Amazon River carbon dioxide outgassing fuelled by wetlands

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River systems connect the terrestrial biosphere, the atmosphere and the ocean in the global carbon cycle¹. A recent estimate suggests that up to 3 petagrams of carbon per year could be emitted as carbon dioxide (CO₂) from global inland waters, offsetting the carbon uptake by terrestrial ecosystems². It is generally assumed that inland waters emit carbon that has been previously fixed upstream by land plant photosynthesis, then transferred to soils, and subsequently transported downstream in run-off. But at the scale of entire drainage basins, the lateral carbon fluxes carried by small rivers upstream do not account for all of the CO₂ emitted from inundated areas downstream^{3,4}. Three-quarters of the world's flooded land consists of temporary wetlands⁵, but the contribution of these productive ecosystems⁶ to the inland water carbon budget has been largely overlooked. Here we show that wetlands pump large amounts of atmospheric CO₂ into river waters in the floodplains of the central Amazon. Flooded forests and floating vegetation export large amounts of carbon to river waters and the dissolved CO₂ can be transported dozens to hundreds of kilometres downstream before being emitted. We estimate that Amazonian wetlands export half of their gross primary production to river waters as dissolved CO₂ and organic carbon, compared with only a few per cent of gross primary production exported in upland (not flooded) ecosystems^{1,7}. Moreover, we suggest that wetland carbon export is potentially large enough to account for at least the 0.21 petagrams of carbon emitted per year as CO₂ from the central Amazon River and its floodplains⁸. Global carbon budgets should explicitly address temporary or vegetated flooded areas, because these ecosystems combine high aerial primary production with large, fast carbon export, potentially supporting a substantial fraction of CO₂ evasion from inland waters.

In the global carbon cycle, rivers act not only as vectors from land to ocean but also as significant sources of CO_2 to the atmosphere. The amount of carbon that leaves the terrestrial biosphere through inland waters is much larger than the amount that ultimately reaches the ocean¹. There is a growing consensus that outgassed carbon from inland waters originates from land, where it was fixed by terrestrial plants, then recycled within soils and finally exported to surface waters^{1,2}. In water, the respiratory destruction of terrestrial organic carbon predominates over photosynthetic production^{9,10}. However, other sources such as soil and groundwater CO_2 , which are particularly significant in small streams, or wetland carbon, are necessary to balance CO_2 evasion at the global scale^{2,4}. Over the past few years, estimates of the outgassing flux have substantially increased, in parallel with the development of remote sensing tools able to capture flooding². Of the maximum 15% of global land area occupied by water, 9% is seasonally flooded⁵. Temporary and

vegetated waters are grouped under the generic term of wetlands. Wetlands are among the most productive ecosystems on Earth⁶ and behave as net carbon sinks owing to their efficient storage of carbon in waterlogged soils¹¹. Yet they have been considered atmospheric CO₂ sources in inland water inventories^{2,8}. Therefore, a better understanding of the carbon flows through the boundaries of wetlands with uplands, the atmosphere and rivers is crucial to determine an accurate continental carbon budget.

In this study, we examined the central Amazon River–floodplain system, which comprises the open waters and wetlands located in the 1.77-million-km² reference quadrant of the central Amazon basin that have been characterized in detail with Synthetic Aperture Radar (SAR) imagery¹² (Fig. 1b). Approximately 14% of this quadrant is occupied by wetlands; that is, temporary or vegetated waters in the floodplain, which are 96% inundated during high-water periods and 26% inundated during



Figure 1 | **Study area. a**, The Amazon Basin. **b**, The Central Amazon reference quadrant (1.77 million km²). **c**, The section of the Amazon River and the five floodplains investigated in this work. **d**, The Cabaliana and Janauaca floodplains on the Solimões river. **e**, The Canaçari and Miratuba floodplains on the Amazon River. **f**, The Curuai floodplain on the Amazon River.

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low-water periods. Forest occupies about 70% of the entire flooded area during high-water periods¹². These waters emit 210 \pm 60 teragrams of carbon (Tg of C) per year as CO₂, of which approximately half is from the open waters and the other half is from the wetlands⁸. We combined high-resolution field measurements of the partial pressure of carbon dioxide (p_{co_2}) with remote sensing data on the extent of water and vegetation in the floodplain and mainstream. We focused on a section approximately 800 km long located in the farthest-downstream area in the reference quadrant (Fig. 1c). This section is of particular interest because the four characteristic biotopes of the central Amazon River (flooded forest, deep channels, shallow open floodplain lakes and floating macrophytes) are all well represented, although the proportions are different from those in the reference quadrant (Extended Data Table 1). In addition, this section shows a well-defined biogeographic gradient from flooded forests that are dominant upstream to open lakes that are dominant downstream^{12,13}. During eight periods from 2007–2011, we measured the water p_{co_2} continuously in the main channels of the Amazon River and its major tributaries and in five floodplain lakes (Fig. 1d–f). Our instrumental set-up was best suited to assess extreme spatial heterogeneity, including most of the remote and shallow water bodies (Extended Data Fig. 1). Except for some clear waters, such as the Tapajós River, the p_{co_2} in the main river channels was consistent with previous reports⁸ and varied within one order of magnitude, from approximately 1,000 to 10,000 parts per million by volume (p.p.m.v.) (Extended Data Table 2). In floodplain lakes, the p_{co_2} varied by three orders of magnitude, from approximately 20 to 20,000 p.p.m.v. The



Figure 2 | **CO**₂ advection from flooded forest to open waters. a, The process of CO₂ advection could be tested using high-resolution p_{co_2} measurements performed in the Cabaliana Lake region, where waters have a single unidirectional eastward flow (from flooded forest (light grey) to open waters (dark grey and black)). b, Theoretical p_{co_2} distributions in floodplains (top graph) and river channels (bottom graph) calculated by the one-dimensional advection model (Supplementary Methods). The p_{co_2} curves start at a high p_{co_2} of 12,000 p.p.m.v. within wetlands and account for variable transport and degassing intensities. The models are labelled according to the parameters chosen: for example, model k2w40H8 indicates that the gas transfer velocity *k* is normalized to a Schmidt number of 600 and set to 2 cm h⁻¹, the water velocity *w* is set to 40 cm s⁻¹, and the water depth *H* is set to 8 m. Various settings for these three parameters corresponding to typical conditions in rivers and floodplains have been applied (Supplementary Information and Extended Data

Fig. 5). **c**, The track of the ship in Cabaliana Lake and the Solimões river channel in May 2008. Brown arrows indicate the dominant water flows into the lake. **d**, Results of the measurements obtained while underway during the cruise. The conductivity distribution shows that waters from the Solimões river channel were dominant in the western part of Cabaliana Lake but were mixed with waters from the Manacapuru River in the eastern part of the lake. The water p_{co_2} showed a clear decrease from west to east as the distance from the flooded forest increased. The solid black line shows the theoretical p_{co_2} distribution modelled by considering a normalized gas transfer velocity of 12 cm h^{-1} , a water velocity of 10 cm s^{-1} and a water depth of 5 m, as was observed during the cruise. The differences in p_{co_2} at the centre of the lake in the morning and the afternoon were attributed to photosynthesis by phytoplankton, which were abundant in the lake. extreme heterogeneity in the floodplains (Extended Data Figs 2 and 3) was related to the connections between the waters and vegetation at all spatial and temporal scales. At the centre of the open lakes, the water p_{co_2} was highest during high-water periods in the floodplains surrounded by large flooded forests, whereas the lowest values occurred in almost totally isolated lakes during low-water periods and were associated with a high phytoplankton biomass (Extended Data Table 2). There was a net downstream decline in p_{co_2} along the biogeographic gradient; the upstream forested floodplains and channels of the Solimões River always showed higher saturation values than the downstream open lakes and channels of the Amazon River. Finally, within individual lakes and during any season, p_{co_2} increased consistently from open waters to the vicinity of floating macrophytes and flooded forests.

