Perspective

The land-to-ocean loops of the global carbon cycle

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Pierre Regnier[1✉], Laure Resplandy[2], Raymond G. Najjar[3] & Philippe Ciais[4]

Carbon storage by the ocean and by the land is usually quantified separately, and does not fully take into account the land-to-ocean transport of carbon through inland waters, estuaries, tidal wetlands and continental shelf waters—the 'land-to-ocean aquatic continuum' (LOAC). Here we assess LOAC carbon cycling before the industrial period and perturbed by direct human interventions, including climate change. In our view of the global carbon cycle, the traditional 'long-range loop', which carries carbon from terrestrial ecosystems to the open ocean through rivers, is reinforced by two 'short-range loops' that carry carbon from terrestrial ecosystems to inland waters and from tidal wetlands to the open ocean. Using a mass-balance approach, we find that the pre-industrial uptake of atmospheric carbon dioxide by terrestrial ecosystems transferred to the ocean and outgassed back to the atmosphere amounts to 0.65 ± 0.30 petagrams of carbon per year (±2 sigma). Humans have accelerated the cycling of carbon between terrestrial ecosystems, inland waters and the atmosphere, and decreased the uptake of atmospheric carbon dioxide from tidal wetlands and submerged vegetation. Ignoring these changing LOAC carbon fluxes results in an overestimation of carbon storage in terrestrial ecosystems by 0.6 ± 0.4 petagrams of carbon per year, and an underestimation of sedimentary and oceanic carbon storage. We identify knowledge gaps that are key to reduce uncertainties in future assessments of LOAC fluxes.

The land and the ocean carbon reservoirs are key gatekeepers controlling atmospheric carbon dioxide (CO_2) and Earth's climate on annual to centennial timescales. In most carbon budgets, terra firme ecosystems on land and the open ocean (see Box 1 for definitions) are viewed as silos that exchange CO_2 with only the overlying atmosphere[1–3]. In reality, some of the carbon taken up as CO_2 by terra firme ecosystems is transported to the ocean by the 'land-to-ocean aquatic continuum' (LOAC)[4–8] (Box 1), and may return to the atmosphere or be trapped in sediments at each step of its journey[9–16]. The transport and transformation of carbon along the LOAC involve natural processes that have been substantially perturbed by human activities[8,14,17]. Knowledge of this transport and redistribution by the LOAC is required to separate natural and anthropogenic fluxes from total CO_2 fluxes estimated by observational analyses, such as atmospheric inversions, surface-ocean CO_2 surveys or upscaling of eddy covariance ecosystem exchange measurements[18]. Despite recent advances in understanding LOAC processes, for example, refs. [19,20], the separation of natural and anthropogenic CO_2 fluxes still relies on the assumption that the LOAC is a 'river pipeline' of natural carbon flowing from the land to the ocean. This approach, proposed by Sarmiento and Sundquist[21], continues to be used by the Intergovernmental Panel on Climate Change (IPCC)[1,2] and the Global Carbon Project (GCP)[3].

A standard estimate of the LOAC pre-industrial natural carbon flux outgassed in the open ocean using the river pipeline conceptual model is 0.45 ± 0.18 PgC yr^{-1} (ref. [2]). This number is derived from present-day observations of carbon transport at river mouths (0.71 PgC yr^{-1})[5,22,23] assuming that a fraction of this carbon is buried in the ocean (0.26 PgC yr^{-1}) and the rest is outgassed back to the atmosphere[23] (Fig. 1a). This estimate has four main shortcomings: the river input (0.71 PgC yr^{-1}) is lower than recent assessments (for example, refs. [2,9]) giving 0.90 PgC yr^{-1}; it assumes that carbon is transported passively in rivers; it neglects the anthropogenic perturbation of the river carbon transport; and it assumes that all the carbon transported at river mouths then reaches the open ocean, ignoring the role of estuaries, tidal wetlands and continental shelf waters. More recently, Resplandy et al.[24] revised the pre-industrial river carbon transport upwards to 0.78 ± 0.41 PgC yr^{-1}, arguing that a higher riverine supply was needed to match the observed meridional transport of carbon in the ocean (Fig. 1b). After subsequently using the former (for example, ref. [25]) and latter[3,26] estimates, the GCP has most recently evaluated the land-to-ocean carbon flux using the average of both estimates (that is, 0.61 PgC yr^{-1})[27]. These estimates provide, however, limited understanding of the LOAC contribution to the global carbon cycle, as they either do not consider all key carbon pathways or rely on indirect constraints from ocean-tracer observations alone (Fig. 1).

In this Perspective, we replace the river pipeline conceptual model by a more detailed description of the LOAC. Building on recent assessments of global LOAC fluxes[8,19,20,28–55], we estimate pre-industrial and

[1]Biogeochemistry and Modelling of the Earth System-BGEOSYS, Department of Geoscience, Environment and Society, Université Libre de Bruxelles, Brussels, Belgium. [2]Department of Geosciences, High Meadows Environmental Institute, Princeton University, Princeton, NJ, USA. [3]Department of Meteorology and Atmospheric Science, The Pennsylvania State University, University Park, PA, USA. [4]Laboratoire des Sciences du Climat et de l'Environnement – UVSQ, UPSaclay, Gif sur Yvette, France. ✉e-mail: pierre.regnier@ulb.be

Box 1

The land-to-ocean aquatic continuum

The LOAC can be viewed as a succession of connected, chemically and physically active aquatic biogeochemical systems, linking upland soils to the open ocean. The segmentation of the LOAC mostly follows that proposed by ref. [8]. In this segmentation, land should be understood as 'terra firme' terrestrial ecosystems, whereas inland waters comprise streams, rivers, floodplains, lakes, ponds and reservoirs. Coastal waters include estuaries and continental shelf waters[36]. They receive land-derived carbon inputs from inland waters through both river flows and subsurface discharge from fresh groundwater[32,33].

