent of water routing through catchments and consequently the transport of terrestrial C into rivers. In fact, C fluxes from catchments to rivers are often limited by hydrologic transport and therefore increase during high precipitation[69,75,104]. Recent work has demonstrated that indeed a greater percentage of terrestrial GPP is routed to and evaded as CO_2 from river networks in wetter regions, thereby emphasizing the importance of catchment hydrology for plumbing terrestrial and river C fluxes at global scale[62]. Furthermore, increasing DOC concentrations in Swedish rivers over the last decades were linked to elevated precipitation and higher runoff[105], and DIC fluxes are also typically higher during wetter years[106]. Therefore, it is intuitive to assume that climate-induced alterations of catchment hydrology will increase leakage of terrestrial C in some regions (wetter climate) but decrease it in others (drier climate).

Pulsed terrestrial OC subsidies can also influence river ecosystem metabolism at an annual scale. For instance, low snowpack and early snowmelt during a mild winter shifted metabolism toward increased heterotrophy in an alpine river network[107]. Such a shift is unusual and attributable to pulsed terrestrial OC deliveries, transiently fuelling ER and reducing the magnitude of the spring window when these rivers are typically autotrophic[107]. As winters become milder and precipitation increasingly changes from snow to rain[108] in alpine regions, such metabolic shifts may increase CO_2 emissions from alpine rivers.

A second example illustrates the effects of agricultural land conversion on river ecosystem metabolism and GHG (Fig. 3a,b). Land-use change, including deforestation in the Congo basin and conversion of peatlands into oil palm plantations in Southeast Asia, mobilises ancient but bioreactive OM, which, upon arrival in rivers, is respired to CO_2 (refs.[109–111]). Agricultural soils themselves are a major source of OC and nutrients to the world's rivers[20]. These subsidies alter the magnitude and seasonality of GPP and ER of agricultural rivers[112–114]. Besides increasing subsidies to rivers, agriculture can also cause riparian deforestation and channel geomorphology alterations, which further impair river ecosystem metabolism[115,116]. While several studies have pointed to agricultural rivers as significant sources of CO_2 and CH_4 (refs.[117,118]), the apportioning of these sources (i.e., allochthonous *versus* autochthonous) remains poorly studied to date. Disentangling the relationships between agricultural river metabolism and GHG emissions is important given the large contributions from agriculture to global GHG emissions[119].

Changing river flow regimes. While the above examples relate to changes in catchment land-use and hydrology, changing river flow regimes are also important (Fig. 3a,b). Because the atmospheric holding capacity of water is highly sensitive to temperature, precipitation extremes will become more intense and frequent, with impacts on the natural flow regimes of rivers[120]. Droughts will shape the flow regime in some regions, flash floods attributed to storm runoff in others, and many areas will experience longer periods of drought between more extreme flooding[121,122]. Furthermore, river ice extent and duration are declining globally, further transforming the natural flow, light, and gas-exchange regimes of numerous rivers[14].

Globally, a large fraction of rivers are non-perennial, and both the distribution and magnitude of flow intermittency will change with climate and other anthropogenic alterations[123]. These changes will affect river metabolism, but the nature and magnitude of these changes remain uncertain, as do the implications for regional and global C cycling (Fig. 3a,b). As the flow recedes, particularly headwaters, accounting for the bulk of stream length in global river networks, contract and disconnect[124]. With ongoing drying, GPP collapses but ER proceeds, which promotes heterotrophy of non-perennial rivers[125]. These metabolic processes, along with increasing water residence time, induced hypoxia and promoted CH_4 production during an experimentally induced drought in a boreal river[126]. A similar metabolic shift occurred throughout a boreal river network during the 2018 heatwave in Europe[126]. While such droughts are rather uncommon in cold and humid high-latitudinal regions, non-perennial rivers are a common feature of arid and semi-arid regions[123,127]. The paucity of data on ecosystem metabolism and related GHG emissions from non-perennial rivers contrast with their worldwide prevalence[123,127].