Wetland vegetation can support the outgassing of CO₂ in the surrounding water through two mechanisms, which differ in the form of carbon transported by the waters and in the site where respiration occurs (Extended Data Fig. 4). First, litterfall and root exudation release labile organic carbon to the water^{14,15}, where the organic carbon is further decomposed; in this organic carbon pathway, heterotrophic metabolism and outgassing occur concomitantly in the open waters. Second, submerged roots and microbial respiration in wetland soils release CO_2 to the water¹⁶; this CO_2 is then transported to open areas, where outgassing occurs. We investigated the potential magnitude of this latter CO₂ pathway with a one-dimensional model that computes the distance that wetland CO2 is transported before it is emitted (Extended Data Fig. 5). We found that the water movement is fast enough relative to gas exchange to maintain high supersaturation over dozens to hundreds of kilometres without requiring heterotrophic metabolism. The ability of water masses to export wetland CO₂ depends on their velocity, depth, vertical mixing and the gas transfer coefficient k. In a river channel that is 30 m deep with a typical k value⁸ of 15 cm h^{-1} and a water current of 150 cm s^{-1} , only 18% of the CO₂ has been evaded 150 km downstream of the point source (the rest is still dissolved in the river water and is transported further downstream). In contrast, in an open floodplain lake that is 2 m deep with a typical thermally enhanced k value¹⁷ of 12 cm h⁻¹ and a water current of 20 cm s⁻¹, 90% of the wetland CO2 is outgassed 20 km downstream. Our model satisfactorily mimics the spatial p_{co_2} gradient observed in May 2008 along a 20-km transect in Cabaliana Lake, where the water current flows permanently eastward after passing over a large flooded forest area (Fig. 2d).

The CO₂ outgassing fluxes in individual lakes increase with the percentage of the floodplain covered by vegetation (Fig. 3). Lakes that were almost isolated from wetlands had nearly neutral daily CO2 fluxes, whereas lakes connected to large wetlands showed the highest outgassing rates. This relationship was valid in three different seasons for a given lake, which is consistent with the flood pulse concept¹⁸, and also during the same season at different lakes because the vegetation cover decreases downstream. Floodplain vegetation that performs aerial photosynthesis thus drives CO₂ outgassing. The CO₂ pathway apparently dominates in floodplains (Fig. 2), but it also occurs in river channels, as indicated by the strong anomalies in the stoichiometry between dissolved CO₂ and oxygen concentrations. Indeed, respiration of inundated emergent vegetation can release dissolved CO₂ to waters through their roots with no concomitant drawdown of dissolved oxygen, which is supplied from the atmosphere through the leaves^{16,19}. Net heterotrophy in lakes and main channels frequently accounts for less than 20% of the CO₂ outgassing flux^{19,20}, the majority of which is supported by wetlands CO2 from upstream areas (Supplementary Information). Furthermore, the composition of particulate organic matter reveals a transfer of algal- and macrophyte-derived organic carbon from the floodplains to the river channel^{21,22}, and the isotopic composition of respired CO₂ in channels shows seasonally variable contributions from C3 plants, C4 plants and algal material^{20,23}, all of which are well represented in the floodplains. Flooded forest is also a potential major source of biodegradable macromolecules in the Amazon River²⁴. Finally, both the organic carbon and CO₂ pathways are consistent with



Figure 3 | **Vegetation-mediated control of CO₂ outgassing in floodplain lakes.** Symbols correspond to seasons, and colours correspond to sites. CO₂ degassing was computed from the measured p_{co_2} and an average gas transfer velocity and was averaged over the surface area of the lake. Vertical bars indicate two standard deviations induced by the spatial and diurnal variation within each lake at a given season. The surface areas of the open lakes and the surrounding flooded and floating vegetation were obtained from SAR images taken during three seasons (Supplementary Methods). The thick dotted line represents the linear regression line ($r^2 = 0.90$, P < 0.0001); the thin dotted lines delineate the 95% confidence bands of the regression.

the very young ¹⁴C age of the outgassed CO₂, compared with the older terrestrial organic carbon transported by the Amazon River²⁵.

Published metabolic rates^{14-16,25,26} and the extent of vegetation¹² in the floodplains of the central Amazon reference quadrant allow some quantities of carbon supplied by wetlands to the waters to be computed. Flooded forests and floating macrophytes provide, through litterfall and submerged root respiration, a total of -305 ± 120 Tg of C per year of atmospheric carbon to the waters (Extended Data Table 3). This probably conservative estimate is not significantly different from the CO₂ outgassing flux of $+210 \pm 60$ Tg of C per year⁸. Central Amazonian waters thus receive at least as much carbon from semiaquatic plants as they emit to the atmosphere, and the CO₂ net ecosystem exchange of the river system as a whole, including wetlands and open waters, should be nearly neutral. This is consistent with airborne observations over the Amazon, which do not reveal a large unidirectional CO2 outgassing flux from wetland and river surfaces compared to uplands²⁷. Water inside and downstream of a wetland functions similarly to the way soil functions in a forest, in that it rapidly returns a large fraction of the carbon fixed by photosynthesis to the atmosphere. Unlike in the headwaters³, in the central Amazon, the contribution of strictly upland terrestrial carbon to CO2 outgassing is potentially minor compared to the wetland carbon contribution. Unlike terrestrial landscapes that export less than 2% of their gross primary production to inland waters^{1,7}, Amazonian wetlands export half of their gross primary production to waters (Extended Data Table 3). Although more quantitative information is needed on the global distribution of wetland primary productivity and carbon export, the available information²⁸

suggests that wetlands support a large percentage of inland water CO₂ evasion at the global scale.

METHODS SUMMARY

Continuous measurements (once per minute) were performed on eight cruises in the channels and floodplain lakes of the Amazon on a ship equipped for this purpose. River water was continuously pumped from about 50 cm below the surface and delivered to the different equipment and sensors. Water p_{co} , was measured using a marble-type equilibrator²⁹ (see online Methods) connected to an infrared gas analyser, which was calibrated before and after each cruise. The response time was estimated to be 3 min. The water temperature, conductivity and turbidity were measured in an overflowing bucket using a multiprobe, which was calibrated every 10 days. Fluorescence was measured using a BBE Moldaenke Fluoroprobe. The position was recorded using a global positioning system (GPS). During low-water periods, shallow and remote lakes were surveyed using a small boat and a 12-V version of the measurement set-up. The total number of geo-referenced measurements was 45,786. The water and flooded vegetation surface areas were derived from SAR data acquired using the PALSAR space-borne sensor (see Supplementary Methods). Within the five floodplains sampled and for the three campaigns at high, intermediate and low water, the flooded areas were divided among open water, flooded forest and floating vegetation.