Coastal waters are also strongly connected to tidal wetlands (mainly tidal marshes and mangroves), which extract CO_2 from the atmosphere and export carbon laterally towards estuaries and continental shelf waters[64]. In addition, submerged vegetation (seagrass and macroalgae) present in estuaries and on continental shelves has an important role in carbon burial and air–water CO_2 exchange[34]. Our analysis explicitly accounts for tidal wetlands and submerged vegetation—together referred to as 'blue carbon'. Estuaries comprise alluvial estuaries dominated by the tide, small deltas, lagoons and fjords[112], and carbon fluxes through the air–water interface were estimated separately for each type, whereas burial was estimated separately for fjords and collectively for the other estuarine types. Continental shelf waters correspond to the shallow part of the ocean down to the shelf break, typically located at around 200-m water depth[36]. The open ocean is defined here as the global ocean minus the portion covered by continental shelves.

anthropogenic LOAC carbon transfers using the more complete representation given in Fig. 1c. We discuss the magnitude and underlying processes of land-to-ocean carbon transfers during pre-industrial times, how much have human activities perturbed these transfers, and how this perturbation has decoupled the uptake of anthropogenic CO_2 from carbon storage in the terra firme and ocean reservoirs. We conclude by identifying key knowledge gaps in LOAC research and discussing how to reduce uncertainties in future estimates of LOAC fluxes.

Perturbed LOAC carbon cycle

The realistic conceptual framework drawn in Fig. 1c is used to quantify each LOAC carbon flux and provide a full closure of the global carbon budget from terra firme ecosystems to the open ocean. We apply a mass-balance approach, relying on the recent advances and syntheses of LOAC observational data, complemented by statistical and process-based models. We quantify these fluxes for present-day conditions (roughly 1990 to present), then estimate the anthropogenic perturbation for each of the LOAC fluxes, and finally quantitatively constrain the pre-industrial equilibrium state (see Supplementary Information for details). Our approach differs from the global carbon budgets of the IPCC and GCP, which did not fully resolve the complexity of the LOAC and assumed that LOAC fluxes remained equal to their pre-industrial values[2,3]. A latitudinal decomposition is also performed, which enables an independent comparison with the revised independent top-down estimate from ref. [24].

To constrain the present-day LOAC fluxes, we have prioritized spatially and temporally resolved, observation-based assessments (Table 1) derived from a systematic search of more than 100 peer-reviewed publications, of which about half have been published over the past decade (Supplementary Table 2). The vast majority of LOAC fluxes are quantified using spatially resolved climatologies (albeit at different resolutions, Table 1), except the estuarine burial, the tidal wetland fluxes and the submerged vegetation fluxes, which are based on a global mean area-based flux density. It is, however, important to stress that even in the cases based on flux density, we used distinct values per estuarine type (tidal systems and deltas, lagoons, and fjords) and vegetation type (mangroves, marshes, seagrasses and macroalgae). When studies did not report the time frames covered by their assessment, we assumed that present-day LOAC fluxes were broadly representative of the past three decades (1990 to present; Supplementary Table 2) and that these fluxes have remained constant over this relatively short period. Only in a few cases, where the spatial resolution of the model products was unambiguously better than the observational evidence, we have selected model-derived estimates. These cases include the continental shelf carbon burial (and accumulation), which was partly derived from model estimates, and the river-to-estuary export flux, which was constrained using a hybrid approach. At the global scale, these model-derived estimates match reasonably well the spatially coarser, observation-based assessments (Supplementary Section 1, Supplementary Table 2).

The present-day carbon cycle

The starting point in evaluating the present-day carbon budget (roughly 1990 to present) shown in Fig. 2a (step 1 in Supplementary Section 0) is the lateral flux at river mouths where the water enters estuaries: this is the best-constrained lateral carbon transport along the LOAC[20]. Our estimate of this lateral flux, 0.95 ± 0.15 PgC yr^{-1} (F_{IE}, see Table 1 and Fig. 1c for LOAC flux names) is based on the latest assessments of carbon carried by rivers[28–31], but also includes groundwater sub-sea carbon discharge[32,33] (Supplementary Section 1). The groundwater carbon discharge is highly uncertain[32,33], but it is a relatively minor pathway for land-to-ocean carbon transfers, probably not exceeding 0.1–0.2 PgC yr^{-1}. Downstream of river mouths, we estimate using recent syntheses (Supplementary Section 1)[34–38] that the net uptake of atmospheric CO_2 by tidal wetlands, estuaries and continental shelf waters ($F_{AW} - F_{EA} + F_{AC}$) adds 0.40 ± 0.15 PgC yr^{-1} to the carbon carried by rivers towards the open ocean. This atmospheric CO_2 uptake is incidentally in balance with carbon burial in coastal sediments ($F_{WS} + F_{ES} + F_{CS}$; Supplementary Section 1)[39–45], so that the net lateral transfer of carbon at the river-–estuary boundary (F_{IE}) equals the transfer between continental shelf waters and open ocean (F_{CO}; Fig. 2a).

Moving upstream to the continental segments of the LOAC (left side of Fig. 1c), we note that the amount of carbon leached from the land to the LOAC cannot be assessed from observations. Therefore, this flux was constrained from mass balance, starting again from the well established lateral flux at river mouths, F_{IE}. Upstream of the river–estuary interface, we revised the estimates of carbon evasion from inland waters to the atmosphere (F_{IA} = 1.85 ± 0.50 PgC yr^{-1}; Supplementary Section 1)[19,46–48] and the inland-water carbon burial (F_{IS} = 0.15 ± 0.10 PgC yr^{-1}; Supplementary Section 1)[49]. These estimates of carbon evasion and burial account for the contribution of streams, rivers, ponds, lakes and reservoirs, but exclude the largely unknown and yet potentially large fluxes from floodplains. Despite significant uncertainties, these revisions yield a massive lateral carbon loss from terra firme ecosystems to inland waters of 2.95 ± 0.55 PgC yr^{-1} (F_{LI}).