Increasing flood frequency, associated with climate change, will also have important yet poorly understood effects on river metabolism. A recent study covering 222 US rivers showed that more variable flow regimes (i.e., higher 'flashiness') reduced both annual GPP and ER, with an even stronger effect on the latter[37]. High flood-related flows regularly perturb benthic primary producers and can ultimately erode them, thereby reducing annual GPP in shallower rivers. The pronounced effect of flow disturbance on annual ER was attributed to short mean OC residence times, potentially decoupling river ER from the supply rate of terrestrial OC[37]. Such disturbances of ecosystem metabolism appear particularly pronounced in urban rivers, which experience frequent 'flashy' flows during heavy rain because of the imperviousness of their catchments[128–130]. As suggested by Bernhardt and colleagues[37], increasingly perturbed flow regimes may limit the accumulation and storage of primary producer biomass and terrestrial OC, which would have implications for river food webs.

The effects of shrinking ice cover on river flow regimes may be even more pronounced than those of droughts and floods. However, it is currently difficult to predict how changes in ice cover influence river ecosystem metabolism beyond the mere assumption that increased light availability may increase annual GPP[131].

River impoundment and associated water management can also affect river metabolism and GHG emission. Dams retain sediments, OC and nutrients with profound impacts on the biogeochemistry of rivers and the coastal ocean[77,78,80,132]. Depending on their age, geography and operation, reservoirs can emit large amounts of CO_2 and CH_4 to the atmosphere[66,133,134]. The influence of reservoirs on river ecosystem metabolism and GHG emissions does not stop at the dam. Rather it can extend downriver. For instance, water clarity and hydropeaking can affect GPP downriver of the Glen Canyon Dam (Colorado River)[135], while CO_2 and CH_4 leaking from a reservoir through the tailwaters can lead to a 'carbopeaking' downriver of major dams (e.g., ref.[136]).

Underlying the GHG production and emissions from reservoirs are the combined effects of increased water residence time, temperature, nutrient and OC accumulation, and related ecosystem metabolism. For instance, accumulated OC and elevated temperature foster ER and CO_2 production in the oxygenated waters of reservoirs, while methanogenesis and CH_4 production dominate metabolism in the deeper anoxic waters and sediments (e.g., ref.[132]). Furthermore, reservoirs facilitate algal blooms, thereby transiently shifting the metabolism towards autotrophy. Such a shift towards autotrophy in large and nutrient-rich rivers in Asia has been attributed to damming[137] as has the decrease in CO_2 evasion (32%) from Chinese rivers over the last three decades[103]. These observations would benefit from better mechanistic insights. Dam removal after decommissioning offers useful opportunities to gain these insights.

River ecosystem deoxygenation and health. Many of the global-change impacts on river ecosystem metabolism illustrated above can ultimately lead to eutrophication and further to deoxygenation when ER outweighs oxygen resupply from GPP or atmospheric exchange. As a consequence, river metabolism switches from an aerobic to an anaerobic state. Such a state shift triggers alternative metabolic pathways, foremost denitrification and methanogenesis with the production of the potent greenhouse gases nitrous oxide[138] and CH_4 (ref.[139]), respectively. Deoxygenation is increasingly well documented in tidal zones, coastal waters[140] and lakes[141]. While hypoxia has been well known from the hyporheic zone in rivers (e.g,, ref. [142]), it is only recently that we are becoming aware of its spatiotemporal extent at the ecosystem scale in rivers[128,143]. In rivers, large-scale deoxygenation can imperil biodiversity, impose barriers to fish migration, kill fish, and compromise water quality, thereby jeopardizing ecosystem health and services.

Priorities for river network research

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

Observing System (RIOS) (Fig. 4), similar to those existing for terrestrial (e.g., ICOS[144]), lake (e.g., GLEON[145]) and marine (e.g., ARGO floats[146]) domains.