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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- 1. Cole, J. J. *et al.* Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10**, 172–185 (2007).
- Aufdenkampe, A. K. *et al.* Rivers key to coupling biogeochemical cycles between land, oceans and atmosphere. *Front. Ecol. Environ.* 9, 53–60 (2011).
- Davidson, E. A., Figueiredo, R. O., Markewitz, D. & Aufdenkampe, A. K. Dissolved CO₂ in small catchment streams of eastern Amazonia: a minor pathway of terrestrial carbon loss. *J. Geophys. Res.* **115**, G04005 (2010).
- Butman, D. & Raymond, P. A. Significant efflux of carbon dioxide from streams and rivers in the United States. *Nature Geosci.* 4, 839–842 (2011).
- Downing, J. A. Global limnology: up-scaling aquatic services and processes to planet Earth. Verh. Int. Verein. Limnol. 30, 1149–1166 (2009).
- Whittaker, R. H. & Likens, G. E. in *Primary Productivity of the Biosphere* (eds Lieth, H. & Whittaker, R. H.) 305–328 (Springer, 1975).
- Schulze, E. D. et al. The European carbon balance. Part 4: integration of carbon and other trace-gas fluxes. Glob. Change Biol. 16, 1451–1469 (2010).
- Richey, J. E., Melack, J. M., Aufdenkampe, A. K., Ballester, V. M. & Hess, L. L. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO₂. *Nature* **416**, 617–620 (2002).
- Battin, T. J. et al. Biophysical controls on organic carbon fluxes in fluvial networks. Nature Geosci. 1, 95–100 (2008).
- Duarte, C. M. & Prairie, Y. T. Prevalence of heterotrophy and atmospheric CO₂ emissions from aquatic ecosystems. *Ecosystems* 8, 862–870 (2005).
- Kayranli, B., Scholz, M., Mustafa, A. & Hedmark, A. Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30, 111–124 (2010).
- Hess, L. L., Melack, J. M., Novo, E. M., Barbosa, C. C. F. & Gastil, M. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. *Remote Sens. Environ.* 87, 404–428 (2003).
- Maurice-Bourgoin, L. *et al.* Temporal dynamics of water and sediment exchanges between the Curuaí floodplain and the Amazon River, Brazil. *J. Hydrol.* 335, 140–156 (2007).

- Schöngart, J., Wittmann, F. & Worbes, M. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 347–388 (Springer, 2010).
- Engle, D. L., Melack, J. M., Doyle, R. D. & Fisher, T. R. High rates of net primary production and turnover of floating grasses on the Amazon floodplain: implications for aquatic respiration and regional CO₂ flux. *Glob. Change Biol.* 14, 369–381 (2008).
- Hamilton, S. K., Sippel, S. J. & Melack, J. M. Oxygen depletion and carbon dioxide and methane production in waters of the Pantanal wetland of Brazil. *Biogeochemistry* **30**, 115–141 (1995).
- Polsenaere, P. et al. Thermal enhancement of gas transfer velocity of CO₂ in an Amazon floodplain lake revealed by eddy covariance. *Geophys. Res. Lett.* 40, 1734–1740 (2013).
- Junk, W. J., Bayley, P. B. & Sparks, R. E. The flood pulse concept in river–floodplain systems. in *Proc. Int. Large River Symp.* (ed. Dodge, D. P.) *Can. J. Fish. Aquat. Sci. Spec. Publ.* **106**, 110–127 (1989).
- Devol, A. H. et al. Seasonal variation in chemical distributions in the Amazon (Solimões) River: a multiyear time series. *Glob. Biogeochem. Cycles* 9, 307–328 (1995).
- Ellis, E. E. et al. Factors controlling water-column respiration in rivers of the central and southwestern Amazon Basin. *Limnol. Oceanogr.* 57, 527–540 (2012).
- Mortillaro, J. M. et al. Particulate organic matter distribution along the Lower Amazon River: addressing aquatic ecology concepts using fatty acids. PLoS ONE 7, e46141 (2012).
- Moreira-Turcq, P. et al. Seasonal variability in concentration, composition, age and fluxes of particulate organic carbon exchanged between the floodplain and Amazon River. Glob. Biogeochem. Cycles 27, 119–130 (2013).
- Quay, P. D. et al. Carbon cycling in the Amazon River: implications from the ¹³C compositions of particles and solutes. *Limnol. Oceanogr.* 37, 857–871 (1992).
- Ward, N. D. et al. Degradation of terrestrially derived macromolecules in the Amazon River. Nature Geosci. 6, 530–533 (2013).
- Mayorga, E. et al. Young organic matter as a source of carbon dioxide outgassing from Amazonian rivers. Nature 436, 538–541 (2005).
- Worbes, M. in The Central Amazon Floodplain: Ecology of a Pulsing System (ed. Junk, W. J.) 223–265 (Springer, 1997).
- Lloyd, J. et al. An airborne regional carbon balance of Central Amazonia. Biogeosciences 4, 759–768 (2007).
- AseImann, I. & Crutzen, P. J. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. J. Atmos. Chem. 8, 307–358 (1989).
- Abril, G., Richard, S. & Guérin, F. In situ measurements of dissolved gases (CO₂ and CH₄) in a wide range of concentrations in a tropical reservoir using an equilibrator. *Sci. Total Environ.* **354**, 246–251 (2006).

Supplementary Information is available in the online version of the paper.

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Author Contributions G.A., J.-M.M., P.M.-T., L.F.A., T.M. and M.F.B. conceived and designed the study. G.A. coordinated project and fieldwork. G.A., J.D., M.F.L.d.S. and N.S. performed the p_{co_2} measurements. J.-M.M. and E.L.S. analysed the remote sensing data. L.F.A. measured Chl a and fluorescence. L.V. and F.R. measured respiration. All authors contributed to the interpretation of the data. G.A. wrote the manuscript, J.-M.M., L.F.A. and F.R. contributed to the interpretation of the Mata. G.A. wrote the manuscript, J.-M.M., N.S. and M.F.B. commented on the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to G.A. (g.abril@epoc.u-bordeaux1.fr).

LETTER RESEARCH

METHODS

Study site and remote sensing. The central Amazon river-floodplain system is defined as the waters and wetlands located in the 1.77-million-km² reference quadrant of the central Amazon basin that has been characterized in detail using SAR imagery¹² (referred to as 'quadrant b'; Fig. 1b). We focused our fieldwork and remote sensing analysis on a secondary 0.288-million-km² quadrant inside the eastern limit of quadrant b, which was referred to as 'quadrant c' (Fig. 1c). Quadrant c is located in the downstream section of the Amazon River in Brazil, from the city of Manacapuru on the Solimões River upstream of its confluence with the Negro River to the Amazon River in front of the city of Santarem at the confluence of the Amazon with the Tapajós River (Fig. 1c). In this region, waters flowing from the Andes are rich in suspended matter and nutrients, have the highest conductivity and are termed 'white'30. Waters draining the primarily lowland podzol soils are rich in dissolved organic matter and intensely coloured by humic material, have low conductivity and are called 'black'. Finally, relatively transparent waters draining the Precambrian Shields are poor in organic and inorganic material, have low-to-intermediate conductivity and are called 'clear'. The main tributaries of the Amazon River sampled were the Solimões and Madeira (white), the Manacapuru and Negro (black), and the Urubu and Tapajós (clear). The Amazon River flood is characterized by relatively low interannual variability but strong water level differences between the low-water (October-November) and high-water stages (May-June). The annual water level within the main stream reaches approximately 8 m near Santarem station and up to 12 m at Manacapuru station on the Solimões River. The floodplains are connected to the river's main stem by a complex system of channels (called Paranás) that vary as a function of the flood level³¹. Spilling over the riverbanks usually occurs during the peak inundation phase^{31,32}. These environments participate significantly in the transfer of water and matter from the Andes to the Atlantic Ocean; approximately 5% of the annual water discharge of the Amazon is estimated to travel through the floodplain33.