To recast the present-day LOAC carbon fluxes in the context of the global carbon budget, we select the 2005–2014 decade as an example. Selecting a shorter time frame is needed to constrain the rapidly evolving fossil fuel emissions, atmospheric CO_2 growth rate and open-ocean uptake. During this period, the open-ocean CO_2 uptake from the atmosphere (F_{AO}) is estimated at 1.85 ± 0.95 PgC yr^{-1} using three data-driven products based on surface-ocean partial pressure of CO_2 (p_{CO_2}) meas-

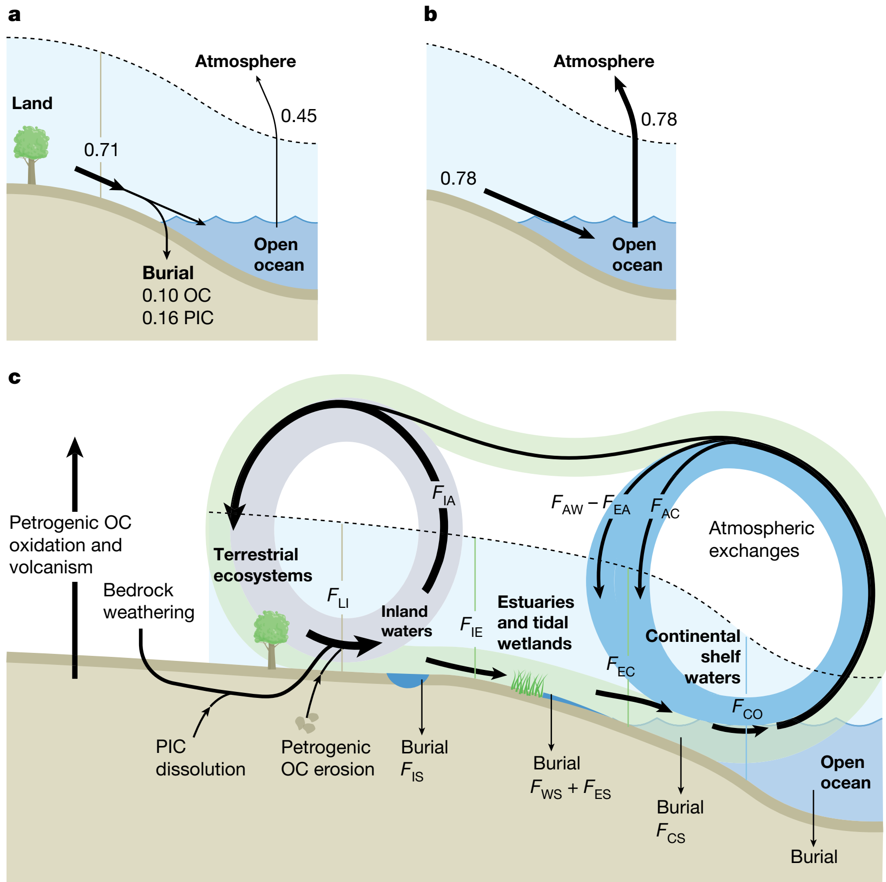

Fig. 1 | Approaches to quantify the pre-industrial carbon budget. **a**, According to the 'river pipeline' model[23]. **b**, According to the meridional carbon transport by the ocean[24]. **c**, According to the LOAC carbon loop model from this study. The LOAC loop model explicitly accounts for LOAC segments ignored in traditional global carbon budgets. It splits 'land' into 'terra firme ecosystems' and 'inland waters' and adds the overlooked contributions of 'estuaries and tidal wetlands' and 'continental shelf waters' to the overall carbon budget. The full LOAC loop can be decomposed into one long-range carbon loop (green) connecting terra-firme ecosystems to the open ocean and two short-range carbon loops respectively connecting terra firme ecosystems to inland waters in the upstream portion of the LOAC (grey), and tidal wetlands and shelf waters to the open ocean in the downstream portion of the LOAC (blue). The units in panels **a**, **b** are PgC yr^{-1}. OC stands for organic carbon and PIC for particulate inorganic carbon. See Table 1 for LOAC flux nomenclature.

urements, which show remarkable agreement over the given time frame (Supplementary Table 2)[56–58]. Closure of the present-day atmospheric carbon budget using this ocean uptake, our new LOAC fluxes and fossil fuel emissions (8.90 PgC yr^{-1}), and the atmospheric CO_2 growth rate (4.40 PgC yr^{-1}) reported by the GCP[3] yields a CO_2 uptake by terra firme ecosystems of 4.10 ± 1.50 PgC yr^{-1} (F_{AL}; Fig. 2a; see Supplementary Sections 0, 1 for further details). A substantial fraction of this carbon uptake is not stored in situ but feeds into the LOAC where it is largely recycled back to the atmosphere, suggesting a rapid carbon turnover between terra firme ecosystems and inland waters.

The anthropogenic perturbation

Instead of using the concept of a river pipeline, we revise the anthropogenic carbon budget to include each segment of the LOAC (Fig. 2a, step 2 in Supplementary Section 0, see details in Supplementary Section 2). We find that the anthropogenic perturbation notably increased the lateral transfer of carbon from terra firme ecosystems to inland waters by 0.60 ± 0.40 PgC yr^{-1} (F'_{LI}; Supplementary Section 2). This enhancement of the carbon leached from terra firme ecosystems mostly intensifies inland water outgassing and burial (Supplementary Section 2)[50–52] so that the carbon flux at the river–estuary interface increases by only 0.10 ± 0.05 PgC yr^{-1} (F'_{IE}) from its pre-industrial value, in agreement with global and regional assessments[31,50,53,54]. In addition, the anthropogenic perturbations of atmospheric CO_2 exchanges and burial downstream of the river–estuary interface largely offset each other[8,39,55]. As a result, the net anthropogenic transport perturbation only marginally grows from the river–estuary interface to the shelf–open-ocean interface to reach 0.15 ± 0.15 PgC yr^{-1} (F'_{CO}; Fig. 2a, Supplementary Section 2).