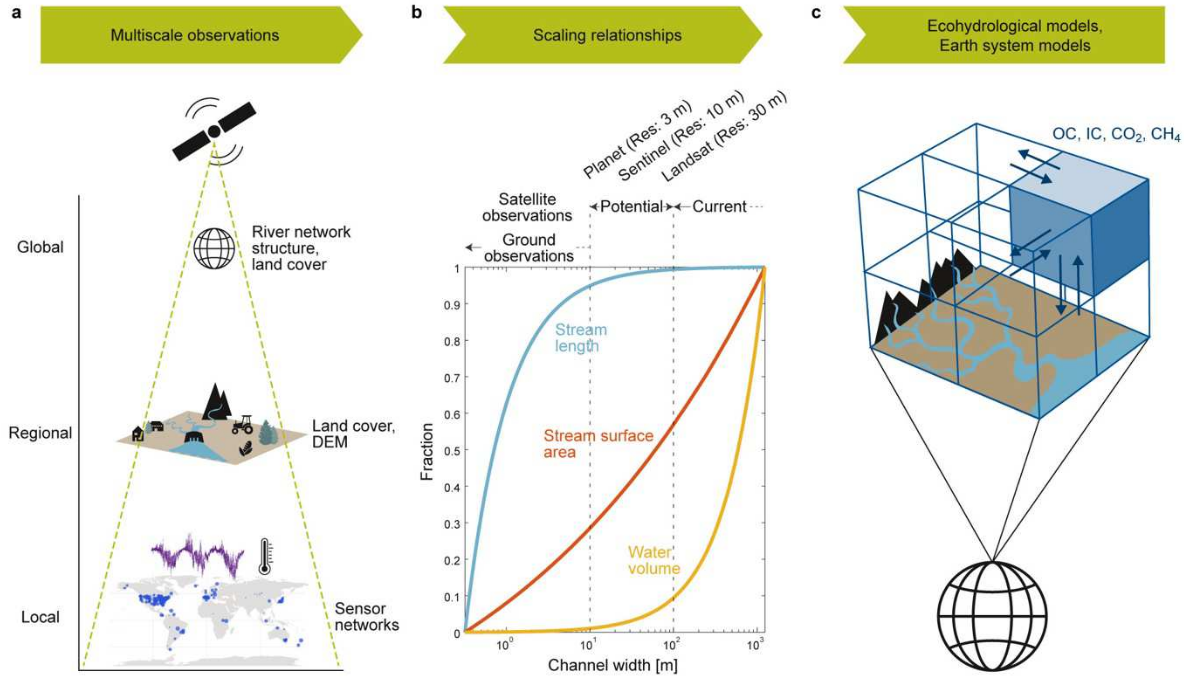


Figure 4. A global River Observation System (RIOS). (a) Multiscale observations integrate data from distributed sensor networks, field surveys and satellite imagery. Sensor networks provide time series of ecosystem metabolism, GHGs and environmental drivers, taking into account the nested organisation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

The first key challenge is to better constrain the uncertainty associated with river network metabolism and how it influences our conceptualization of various C fluxes at both local and large spatial scales (Fig. 2). To achieve this major endeavour, a key research priority is to dramatically increase the number of multiannual time series of ecosystem metabolism, GHG emissions and related metadata, covering a broad spectrum of river ecosystems. Here the focus should be to facilitate measurements at the network scale that helps fill geographic (i.e., tropics, high-latitude and high-altitude regions) and knowledge (e.g., network responses to flow extremes and changing climate) gaps. Filling these gaps is greatly facilitated by the recent improvements in O_2 and other sensors and statistical approaches[31,32], however a further priority is the development of next-generation inexpensive GHG sensors and further support and research on creating networks of "smart" sensors. This effort must be accompanied by the proper training of staff to maintain sensors. Furthermore, water quality data from governmental agencies should be better leveraged to complement time series from sensors[32,148]. Increasing the quantity and quality of river metabolism and GHG time series requires coordinated approaches steered by working groups and facilitated by the use of standardized protocols. Recent advances in information and communications technology, as well as in the governance of complex sensor networks, including ensuring data availability, will facilitate the implementation of this effort[149,150]. Given the scale of the endeavour, the research community will need to secure large-scale, collaborative and transnational funding to also better include the Global South.