Five floodplain systems were selected for fieldwork and remote sensing (Fig. 1 and Extended Data Table 1c). Farthest upstream, the Cabaliana and Janauacá floodplains receive large inputs of waters from the Solimões River and are surrounded by large areas of flooded forest (Fig. 1c, d). In the Cabaliana, the conductivity is similar to that of the Solimões (70–100 μ S cm⁻¹), but the turbidity is much lower because of sediment retention in the flooded forest that acts as a filter. In the Janauacá, the conductivity is slightly lower (33-70 µS cm⁻¹) because of clear water contributed by local drainage. Downstream of the Amazon-Madeira confluence, the Canaçari and Miratuba mainly receive waters from the flooding of the Amazon and Madeira rivers, respectively (Fig. 1e). Miratuba Lake is well surrounded by flooded forest and is almost completely dry at low water (Fig. 1e). The Canaçari is a very homogeneous lake with approximately the same depth all over, and is disconnected from flooded forest most of the year. The Canaçari receives white waters from the Amazon and occasionally clear waters from the Urubu River that drains the northern local basin. Finally, in the farthest-downstream part of our study area, the Várzea of Curuai is composed of more than 30 interconnected lakes temporarily or permanently connected to the Amazon main stem by small channels³⁴ (Fig. 1f).

We used L-band SAR radar remote sensing images to monitor the extent of flooding at different stages in the five floodplains from 2007 to 2010. Several studies using a time series of L-band SAR satellite images reported excellent classification results in the quadrant under study^{12,35,36}. The mapping accuracy was shown to increase with the number of images included in the time series (up to eight images³⁶), which allowed the flood dynamics to be retrieved with an accuracy higher than 80%. The satellite images were acquired by the PALSAR space-borne sensor in wide-beam mode with 250-km-wide images and a resolution of 100 m. The PALSAR resolution allowed us to quantify the area of large lakes and flooded forest, but not small channels, in the floodplain. Because the area studied in this work extends over more than 800 km from east to west, five PALSAR wide-beam frames and eight images per frame were considered. The water-level range corresponding to the image acquisition agrees well with the maximum water level at the Obidos water gauge on the Amazon River, from 1.29 m to 8.56 m, and at the Manacapuru water gauge on the Solimões River, from 8.41 m to 20.43 m.

Flood maps were derived using an algorithm that allows the retrieval of the flood dynamics and the primary landscape units³⁶ with an accuracy better than 80% considering all landscape units and better than 90% for the forested areas. All images were co-registered and ground-corrected using the Shuttle Radar Topography Mission digital elevation model (http://srtm.csi.cgiar.org/) and georeferenced with MapReady software, available from the Alaska Satellite Facility. Speckle reduction was achieved by both temporal and spatial filtering using a specific algorithm for SAR image time series³⁷ and the Lee-Sigma filter³⁸. Filtered multitemporal images were segmented into homogeneous regions using the multi-resolution segmentation algorithm of the eCognition software (http://www.ecognition.com/). The scale and

shape parameter values that control the merging procedure were tested and applied uniformly to preserve the main floodplain landscape units. Then, a parallelepiped classifier was used to attribute a status regarding flooding to each segment: never flooded (NF), occasionally flooded (OF), and permanently flooded (PF). The classifier also provides the general type of land cover: open water, bare soil, savannah, forest. Combining all the images and scanning the time series from the lowest water level to the highest water level allowed the flooded surface areas to be retrieved at the minimum, maximum and intermediate flood levels for each landscape unit. The area flooded was assessed for each floodplain system to provide the variation in the areas of the flooded forests, the floating vegetation that emerges at the water surface, and the open waters of the floodplain lakes.

In quadrant c (Fig. 1), 31,435 km² are seasonally flooded, of which 37.7% is occupied by floodable forests, 10.1% by floating macrophytes, 17.6% is occupied by permanent river channels, 13.1% is permanent open lakes in the floodplain, and 21.1% is temporary open waters in the floodplain. Compared to the central Amazon reference quadrant (quadrant b in Fig. 1), open waters in the floodplain comprise more of our study area (Extended Data Table 1a, b). This sampling area thus provides a large array of floodplain conditions, from predominantly flooded forest floodplains, as in most of quadrant b, to open lakes that are more disconnected from wetland vegetation. There is a clear gradient in floodplain vegetation along this river section, beginning from the dominant flooded-forest coverage upstream on the Solimões River, which represents up to 75% of the total flooded area, and ending with the open-lake coverage dominant downstream on the Amazon River¹³, in which only 10% of the floodplain is occupied by forest. The Curuai floodplain (2,333 km²) and the Cabaliana floodplain (1,822 km²) are the largest wetlands, whereas the Janauaca floodplain extends over only 216 km² at high water. The five floodplains studied show a downstream-decreasing trend of floodedforest coverage (Extended Data Table 1c).

Field work. The CARBAMA database is the largest data set of water p_{co_2} and ancillary parameters (temperature, conductivity, dissolved oxygen, fluorescence and turbidity) recorded in a large tropical river–floodplain system. The total number of p_{co_2} measurements obtained was 47,786 (Extended Data Table 2), which, with a frequency of one measurement per minute, represents 32 days of continuous measurements while underway in the Amazon River, tributaries and five floodplain lakes. The eight cruises were distributed along the Amazon hydrograph to sample low water (November 2007, October 2008 and October 2009), rising water (January 2007 and January 2011), high water (May 2008 and June 2009), and falling water (August–September 2010).

The cruises consisted of continuous measurements while underway (Extended Data Fig. 1), as well as discrete water sampling for chlorophyll a (Chl a) analysis. The continuous measurement system consisted of a circuit of river water installed in a typical Amazonian ship, with a bypass at the engine cooling water inlet located at a depth of about 40 cm. This water flowed gravimetrically into a five-litre bucket located in the vessel's hold that contained a submerged 220-V pump that raised water 5 m at a rate of 8 litres per minute. The water was allowed to overflow the bucket, and the inflow was optimized to exclude gas bubbles and reduce water residence time in the bucket, even when the ship was sailing at maximum speed, around $20 \,\mathrm{km} \,\mathrm{h}^{-1}$. The pump pushed water from the ship's hold to a one-litre bucket, which was also continuously overflowing, located on the side of the boat. The water volume in this second bucket at deck level was minimized because it contained an Yellow Spring Instruments (YSI) multisensory probe that recorded ancillary parameters and a 12-V submerged pump that delivered water at a constant flow to the equilibrator (about one litre per minute) and to a closed circuit passing through a BBE-Moldaenke fluorimeter (2-3 litres per minute). There was a height difference of approximately 2 m between the first bucket in the hold and the container with the sensors; the equilibrator was placed approximately 1 m above the deck floor. By adding salt to the first bucket and measuring the conductivity in the second bucket, we determined the maximum water residence time to be 2.5 min. Comparison with direct measurements in the river revealed that the water temperature increased by no more than 0.5 °C in the circuit. There was no notable difference in the oxygen concentrations measured with the same optode inside and outside the water circuit. A Garmin global positioning system recorded the position every minute. The instrumental set-up was also converted to a 12-V version that could be used on small boats able to enter large, remote shallow lakes inaccessible to vessels at low water levels (Extended Data Fig. 1). In this case, the 12-V pump and the YSI probes were submerged directly from the side of the boat.