The open-ocean anthropogenic CO_2 sink[59,60] (F'_{AO}; Fig. 2a) is estimated to be 2.50 ± 1.00 PgC yr^{-1}, as derived from the present-day total CO_2 uptake (1.85 ± 0.95 PgC yr^{-1}; ref. [56]) minus the pre-industrial outgassing derived from our LOAC assessment (0.65 ± 0.30 PgC yr^{-1}; see next section). The anthropogenic change in carbon storage in the open ocean, however, amounts to 2.65 ± 1.00 PgC yr^{-1}. It is larger than the anthropogenic CO_2 uptake by the ocean because 0.15 ± 0.15 PgC yr^{-1} of anthropogenic carbon is received laterally from shelf waters (Supplementary Section 0). Conversely, the anthropogenic CO_2 sink of terra firme ecosystems obtained from closure of the anthropogenic carbon budget amounts to 2.30 ± 1.50 PgC yr^{-1} (F'_{AL}; Supplementary Section 2). This sink is substantially larger than the net anthropogenic carbon storage on land of 1.70 ± 1.55 PgC yr^{-1}, because of the leaching of anthropogenic carbon to inland waters. We note that partly owing to the propagation of significant uncertainties in lateral carbon fluxes, the impact of the LOAC on the anthropogenic carbon storages in the land and the open ocean is subject to uncertainties of the order of 50–100% at the 2σ level.

Pre-industrial LOAC carbon cycle

In our conceptual framework, we derived the pre-industrial state for all LOAC fluxes (Table 1) by subtracting the anthropogenic perturbation

Table 1 | Quantification of the LOAC carbon fluxes and their 2σ uncertainties

Symbol	Name	Present day	Confidence	Uncertainty	Method	Spatially resolved flux	Temporal variability	Perturbation *F*'	Confidence	Uncertainty	Pre-industrial *F*°	Uncertainty
F_{IA}[a]	Outgassing from inland waters	1.85	L/M	0.51	d	Yes	No	0.40	L	0.40	1.45	0.65
F_{IS}[a]	Burial in inland waters	0.15	L/M	0.10	d	Yes	No	0.10	L	0.05	0.05	0.11
F_{IE}[a]	Lateral flux from inland waters to estuaries	0.95	M/H	0.17	d, m[b]	Yes	S, IAV[c]	0.10	L	0.05	0.85	0.18
F_{LI}[d]	Lateral flux from land to inland waters	2.95	L/M	0.54	b	NA	NA	0.60	L	0.41	2.35	0.68
$F_{AW} - F_{EA}$[a]	C uptake by tidal wetlands—estuarine outgassing	0.10	L	0.12	d	Yes/SA only[e]	No	−0.10	L	0.07	0.20	0.13
$F_{WS} + F_{ES}$[a]	C burial in tidal wetlands and estuaries	0.10	L/M	0.03	d	SA only[f]	No	−0.05	L	0.05	0.15	0.06
F_{EC}[d]	Lateral flux from estuaries to continental shelf waters	0.95	L/M	0.21	b	NA	NA	0.05	L	0.10	0.90	0.23
F_{AC}[a]	C uptake by continental shelf waters	0.30	M/H	0.08	d	Yes	S[c]	0.20	L	0.10	0.10	0.13
F_{CS}[a]	Burial on continental shelves and DIC accumulation in the water column	0.30	L/M	0.11	m[b]	Yes	No	0.10	L	0.05	0.20	0.12
F_{CO}[d]	Lateral C export from continental shelf waters to the open ocean	0.95	L/M	0.25	b	NA	NA	0.15	L	0.15	0.80	0.29

Throughout the paper, a present-day flux from reservoir A to reservoir B is denoted by $F_{AB} = F°_{AB} + F'_{AB}$, with $F°_{AB}$ and F'_{AB} corresponding to pre-industrial and anthropogenic perturbation terms, respectively; see Supplementary Box 0 for carbon flux nomenclature. Confidence in the values selected for this study is specified for the present-day fluxes, using the IPCC nomenclature (VL, very low; L, low; M, medium; H, high; VH, very high). The confidence for all LOAC perturbation fluxes is considered low (L). Methodology (d, data; m, model; b, budget closure) and the spatiotemporal resolution of each flux are also reported (NA, not applicable). See Supplementary Table 1 for non-rounded present-day fluxes and a quantification of terrestrial, open-ocean and geological fluxes of the global carbon budget.

[a]Fluxes derived from bottom-up estimates.

[b]F_{IE} modelled values for dissolved inorganic carbon (DIC) and DOC, except subsurface flux, hybrid approach for particulate organic carbon (POC, observed POC yields combined with simulated sediment loads); F_{CS} semi-empirical model for particulate inorganic carbon; reactive-transport model driven by observed forcing fields for POC; modelled DIC accumulation.

[c]Seasonal variability (S) and interannual variability (IAV) for dissolved carbon compounds.

[d]Fluxes calculated from mass balance.

[e]Flux computed from (partly) spatially resolved flux density per estuary type and from a global mean flux density per vegetation type, both combined with spatially resolved surface areas (SAs).

[f]Flux computed from global mean flux density (per estuary/coastal vegetation type) and spatially resolved SA.

from the present-day LOAC budgets described in the previous sections (step 3 in Supplementary Section 0, Fig. 2b). As a result, the uncertainties in the pre-industrial carbon fluxes grow further, highlighting the challenge to reach a closure of the carbon budget that includes the LOAC before human perturbations. Our analysis suggests that pre-industrial terra firme ecosystems were taking up 1.80 ± 0.75 PgC yr^{-1} of atmospheric carbon, as CO_2 ($F°_{AL}$), which was entirely channelled to inland waters. The weathering of the bedrock[22,29,61,62] ($F°_{WI}$; see Supplementary Box 0 for the nomenclature of geological fluxes) and the lateral transfer of eroded petrogenic and old soil organic carbon[28] ($F°_{FI}$) added 0.40 ± 0.15 PgC yr^{-1} and 0.15 ± 0.20 PgC yr^{-1}, respectively, leading to a total lateral transfer of 2.35 ± 0.70 PgC yr^{-1} from soils to inland waters during pre-industrial times. Most of this carbon was processed in inland waters by the upstream short-range carbon loop (grey, Fig. 1c), and only 0.85 ± 0.20 PgC yr^{-1} flowed through the river–estuary interface ($F°_{IE}$) as part of the long-range carbon loop (green, Fig. 1c).