The second key challenge relates to the upscaling of measured C fluxes from individual river segments to river networks. This requires the integration of multi-scale ground (i.e., sensor networks) and satellite observations with scaling laws, and further with catchment-scale mechanistic models. Today, satellites offer opportunities to quantify river network topology[151,152], surface[68] and inundation area[17], water storage[18], discharge[153,154], suspended sediments[155], and ice cover[14]. Advances in remote sensing are promising and shall soon provide data that are also relevant to ecosystem processes and C biogeochemistry[156] (Table SI 6). However, satellite imagery still leaves substantial data gaps. Global satellite analysis of river surface area currently excludes narrow rivers (< 90 m wide), thereby excluding the majority of the world's rivers[68,157] (Fig. 4). Furthermore, riparian vegetation still poses an unresolved problem in detecting and characterising these narrow rivers. Therefore, a key research priority would be to unify new remote sensing methods related to riparian vegetation, ice cover, and suspended sediment concentration to quantify channel width and light availability (a main driver of GPP) in the world's smallest and largest rivers .

Simple scaling laws can be used to predict how channel length and flow geometry (i.e., water depth, velocity and width) change through river networks (Fig. 4) (*Supplementary Information*). Owing the to universal features of river networks[158], they are also used to integrate river GPP[57], DOC transport and uptake[75,159], as well as GHG emissions (e.g., N_2O, ref.[160,161]) over entire networks and probe constraints on these processes. However, the applicability of scaling laws for river ecosystem science has limitations. Scaling laws often only resolve steady state conditions, thus not accounting for the dynamic nature of river networks (e.g., expansion and contraction). New mapping[68,123,151,152], modelling[162] and conceptual frameworks[163] will facilitate predictions of the spatiotemporal dynamics of river networks, which seems particularly important for headwaters that are often non-perennial[164]. Furthermore, scaling relationships require validation across the entire spectrum of river sizes, particularly the smallest perennial rivers within networks that do not become infinitely small[165]. Therefore, a priority for the research community is the development of integrated global field campaigns to resolve problems with scaling laws and unify the scales of ground and satellite observations in small and large rivers. This entails recruiting scientists and volunteers to make relatively simple measurements (e.g., stream width) using standardized protocols across a broad range of rivers.

Finally, our ability to understand, and thus predict, large-scale river C dynamics and impacts would benefit from improved iterative interactions between observations and simulations. However, current biogeochemical modelling frameworks often still fail to properly represent river ecosystem processes, particularly metabolism, and the fate of the various C forms at relevant spatial and temporal scales. Furthermore, most modeling frameworks fall short of integrating C cycling with nutrient cycling and deoxygenation, which appears critical though given the global change impacts on these latter processes. Therefore, opportunities to adapt and improve modeling frameworks (e.g., IMAGE-DGNM[72], Tethys-Chloris[166]) are numerous. Given the dynamic nature of river networks, also these latest modeling frameworks (e.g., ref. [72]) would need to resolve river ecosystem processes at daily scales — still a computational challenge. A key research priority therefore is to integrate the global rivers into ESMs used to project climate change in response to anthropogenic CO_2 emissions, still ignoring the fraction of the terrestrial C sink leaking to river networks. In fact, the exclusion of this leakage, despite its large uncertainty, biases estimates of the terrestrial net C uptake (too low) and biospheric C stock increase (too high)[64].

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

Acknowledgments

The following funding sources are acknowledged: TJB, The NOMIS Foundation, SNF (IZSEZO_181491, 200021_163015); RL, ANR "Investissements d'avenir" (ANR-16-CONV-0003_Cland); ESB and ROH, US NSF grant #1442439 (StreamPULSE); ERH, US NSF grant #1926426; PAR, US NSF grant #1840243; TM and JAR, Yale Institute for Biospheric Studies; Pre, BELSPO (ReCAP, FedTwin), EU Horizon 2020 VERIFY (grant agreement no. 776810) and ESM2025 - Earth System Models for the Future - (grant agreement no. 101003536). LR, Research Grants Council of Hong Kong (grant no. 17300621). Katharina Peter designed the figures.

Contributions

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

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