In a marble-type equilibrator, water flows from the top to the bottom (0.7–1 litre per minute), while a constant volume of air (about 0.5 litres per minute) flows from the bottom to the top; surface gas exchange is optimized around the marbles, and the volumes of water and air are minimized by the presence of the marbles. p_{co_2} in the air circuit tends rapidly to equilibrate to the water p_{co_2} value^{29,39}. The pump delivers air from the top of the equilibrator. The air from the equilibrator passes

first through a water trap, then through a desiccation tube (10 cm long, 2 cm in diameter) containing a desiccant (Drierite), then through the air pump, the gas analyser, a gas flow meter, and finally, back to the bottom of the equilibrator^{29,39}. All tubes are made of Tygon or polytetrafluoroethylene (both gas-tight plastics) and the connections are also gas-tight. If the equilibrator is bypassed, the air circuit loses less than 1 p.p.m.v. of CO₂ per minute at about 3,000 p.p.m.v. The drying tube was intentionally small to limit the effect of the interaction of Drierite with CO₂ (adsorption/desorption), which increases the response time of the system⁴⁰. We changed the Drierite in the tube every day and flushed the system with atmosphere for half an hour before measurements. The Drierite was regularly regenerated on board using a hairdryer. In the laboratory, before and after each cruise, the LICOR gas analyser was calibrated in the 0-20,000 p.p.m.v. range by nitrogen passing through soda lime to calibrate the zero and by a gas standard certified at 5,000 \pm 30 p.p.m.v. (Air Liquide) to calibrate the span. The linearity was checked using another standard at 500 ± 8 p.p.m.v. During cruises, as advised by the manufacturer, we regularly checked the zero of the instrument by passing air over soda lime, and we reset the zero when the deviation was more than ± 10 p.p.m.v. After the cruise, the maximum deviation with the 5,000 p.p.m.v. standard was \pm 90 p.p.m.v., that is, less than 2%.

The YSI multiprobe measured the water temperature, conductivity, dissolved oxygen, pH and turbidity. We applied the calibration procedures recommended by the manufacturer. Calibration was performed at the beginning of each cruise and at the middle of cruises that lasted more than 10 days. The BBE-Moldaenke Fluoroprobe is a submersible spectral fluorometer that allows continuous recording of total in vivo fluorescence and discriminates among the main spectral groups of phytoplankton (that is, diatoms and dinoflagellates, blue-green algae, cryptophytes and green algae) on the basis of the relative fluorescence intensity of Chl a at 680 nm (because of the Photosystem II core pigments) after sequential excitation of the antenna and accessory pigments by five light-emitting diodes at 450 nm, 525 nm, 570 nm, 590 nm and 610 nm (refs 41, 42). The Chl a concentration was measured in two to three discrete water samples collected in each floodplain and river. The samples were filtered through Whatman 47-mm GF/F glass-fibre filters, stored frozen (in liquid nitrogen) until the return to the laboratory, and then extracted in 90% acetone overnight. Fluorescence measurements were performed using a Turner Designs 10-AU fluorometer before and after acidification with hydrochloric acid43.

Respiration in river and lake surface waters was measured with 24-h incubations. Fifteen calibrated 60-ml Biochemical Oxygen Demand (BOD) bottles were filled with a well-homogenized and re-oxygenated (about 80% saturated) water sample. Five bottles were used for time zero, and ten were incubated in the dark at the temperature of the river water. Five bottles were fixed at 12 h, and the last five bottles were fixed at 24 h. In floodplain lakes, where phytoplanktonic production may occur, oxygen production in the light was measured by applying the same procedure, except that the samples were incubated on-deck at incident light, in a bucket thermostated with lake water. The oxygen concentrations were measured onboard the vessel with Winkler titration. Respiration and production were calculated from the linear regression of the oxygen concentration as a function of time; the correlation coefficient was greater than 0.90. The respiration rates were multiplied by the water depth to estimate the depth-integrated respiration, with an assumption of vertical homogeneity²⁰. In the case of turbid river channels, where water depth is high and light penetration is very low, we assume that phytoplanktonic production does not occur and that the net heterotrophic metabolism equals the depth-integrated respiration²⁰. With floodplain lakes, we made this assumption only for the high-water period, when phytoplankton biomass was low.

Flux computation. The air-water flux of CO_2 was calculated from the water temperature and p_{co} , according to:

$F(CO_2) = k\alpha \Delta p_{co_2}$

where k is the gas transfer velocity of CO₂ (in units of cm h⁻¹ or m s⁻¹), α is the solubility coefficient of CO₂ (in mol kg⁻¹ atm⁻¹), and Δp_{co_2} is the air–water gradient of p_{co_2} (in atm). The atmospheric p_{co_2} measured every day at the beginning and end of the equilibrator records was 402 ± 24 p.p.m.v. and did not significantly change with the seasons, between morning and evening, or between lakes and channel sites; this average atmospheric value was used for all flux calculations, and Δp_{co_2} was largely driven by fluctuation in the water p_{co_2} . We used the polynomial formulation that gives the solubility coefficient α as a function of water temperature⁴⁴. The gas transfer velocity k was calculated from the gas transfer velocity normalized to a Schmidt number of 600 that corresponds to CO₂ at 20 °C (ref. 45):

 $k = k_{600} (600/\text{Sc})^n$

where k_{600} is the normalized gas transfer velocity, Sc is the Schmidt number of a given gas at a given temperature⁴⁶, and *n* equals 2/3 in floodplain lakes and 0.5 in the more turbulent river channels⁴⁷.

Despite numerous studies on the subject, important uncertainty still remains regarding the parameterization of k_{600} in lakes, particularly in Amazon floodplain lakes. The widely used parameterizations based on wind speed^{47,48} do not account for other drivers (or inhibitors) of turbulence at the water-air interface, such as the friction of the current on the bottom^{49,50}, evaporative heat gain and loss and the associated buoyancy fluxes^{51,52}, or the release of organic molecules that might behave as surfactants⁵³ by wetland vegetation⁵⁴. Recently, several authors^{52,55} have hypothesized that the k_{600} value of 2.7 cm h⁻¹ used in previous estimates of CO₂ outgassing from the Amazon floodplains⁸ is underestimated by a factor of four to five. Experimental data of k_{600} based on eddy covariance¹⁷ confirm this underestimation exclusively in open lakes under high light incidence and heat flux; on the contrary, the k_{600} values may be much lower within a flooded forest, where no k_{600} data are available, where waters are protected from heat and wind by the canopy, where organic surfactants may be particularly abundant⁵⁴ and which represent 70% of the floodable area in the Amazon¹². Because of the paucity of reliable information on k_{600} in floodplains, we provide average CO₂ fluxes from floodplains based on the value of 2.7 cm h^{-1} , and this value has the advantage of allowing quantitative comparison with the CO₂ fluxes reported previously⁸. When a more precise k_{600} value seems necessary, for instance, in the quantitative comparison between respiration rates and outgassing fluxes, or for the calculation of the distance of wetland CO₂ export, we apply the Cole and Caraco relationship⁴⁸ to the wind speeds at 10 m measured on the roof of the vessel at stations during the cruise. For the river channels, we use the value of 8.2 cm h^{-1} used by Richey *et al.*⁸ and based on direct measurements of O2 and ²²²Rn accumulation in free-floating chambers^{56,57}. In all cases, the chosen k_{600} values are specified in the text. It is worthwhile to note that none of the main conclusions of our paper is affected by the choice of the k_{600} value.

The revised carbon budget was computed at the scale of quadrant b, multiplying published metabolic rates^{14-16,26,58-70} by their respective surface area (Extended Data Table 3).