Downstream of the river–estuary interface, the CO_2 uptake by tidal wetlands in the downstream short-range carbon loop (blue, Fig. 1c) was twice that of today ($F°_{AW} - F°_{EA}$ = 0.20 ± 0.15 PgC yr^{-1}; Supplementary Sections 1, 2) and continental shelf waters were also taking up a small amount of atmospheric CO_2 ($F°_{AC}$ = 0.10 ± 0.15 PgC yr^{-1}). Altogether, 1.15 ± 0.25 PgC yr^{-1} entered coastal waters during pre-industrial times, about three-quarters of which was delivered by rivers and groundwater (0.85 ± 0.20 PgC yr^{-1}) and one-quarter taken up from the atmosphere by

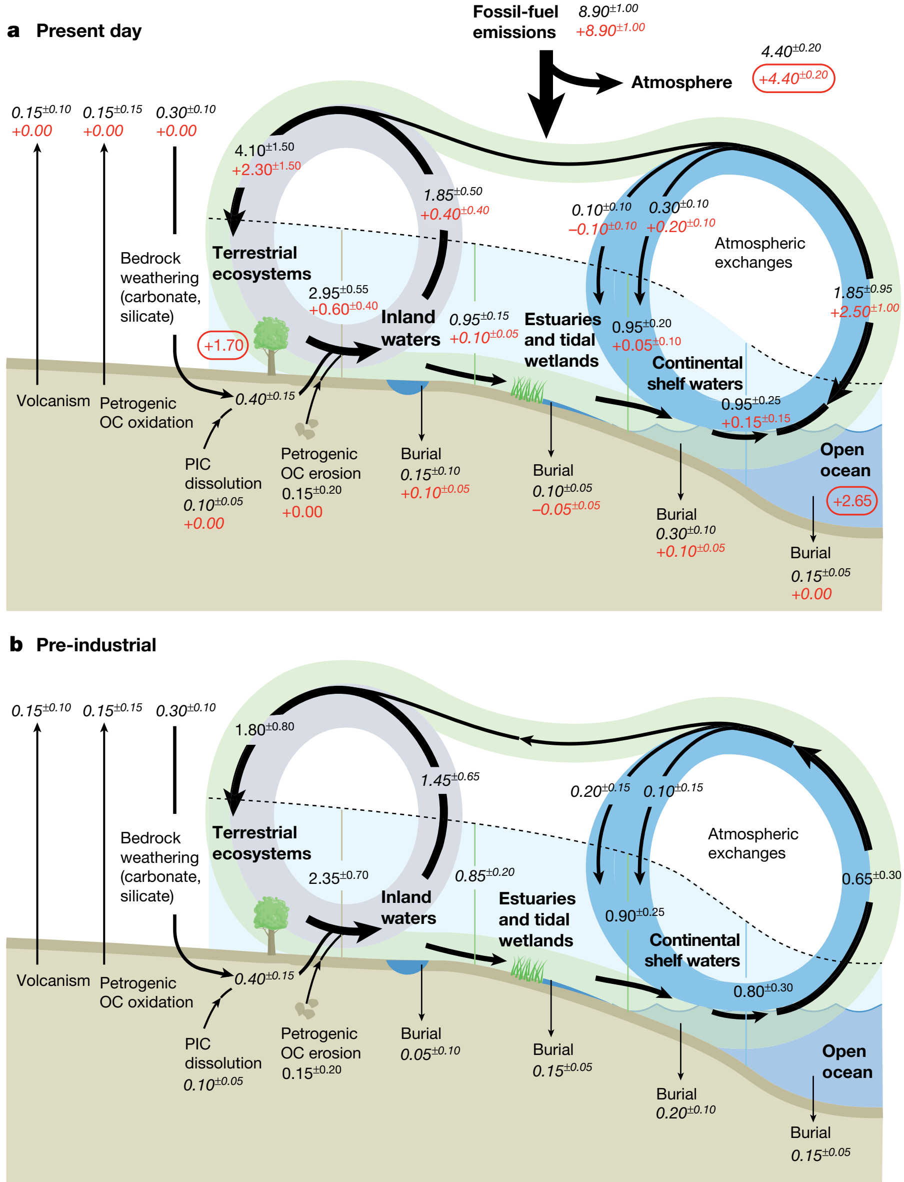

Fig. 2 | The global carbon budget with LOAC fluxes. **a**, The contemporary global carbon budget (numbers in black, period 2005–2014) and its anthropogenic perturbation (numbers in red). **b**, The pre-industrial global carbon budget. The decomposition of the pre-industrial carbon cycle into the inorganic weathering loop and a non-weathering loop driven by organic carbon fluxes is presented in Supplementary Section 3. All fluxes in italics are derived from bottom-up estimates; other fluxes were constrained from a mass balance. The methodology for constraining uncertainties is described in the Supplementary Information, applied to both present-day fluxes (Supplementary Section 1) and anthropogenic perturbation fluxes (Supplementary Section 2). The units are PgC yr^{-1}. All fluxes have been rounded to ±0.05 PgC yr^{-1}.

estuaries, tidal wetlands and shelf waters (0.30 ± 0.20 PgC yr^{-1}). Of this total influx of carbon to coastal waters, about 30% (0.35 ± 0.15 PgC yr^{-1}) was buried in coastal sediments (Supplementary Sections 1, 2), yielding a carbon transfer from continental shelf waters to the open ocean of 0.80 ± 0.30 PgC yr^{-1} (F°_{CO}). In the open ocean, 0.15 ± 0.05 PgC yr^{-1} of this transfer was permanently buried in sediments (F°_{OS}), whereas the remaining 0.65 ± 0.30 PgC yr^{-1} was outgassed to the atmosphere (F°_{AO}). This perspective on the global carbon cycle therefore suggests that the three pre-industrial carbon loops were transferring a net amount of 0.65 ± 0.30 PgC yr^{-1} from the atmosphere to the land and the LOAC, and back from the open ocean to the atmosphere.