- Sioli, H. Hydrochemistry and geology in the Brazilian Amazon region. *Amazoniana* 3, 267–277 (1968).
- Mertes, L. A. K., Dunne, T. & Martinelli, L. A. Channel–floodplain geomorphology along the Solimões-Amazon River, Brazil. *Geol. Soc. Am. Bull.* 108, 1089–1107 (1996).
- Trigg, M. A., Bates, P. D., Wilson, M. D., Schumann, G. & Baugh, C. Floodplain channel morphology and networks of the middle Amazon River. *Wat. Resour. Res.* 48, W10504 (2012).
- Alsdorf, D., Han, S.-C., Bates, P. & Melack, J. Seasonal water storage on the Amazon floodplain measured from satellites. *Remote Sens. Environ.* **114**, 2448–2456 (2010).
- Bonnet, M. P. et al. Floodplain hydrology in an Amazon floodplain lake (Lago Grande de Curuai). J. Hydrol. 349, 18–30 (2008).
- Rosenqvist, A., Forsberg, B. R., Pimentel, T., Rauste, Y. A. & Richey, J. E. The use of spaceborne radar to model inundation patterns and trace gas emissions in the central Amazon floodplain. *Int. J. Remote Sens.* 23, 1303–1328 (2002).
- Martinez, J. M. & Le Toan, T. Mapping of flood dynamics and spatial distribution of vegetation in the Amazon floodplain using multitemporal SAR data. *Remote Sens. Environ.* **108**, 209–223 (2007).
- Quegan, S., Le Toan, T., Yu, J. J., Ribbes, F. & Floury, N. Multitemporal ERS SAR analysis applied to forest monitoring. *IEEE Trans. Geosci. Rem. Sens.* 38, 741–753 (2000).
- Lee, J. S. A simple speckle smoothing algorithm for synthetic aperture radar images. *IEEE Trans. Syst. Man Cybern.* 13, 85–89 (1983).
- Frankignoulle, M., Borges, A. & Biondo, R. A new design of equilibrator to monitor carbon dioxide in highly dynamic and turbid environments. *Water Res.* 35, 1344–1347 (2001).
- Santos, I. R., Maher, D. T. & Eyre, B. D. Coupling automated radon and carbon dioxide measurements in coastal waters. *Environ. Sci. Technol.* 46, 7685–7691 (2012).
- Beutler, M. et al. A fluorometric method for the differentiation of algal populations in vivo and in situ. Photosynth. Res. 72, 39–53 (2002).
- MacIntyre, H. L., Lawrenz, E. & Richardson, T. L. in *Chlorophyll a Fluorescence in Aquatic Sciences: Methods and Applications* (eds Suggett, D. J. *et al.*) 129–169 (Developments in Applied Phycology 4, Springer, 2010).
- Lorenzen, C. J. Determination of chlorophyll and pheopigments: spectrophotometric equations. *Limnol. Oceanogr.* 12, 343–346 (1967).
- Weiss, R. F. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Mar. Chem. 2, 203–215 (1974).
- Jähne, B. et al. On parameters influencing air-water exchange. J. Geophys. Res. 92, 1937–1949 (1987).
- Wanninkhof, R. Relationship between gas exchange and wind speed over the ocean. J. Geophys. Res. 97, 7373–7382 (1992).
- Guérin, F. et al. Gas transfer velocities of CO₂ and CH₄ in a tropical reservoir and its river downstream. J. Mar. Syst. 66, 161–172 (2007).



- Cole, J. J. & Caraco, N. F. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF₆. *Limnol. Oceanogr.* 43, 647–656 (1998).
- Zappa, C. J. et al. Environmental turbulent mixing controls on air-water gas exchange in marine and aquatic systems. *Geophys. Res. Lett.* 34, http://dx.doi.org/ 10.1029/2006GL028790 (2007).
- Abril, G., Commarieu, M. V., Sottolichio, A., Bretel, P. & Guérin, F. Turbidity limits gas exchange in a large macrotidal estuary. *Estuar. Coast. Shelf Sci.* 83, 342–348 (2009).
- MacIntyre, S. *et al.* Buoyancy flux, turbulence, and the gas transfer coefficient in a stratified lake. *Geophys. Res. Lett.* **37**, L24604 (2010).
- Rudorff, C. M., Melack, J. M., MacIntyre, S., Barbosa, Ć. C. F. & Novo, E. M. L. M. Seasonal and spatial variability of CO₂ emission from a large floodplain lake in the lower Amazon. J. Geophys. Res. **116**, G04007 (2011).
- Salter, M. E. et al. Impact of an artificial surfactant release on air-sea gas fluxes during deep ocean gas exchange experiment II. J. Geophys. Res. 116, C11016 (2011).
- Parolin, P. *et al.* Central Amazon floodplain forests: tree survival in a pulsing system. *Bot. Rev.* **70**, 357–380 (2004).
- Richey, J. E., Krusche, A. V., Johnson, M. S., da Cunha, H. B. & Ballester, M. V. in Amazonia and Global Change (eds Keller, M. et al.) 489–504 (Geophys. Monogr. Ser. 186, AGU, 2009).
- Devol, A. H., Quay, P. D., Richey, J. E. & Martinelli, L. A. The role of gas exchange in the inorganic carbon, oxygen and ²²²Rn budgets of the Amazon River. *Limnol. Oceanogr.* 32, 235–248 (1987).
- Alin, S. R. et al. Physical controls on carbon dioxide transfer velocity and flux in lowgradient river systems and implications for regional carbon budgets. J. Geophys. Res. 116, G01009 (2011).
- 58. Junk, W. J. & Piedade, M. T. F. Biomass and primary production of herbaceous
- plant communities in the Amazon floodplain. *Hydrobiology* 263, 155–162 (1993).
 59. Malhi, Y. & Grace, J. Tropical forests and atmospheric carbon dioxide. *Trees* 15, 332–337 (2000).

- Horna, V., Zimmermann, R., Müller, E. & Parolin, P. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 223–241 (Springer, 2010).
- Worbes, M. in The Central Amazon Floodplain: Ecology of a Pulsing System (ed Junk, W. J.) 223–265 (Springer, 1997).
- Saatchi, S. S., Houghton, R. A., Dos Santos Avala, R. C., Soares, J. V. & Yu, Y. Distribution of aboveground live biomass in the Amazon basin. *Glob. Change Biol.* 13, 816–837 (2007).
- Meyer, U., Junk, W. J. & Linck, C. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 163–178 (Springer, 2010).
- Parolin, P., Wittmann, F. & Schöngart, J. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 105–126 (Springer, 2010).
- Piedade, M. T. F., Ferreira, C. S., de Oliveira Wittmann, A., Buckeridge, M. & Parolin, P. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 127–139 (Springer, 2010).
- Junk, W. J., Piedade, M. T. F., Parolin, P., Wittmann, F. & Schöngart, J. in Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management (eds Junk, W. J. et al.) 511–540 (Springer, 2010).
- Morison, J. I. L. *et al.* Very high productivity of the C4 aquatic grass *Echinocloa polystachya* in the Amazon floodplain confirmed by net ecosystem CO₂ flux measurements. *Oecologia* **125**, 400–411 (2000).
- Costa, M. Estimate of net primary productivity of aquatic vegetation of the Amazon floodplain using Radarsat and JERS-1. Int. J. Remote Sens. 26, 4527–4536 (2005).
- 69. Melack, J. M. et al. in Amazonia and Global Change (eds Keller, M. et al.) 525–542 (Geophys. Monogr. Ser. 186, AGU, 2009).
- Moreira-Turcq, P. et al. Carbon sedimentation at Lago Grande de Curuai, a floodplain lake in the low Amazon region: insights into sedimentation rates. Palaeogeogr. Palaeoclim. Palaeoecol. 214, 27–40 (2004).





Extended Data Figure 1 | Instrumental set-up for continuous measurement of p_{co_2} and ancillary parameters while underway in the Amazon River and

floodplain lakes. Side-view diagrams of both boats are illustrated with photos of the equipment. See detailed description in the Methods.

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lakes primarily originates from the flooding of the Solimões and Amazon rivers with modest contribution from local drainage. **c**, The distribution of water p_{co_2} at maximum flooding shows the predominance of supersaturation with a net decrease downstream, in parallel with the extent of vegetation in the floodplains (percentage of total floodplain area is given in parentheses for each lake).



Extended Data Figure 3 | **Continuous record of water** p_{co_2} **in the Amazon River, its tributaries and floodplain lakes during the low water of October 2009. a**, Track of the ship in the main stem (brown), floodplain lakes (green), and major tributaries (blue). Land occupation derived from SAR data is shown as flooded forest (light grey), temporary open waters (dark grey) and permanent open waters (black). **b**, Conductivity values show that water in the floodplain lakes primarily originates from the flooding of the Solimões and Amazon rivers with modest contribution from local drainage. **c**, The distribution of water p_{co_2} shows large contrasts between channel and floodplains, with a significant decrease downstream (as during the high water), in parallel with the extent of vegetation in the floodplains (percentage of total floodplain area is given in parentheses for each lake). Undersaturation in p_{co_2} occurs at low water in dense phytoplankton blooms in almost isolated lakes.



Extended Data Figure 4 | Conceptual diagram for carbon dioxide outgassing fuelled by Amazonian wetlands. In flooded forests, aerial gross primary production absorbs CO₂ from the atmosphere and sequesters part of this carbon in wood. Most of the sequestration in wood occurs during the terrestrial phase and is supposed to be balanced by natural tree mortality associated with channel migration. Leaves and wood also respire CO₂ back to the atmosphere. Litter falls from flooded trees primarily during flooding and constitutes a significant organic carbon input to the water. Floating plants in the Amazon grow above the water level, where they perform aerial photosynthesis, and as the water level progressively rises, their biomass is recycled and decomposes underwater. Because no significant burial of macrophyte material is observed in sediment, it is assumed that all their annual net primary production (NPP) is transferred to water as organic carbon (litter fall). Below water, the respiration of roots of flooded trees and floating macrophytes releases CO₂ to the water. With the establishment of anoxic conditions in forest soils, tree metabolism deviates to an anaerobic pathway that generates fermentation products, which are exuded from the roots into the surrounding water. Carbon flux between the Amazonian wetlands and rivers thus occurs through two distinct pathways. CO₂ export from the wetlands is derived from

root and sediment respiration within the wetlands, whereas organic carbon export from the wetlands is derived from litter fall and from fermentative products released by roots. Quantitative information is missing for the latter exudation flux. In rivers and floodplains, water movement is fast enough relative to gas exchange to generate a lateral CO₂ flux with the water mass, and this flux should be taken into account in the interpretation of the spatial and temporal patterns of CO₂ outgassing. In water and sediments of the entire aquatic system, microbial heterotrophic respiration continuously converts organic carbon to CO2. In open lakes, phytoplankton uses CO2 dissolved in water (that is, primarily derived from the surrounding wetland vegetation) and infrequently uses atmospheric CO_2 because the lakes were rarely net CO_2 sinks on a daily basis. The phytoplankton biomass produced in open lakes constitutes an additional source of biodegradable organic carbon. Both C3 and C4 plants are well represented in the wetland. Isotopic and molecular tracers may distinguish woody from non-woody material. However, it is difficult to differentiate woody material from the flooded forest and woody material from the non-inundated forest, particularly as many species are common to both. More detailed discussion and references can be found in the Supplementary Information.

d



	w	k ₆₀₀	Н	D 1⁄2	T ½
	cm s⁻¹	cm h⁻¹	m	km	days
In floodplains					
Open lake at high waters without thermal effect on gas exchange	40	2	8	284	8,2
Open lake at high waters with thermal effect on gas exchange	40	12	8	47	1,4
Open lake at low waters without thermal effect on gas exchange	5	2	2	9	2,1
Open lake at low waters with thermal effect on gas exchange	5	12	2	1	0,3
In River channels					
Large, wind exposed and deep channel at low water	50	30	25	74	1,7
Large, wind exposed and deep channel at high water	150	30	40	355	2,7
Small, wind protected tributary	50	15	8	47	1,1

Extended Data Figure 5 | Modelling how far dissolved CO₂ is transported before being outgassed. a, We assessed the potential for lateral CO₂ transport in rivers and floodplains using a simple one-dimensional model that

simultaneously calculates the CO₂ lost by outgassing and the CO₂ that remains dissolved in water and is transported downstream by the currents. The model starts from a point source in the wetland (set here at 12,000 p.p.m.v., which is a typical value observed in the vicinity of a flooded forest; Fig. 2b). The iteration time was 1 min. In the model, $F(CO_2)$ is calculated from p_{co_2} , using representative values of k_{600} . The quantity of CO₂ lost to the atmosphere during one iteration is subtracted from the initial CO₂ quantity present in a column of water of a determined depth *H*. Note that this procedure is adequate only for acidic, non-buffered waters, such as those in the Amazon. **b**, **c**, When integrated (Supplementary Information), the equation gives a one-phase exponential

decay function of p_{co_2} versus the distance *x*, the water current velocity *w*, the normalized gas transfer velocity k_{600} , and the water depth *H*. The curves give the potential extent of p_{co_2} saturation that can be maintained without the necessity of aquatic respiration (Fig. 2b). DV_2 is the half-evasion distance, which is the theoretical distance the water mass travels before outgassing half of its initial excess CO₂. TV_2 is the associated half-evasion time. **d**, Typical half-evasion distances of wetland CO₂ in river-floodplain systems vary from less than 1 km in a shallow, stagnant, wind- and heat-protected lake to more than 300 km in a deep and fast-flowing river. This illustrates, on the one hand, how far wetland CO₂ can be exported downstream, and on the other hand, the large heterogeneity of the transport and outgassing processes in the river-floodplain complex.

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Extended Data Table 1 | Surface area of flooded land and aquatic biomes in the Central Amazon and study sites

а	All land	Quadrant-b	Quad	rant-c			
a All I Tota May Fra Rivi Floo Floo Floo Floo Floo Floo Floo Flo	Total area (km ²)	Total area (km ²) 1 770 000		3 000			
	Maximum flooded (km	²) 243 000	31	435			
	Fraction of flooded lan	d 14%		11%			
L						_	
D	Fraction of flooded lan	d	Quad	rant-b	Quadrant-c	_	
	River channels perman	nent waters	14% 1%		18%	_	
	Floodplain permanent	open water (lakes)			13%		
	Floodplain temporary of	open water (lakes)	ţ	5%	21%		
	Floodable forest		69	9%	38%		
	Floating macrophytes		11	11% 10		_	
с	Surface of studied floo	dplains	Cabaliana	Janauaca	Miratuba	Canaçari	Curuai
	High water, June 2009						
	Ann name Quadrant-E Total area (km²) 1 770 000 Maximum flooded (km²) 243 000 Fraction of flooded land 14% River channels permanent waters Floodplain permanent open water (lakes) Floodplain temporary open water (lakes) Floodplain temporary open water (lakes) Floodable forest Floating macrophytes Surface of studied floodplains High water, June 2009 Open waters Flooded forest Flooded forest Floating vegetation Total floodplain Total floodplain Low water, October 2009 Open waters Floating vegetation Total floodplain Falling water, August - September 2010 Open waters Flooded forest Flooded forest Flooded forest Flooded f	367	76	422	448	1377	
	F	looded forest	1354	121	208	186	563
	F	loating vegetation	101	19	30	13	393
	Т	otal floodplain	1822	216	660	647	2333
	Low water, October 20	09					
	O	pen waters	139	48	127	363	1108
	F	looded forest	111	1	26	65	41
	F	loating vegetation	26	3	5	2	256
	Т	otal floodplain	276	52	158	430	1405
	Falling water, August -						
	C	pen waters	210	62	204	386	1136
	F	looded forest	464	13	37	71	111
	F	loating vegetation	45	7	14	2	283
	т	otal floodplain	719	82	255	459	1530

a, Surface areas of flooded land in the Central Amazon reference quadrant b (Fig. 1b) and in the study area, quadrant c (Fig. 1c). b, Surface areas of river channels, floodplain open lakes, flooded forest and floating vegetation in quadrants b and c. c, Surface area of floodplain vegetation in the five floodplains studied during three cruises at three water levels.