Despite significant uncertainties in our quantitative assessment, two independent lines of evidence support our diagnosis of the pre-industrial LOAC carbon loops. The first is based on two distinct estimates of the open-ocean anthropogenic CO_2 sink (Supplementary Table 2). We derived our estimate of this anthropogenic sink by adding the present-day observed open-ocean sink (1.85 ± 0.95 PgC yr^{-1}; ref. [56]) and our LOAC-based pre-industrial outgassing (0.65 ± 0.30 PgC yr^{-1}), yielding 2.50 ± 1.00 PgC yr^{-1} for the 2005–2014 period (Fig. 2a). This value is, within uncertainties, the same as the independent estimate of 2.53 ± 0.20 PgC yr^{-1} by ref. [59] (after correction for the anthropogenic perturbation of 0.20 ± 0.10 PgC yr^{-1} on continental shelf waters; Supplementary Section 2). This conclusion holds irrespective of the choice for the present-day open-ocean sink product[56–58]. Our result is also in agreement with ocean interior observations, which indicate that the ocean is taking up 31% of anthropogenic emissions[60] (0.31 × 8.90 − 0.20 = 2.56 PgC yr^{-1} once corrected for the 0.20 PgC yr^{-1} taken up by continental shelf waters).

The second line of evidence is the consistency of our estimates of the LOAC lateral fluxes for broad latitudinal bands with independent

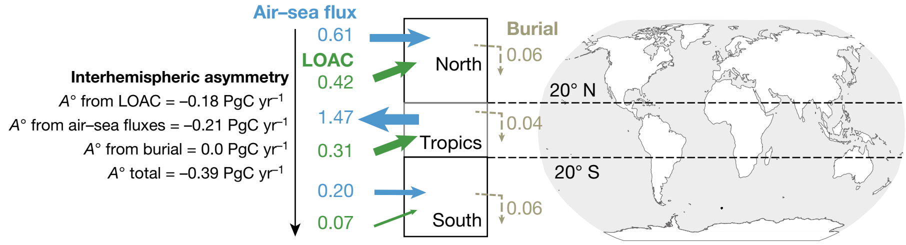

Fig. 3 | Bottom-up estimates of the pre-industrial open-ocean carbon budget in three latitudinal bands. The pre-industrial air–sea flux (blue) is estimated from present-day observations[56] and an assessment of the anthropogenic perturbation[59]. Interhemispheric asymmetries are quantified from the pre-industrial carbon inputs to the open ocean polewards of 20° N and 20° S ($F°_N$ and $F°_S$, defined positive into the ocean) using $A° = (F°_S - F°_N)/2$ (ref. [24]). All fluxes have been rounded to ±0.01 PgC yr^{-1}. Ocean transport and asymmetry are positive northwards. See Supplementary Section 4 for a detailed latitudinal decomposition of the LOAC fluxes (green). Burial (brown) corresponds to burial in the open ocean only.

calculations based on ocean-tracer distributions (Fig. 3). Indeed, the pre-industrial carbon loops connect not only the land and ocean through LOAC lateral transfers but also the Northern and Southern hemispheres through ocean meridional transport[63]. From the latitudinal distribution of the open-ocean fluxes (with LOAC, atmosphere and sediments), we can estimate the steady-state ocean carbon transport between the Southern and Northern hemispheres, also called the pre-industrial interhemispheric carbon asymmetry (Fig. 3). We find that both the carbon asymmetry due to the LOAC ($A°_{CO}$ = −0.18 PgC yr^{-1}) and the net carbon asymmetry ($A°$ = −0.39 PgC yr^{-1}; sum of asymmetries due to LOAC, sediment and atmospheric fluxes) agree with the independent estimates based on ocean interior tracers of ref. [24] ($A°_{\text{land-to-ocean}}$ = −0.17 PgC yr^{-1} and $A°$ = −0.43 PgC yr^{-1}). This latitudinal decomposition of pre-industrial LOAC fluxes also highlights that the atmospheric carbon uptake and burial in coastal regions (estuaries, tidal wetlands and shelves combined) of the Northern and Southern hemispheres roughly compensate each other (Fig. 3). As a result, the ocean transport asymmetry due to the LOAC scales with the asymmetry in riverine carbon exported to estuaries. Despite the uncertainties, this latitudinal decomposition will facilitate the integration into carbon budgets[3] and the interpretation of atmospheric inversions[23].

Implications for the global carbon cycle

Overlooked short-range LOAC loops

Our diagnosis of a pre-industrial open-ocean CO_2 outgassing (0.65 ± 0.30 PgC yr^{-1}) results from the superposition of one 'long range' and two 'short range' LOAC carbon loops (Figs. 1c, 2b). The long-range loop carries carbon from terra firme ecosystems and provides a global river and groundwater carbon flux to estuaries of 0.85 ± 0.20 PgC yr^{-1}, slightly higher than in previous work[8,20,21,23] but consistent with the traditional view of the long-range pre-industrial river loop. Our Perspective highlights the role of the upstream short-range loop that recycles about 80% of the carbon leached from terra firme ecosystems back to the atmosphere before reaching the river–estuary interface, minimizing the transfer of carbon from the land to the ocean (grey, Fig. 1c). Furthermore, we identify the existence of a downstream short-range loop carrying carbon from coastal vegetation (tidal wetlands and submerged vegetation) and shelves to the open ocean, which largely offsets carbon burial in these LOAC segments and contributes to the open-ocean pre-industrial outgassing (blue, Fig. 1c).

The pre-industrial uptake of 'blue carbon' (that is, uptake by tidal wetlands and submerged vegetation) estimated here is in line with recent findings[34,64,65]. Our results suggest that this downstream short-range loop was more active during pre-industrial times than today, and that the uptake of atmospheric carbon by coastal vegetation has decreased by 25–50% under the anthropogenic perturbation, consistent with previous work[34,66–69]. Mean loss rates are about 1.5–2.0% per year for saltmarshes, mangroves and seagrasses[34,69], whereas changes for macroalgae remain uncertain[35,70,71]. The processes involved possibly include the loss of salt marshes, mangroves and seagrasses by human interventions such as land reclamation and pollution, and intensified climate disturbances such as cyclones. The downstream short-range LOAC carbon loop is also fed by a small—admittedly uncertain—pre-industrial CO_2 sink on the continental shelves[39,55]. This sink is probably controlled by the strong uptake in 'cold' biologically active shelf regions[37,55], the efficient exchange[72] of land-derived and marine organic carbon across the shelf[55], and the efficient carbon uptake by submerged vegetation[35].

Evidence for a downstream short-range LOAC carbon loop feeding the pre-industrial ocean outgassing is corroborated by a recent Earth system modelling study[29], suggesting that the long-range loop explains only a pre-industrial outgassing of about 0.3 PgC yr^{-1}, so that there is a missing carbon input that we advocate comes from coastal vegetation and shelves. The existence of this additional input is consistent with observational work showing that macroalgae export about 90% of their dissolved organic carbon (DOC) to the deep ocean[35], that mangroves are the main source of terrigenous DOC in the tropical ocean[73] and that seagrasses may export up to 30% of their organic carbon across the shelf break[74]. In addition, inorganic carbon export from mangroves and tidal marshes to the ocean probably acts as a larger long-term carbon sink than burial in situ[75,76], and this pathway could be a dominant term in the tidal wetland budget[76]. The efficient lateral carbon export to the open ocean is supported by the recently evidenced short residence time of water masses on the shelves[55,72] resulting from the intense three-dimensional circulation and exchanges with the open ocean[77]. This suggests that shelves are less efficient at processing carbon than previously thought[17], thereby reinforcing the imprint of the land and LOAC carbon cycles on the open ocean.

LOAC dissociates CO_2 fluxes from storage

The anthropogenic perturbation of the LOAC has important implications for quantifying the partitioning of anthropogenic carbon storage between the land and the ocean. Part of the anthropogenic CO_2 fixed by terra firme ecosystems increases vegetation and soil carbon stocks, whereas the rest is leached into the LOAC loops. Our quantitative analysis suggests that terra firme ecosystems take up an amount of anthropogenic carbon equal to 26 ± 17% of fossil fuel emissions but store only 19 ± 17%. The rest is leached to inland waters, and subsequently outgassed back to the atmosphere via the upstream short-range carbon loop, or stored in sediments and the ocean. As a result of this leakage of anthropogenic CO_2, the storage of anthropogenic carbon in terra firme ecosystems is lower (by 0.6 ± 0.4 PgC yr^{-1}) and the storage in the open ocean is slightly higher (by 0.15 ± 0.15 PgC yr^{-1}) than estimated by IPCC assessments that do not fully take into account the transfers of anthropogenic carbon by the LOAC[2]. In addition, because of the net anthropogenic CO_2 emissions by the LOAC, the uptake of anthropogenic CO_2 by terra firme ecosystems is also larger than in the IPCC assessment. There might be a silver lining to this view of the anthropogenic CO_2 budget, as sediments and the ocean offer arguably more stable repositories than biomass and soil carbon, which are vulnerable to droughts, fires and land-use change.

The fact that the anthropogenic CO_2 flux into terra firme ecosystems is larger than the anthropogenic carbon storage (Δ'_L) implies that atmospheric inversions of CO_2 fluxes give a systematically higher CO_2 sink than the actual carbon storage change measured by inventories[78]. Our results suggest that inversions or CO_2 budgeting methods could overestimate the increase in terra firme ecosystem carbon storage by about 0.6 ± 0.4 PgC yr^{-1} ($F'_{AL} - \Delta'_L$) globally. To reconcile both approaches, a very accurate estimation of inland water evasion and burial will be needed[78].

Stewardship and management of the carbon buried in the LOAC should be considered to prevent its oxidation and the return of CO_2 to the atmosphere in the future. Blue carbon ecosystems—tidal wetlands and submerged vegetation in estuaries and continental shelves—were notable pre-industrial carbon sinks. This sink has decreased by up to 50% owing to the anthropogenic perturbation[69,71], adding to the growth rate of atmospheric CO_2. If left unprotected from, for example, sea-level rise, pollution and coastal development[79], they will further induce a positive carbon climate feedback that needs to be accounted for.

Challenges in LOAC research

Uncertainties in LOAC fluxes limit our ability to quantitatively constrain the efficiency with which the long-range and short-range carbon loops jointly transfer carbon from the land to the open ocean, as well as the decoupling between anthropogenic CO_2 uptake and carbon storage. Building on recent studies of the LOAC carbon dynamics, we discuss how these uncertainties arise from LOAC complexity and spatiotemporal variability, and identify key challenges and gaps in LOAC research.

The LOAC contribution to the carbon budget varies regionally[80–83], partly reflecting spatial heterogeneities in terrestrial productivity and connectivity between terrestrial and aquatic systems[51,84,85]. At the continental scale, inland and estuarine waters go from being a substantial flux of the land carbon budget in South America, Southeast Asia, Russia and North America to being a marginal contributor in South Asia, Australia and Africa[78]. In support of this variable role of the LOAC, previous work has shown that the fraction of terrestrial net primary production exported as DOC to inland waters is as low as 0.35% along the east coast of the United States[86] and 0.6% in Europe[87], and reaches 1.1% in the Congo Basin and 2.9% in the Amazon Basin. The DOC exports in these tropical watersheds contribute, however, only about one-quarter of the total leaching flux[54,88]. Therefore, the fraction of terrestrial net primary production exported to the inland water network as DOC and dissolved CO_2 reaches values as high as about 4% and 12% in the Amazon and Congo basins, respectively[54]. This regional variability advocates for more analyses at a fine granularity, in addition to those that have been conducted for, for example, Europe[89,90], North America[91] or boreal forests[92]. These regional-scale analyses rely on frameworks similar to our study, but do not necessarily encompass all LOAC carbon fluxes. From the aforementioned assessments, the North American one[91] includes all components of the LOAC, whereas the one for boreal forests[92] ignores the contribution of coastal vegetation and shelves, and the most up-to-date budget for Europe[90] considers only inland waters. Furthermore, the assessments of individual LOAC components are not consistent. For instance, the contribution of small streams[48] is incorporated in only certain inland water carbon budgets.

Fully integrated continental-scale assessments are limited by the lack of continuous, spatially resolved estimates for a few key LOAC fluxes, most notably the ones related to tidal wetlands and submerged vegetation, and estuarine carbon burial (Table 1). As it stands, the spatial distribution of these fluxes merely reflects the surface-area distribution of these ecosystems. Another limitation is the contribution of floodplains, which is sometimes incorporated in inland water flux estimates[83,93], but is not incorporated in other syntheses[8,19], including this one. This is an outstanding issue, given the potentially large contribution of these aquatic systems to the overall carbon budget[85,94–96] (Supplementary Section 1). A proper accounting of floodplains would require a fully integrated view of the terrestrial–aquatic interface, as shown for instance by the model study of ref. [96] for the Amazon Basin. Another issue is the lack of temporally resolved assessments of present-day LOAC fluxes, for which even a precise time frame covered by observations or model results is often not specified (Supplementary Table 2). This knowledge gap is only beginning to be addressed, for instance, by resolving the yearly and seasonal variations in the river to estuary carbon fluxes[31], the diurnal signal in CO_2 emissions from the global fluvial network[97] or the seasonality in the shelf uptake[37]. Furthermore, methodological uncertainties, such as those arising from the estimation of freshwater p_{CO_2} from carbonate equilibria, introduce biases in LOAC fluxes[98,99], and future efforts should be devoted to the resolution of these methodological shortcomings.

The incorporation of anthropogenic perturbations in regional carbon budgets with LOAC fluxes is often missing, incomplete, or provided for different periods or regional scales, leaving us without a fully integrated view covering all ecosystems, carbon pools and processes relevant to the land–ocean continuum. Existing assessments of the perturbation for the upstream short-range loop include: a human-induced increase in carbon burial fluxes tied to damming estimated globally[52] and regionally for European as well as boreal and north-temperate lakes[100,101], a minor change in the river-to-estuary flux estimated globally by models[31,102–104], and changes in inland water CO_2 evasion, which vary regionally (Supplementary Table 3). In temperate regions heavily impacted by land-use change and hydraulic management, such as the contiguous United States[105] and China[106], CO_2 evasion generally decreases, albeit more diverse changes have been observed for Asian rivers[107]. At high latitudes and in the tropics, however, aquatic CO_2 evasion increases owing to accelerated carbon turnover in response to global terrestrial CO_2 fertilization and climate change[50,51,54,108,109]. Major gaps in our understanding of the upstream loop perturbation are estimates of fluxes tied to erosion, and inland water autotrophy. Decadal changes in the tropics are also poorly constrained because observational constraints are at present lacking. Yet, because low latitudes contribute disproportionally to the inland water outgassing[47], we suggest that this region has and will continue to dominate the global perturbation, as supported by the few available predictions of future inland water outgassing (Supplementary Table 3).

Regional estimates of the anthropogenic perturbation in the downstream short-range loop are also very limited. Integrated views of present-day fluxes are only beginning to be established at scales ranging from individual systems[76] to regions and continents[91,110]. Human impacts on these highly heterogeneous systems (estuaries, tidal wetlands and so on) are manifold[79,111], which renders their quantification at the regional scale difficult. Nevertheless, mapping of estuaries, tidal wetlands and submerged vegetation distributions will help identify regions of the globe where the response of the downstream loop is the largest. For example, the continental-scale segmentation of the RECCAP (Regional Carbon Cycle Assessment and Processes) programme indicates that North America is the region that hosts about 40% of the global estuarine and 40% of the saltmarsh surface area, whereas tropical Southeast Asia and Africa host 35% and 20% of the mangrove surface area, respectively[112]. Surface-area reductions—probably the dominant driver of change since pre-industrial times for tidal wetlands and seagrasses—and other anthropogenic drivers evolved at different rates in these regions (Supplementary Table 3), and, therefore, more work is needed to assess how they impact LOAC fluxes in a spatially resolved framework. Finally, recent progress has been achieved in analysing the broad spatial patterns of the shelf anthropogenic carbon sink, both from observations and models. Data coverage is biased towards mid-to-high latitudinal shelves, for which an efficient sink of anthropogenic CO_2 was identified[113] and corroborated by model results[55,114]. In contrast, observations in Arctic and tropical shelves are few[115], and global simulations using physically resolved biogeochemical models suggest that coastal waters could be less efficient sinks for anthropogenic CO_2 in these regions[39,55,114].

Closing the knowledge gaps

Our perspective view of the LOAC helps identify a few key priority areas for further research, which together will help reduce uncertainties in the present-day total and anthropogenic carbon budgets. First, there is a critical need to gather and augment observation-based evidence to better constrain the spatiotemporal variability in present-day LOAC fluxes. In this context, coastal vegetated ecosystems and, to a lesser extent, estuaries should be prime targets in terms of spatial coverage. Of particular importance for the LOAC budget is the need for an improved quantification of the contribution of submerged vegetation—seagrasses and macroalgae—in the overall atmospheric carbon uptake and its subsequent lateral transfer to the open ocean. Better knowledge of temporal variability is also critically needed. Virtually nothing is known regarding decadal trends in LOAC fluxes and there is thus an urgent need to collect long time series of observations against which models can be evaluated. Furthermore, mechanistic studies on key LOAC processes and their potential sensitivity to anthropogenic drivers are also required to build better-informed models. As it stands, models are the only quantitative tools to constrain the LOAC perturbation over the historical period and in the future. Earth system models are only beginning to include LOAC carbon fluxes. Nevertheless, a holistic view of the dominant drivers of changes in the LOAC budget progressively emerge from regional-scale applications, paving the way for global-scale simulations in the near future. Another priority is to improve the representation of the missing processes and LOAC compartments in Earth system models and introduce a full coupling of the land and ocean carbon fluxes in global simulations. As Earth system models are typically too coarse to fully resolve the fine scale of the LOAC, advancing our understanding of LOAC science will also require integrated multiscale approaches, ranging from the local and basin scales to the continental and global scales.

Data availability

Source data for Figs. 1–3, Supplementary Figs. 1, 2 are provided with the paper. All numbers and their associated uncertainties shown in Fig. 2 are synthesized in Supplementary Table 1 and described in detail in Supplementary Sections 1, 2.

Code availability

No code was used to generate the figures in this study.

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Additional information

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Correspondence and requests for materials should be addressed to Pierre Regnier.

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