Extended Data Table 2 | Water pco2, conductivity and Chl a in the river and floodplain lakes of quadrant c

Season		Site	Month	Conductiv	ity	pCO ₂					Chl-a
				(µS cm ⁻¹)	e d	(p.p.m.v.)	80	min	max	N	(µg Litre ⁻ ')
Rising water	Rivers	Solimões	Jan. 2011	Average 98	<u>5.u.</u>	2,286	71	2.135	2.597	1008	1.4
, new g trater		Manacapuru	Jan. 2011	15	1	3,885	430	2,918	4,374	161	5.9
		Negro	Jan. 2011	13	1	2,842	142	2,545	3,191	358	1.1
		Amazon	Jan. 2007	69	1	3,009	112	2,780	3,266	1213	0.7
		Amazon	Feb. 2011	69 54	9	2,555	156	2,175	3,317	2433	1.1
		Urubu	Feb. 2011	11	1	3 4 1 6	739	2,355	4 784	282	4 1
		Tapaiós	Jan. 2007	14	1	413	219	52	798	582	2.7
		Tapajós	Feb. 2011	16	1	1,042	339	457	1,423	283	2.9
	Lakes	Cabaliana	Jan. 2011	97	29	1,736	592	729	3,221	246	25.8
		Janauaca	Jan. 2011	71	25	2,898	1,597	297	6,031	749	4.5
		Miratuba	Feb. 2011	61	9	6,253	826	4,561	7,895	185	4.4
		Curuai	lan 2007	71	3	675	243	306	1 401	900	47.2
		Curuai	Feb. 2011	62	5	2.596	1.429	378	5.672	1076	6.7
High water	Rivers	Solimões	May 2008	80	13	5,726	353	4,517	7,910	702	1.0
		Solimões	June 2009	67	6	9,131	851	7,979	11,557	585	0.3
		Manacapuru	May 2008	9	0	6,602	1,220	4,050	8,615	369	5.1
		Manacapuru	June 2009	3/	19	10,563	845	8,776	11,921	267	3.2
		Negro	June 2009	10	2	4,790	325	4,252	5,303	430	1.0
		Amazon	June 2009	48	11	6.055	723	4.211	7,179	1716	0.5
		Madeira	June 2009	41	0	3,880	193	3,502	4,250	92	1.0
		Urubu	June 2009	34	3	5,869	603	4,071	6,682	189	3.8
		Tapajós	June 2009	17	1	1,209	169	925	1,766	237	4.3
	Lakes	Cabaliana	May 2008	77	6	5,736	2,650	760	12,070	491	18.8
		lanauaca	May 2009	73	3	9,250	1,020	3 431	7 647	2094	15.0
		Janauaca	June 2009	43	2	7.881	1.230	4,195	9.657	2005	2.0
		Miratuba	June 2009	48	3	5,049	457	4,227	5,939	500	2.0
		Canaçari	June 2009	44	2	5,100	624	4,016	7,084	365	2.4
		Curuai	June 2009	45	2	4,427	1,116	2,383	6,670	1209	3.4
Falling water	Rivers	Solimões	Aug. 2010	71	4	4,790	647	3,710	6,500	637	2.7
		Negro	Aug. 2010	9	1	5 116	347	4 128	5,813	359	0.4
		Amazon	Sep. 2010	49	6	4,515	279	3,494	4,947	1639	2.3
		Madeira	Sep. 2010	88	1	1,290	77	1,108	1,621	119	5.8
		Urubu	Sep. 2010	15	4	2,446	520	1,029	3,336	159	8.9
		Tapajós	Sep. 2010	15	6	530	163	197	761	134	5.2
	Lakes	Cabaliana	Aug. 2010	69	3	9,950	860	7,935	12,550	438	10.8
		Miratuba	Aug. 2010 Sep. 2010	59	2	1,930	727	135	2 703	579	30.0
		Canacari	Sep. 2010	51	2	279	245	47	1.032	1920	26.6
		Curuai	Sep. 2010	44	6	256	333	18	1,366	1923	55.8
Low water	Rivers	Solimões	Nov. 2007	95	2	2,199	91	1,908	2,351	761	1.3
		Solimões	Oct. 2008	73	1	2,486	52	2,281	2,595	544	1.5
		Solimoes	Oct. 2009	/1	3	5,348	417	4,489	6,704	5/3	4.6
		Negro	Oct 2008	9	0	2 852	292	2 344	3 433	309	3.0
		Negro	Oct. 2009	8	Ő	3,944	175	3,600	4,484	369	3.3
		Manacapuru	Oct. 2009	11	1	10,718	815	8,716	12,092	245	9.3
		Amazon	Nov. 2007	78	22	2,091	257	1,537	2,721	1270	0.9
		Amazon	Oct. 2008	49	8	2,768	287	1,697	3,397	1349	1.9
		Amazon	Oct. 2009	57	10	4,018	321	3,243	5,041	2118	3.0
		Madeira	NOV. 2007	8/	3	1,381	100	1,239	1,543	9//	1.6
		Madeira	Oct. 2008	77	1	1,954	161	1,120	2.058	81	5.0
		Urubu	Oct. 2009	10	1	1,420	306	819	2,043	262	15.0
		Tapajós	Oct. 2009	17	1	618	143	310	1,023	312	9.8
	Lakes	Cabaliana	Oct. 2009	70	10	6,002	3,115	774	10,411	482	18.1
		Janauaca	Nov. 2007	67	21	1,336	569	454	2,039	51	17.0
		Janauaca	Oct. 2008	41	1	124	101	66	690	88	154.7
		Janauaca	Oct. 2009	58	8	1,268	502	97	4,313	235	35.3
		Canacari	Oct. 2009	44	1	280	304	79	1.628	295	10.8
		Curuai	Oct. 2008	35	4	662	555	25	1,829	279	35.7
		Curuai	Oct. 2009	49	5	482	482	28	2,003	391	47.2

Average, standard deviation (s.d.), minimum and maximum values and number of measurements are reported for p_{co_2} . The total number of measurements was 45,786, which represents 32 days of continuous measurement.

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Extended Data Table 3 | Tentative revised carbon budget for the central Amazon River and wetlands

_		Definition	Method / Source	Rate (MgC km ⁻² yr ⁻¹)			Surface area (1000 km ²)	Carbon flux (TgC y ⁻¹)	
Flooded Forest									
(1)	GPP	NPP + Plant R = NPP + leaf R + wood R + root R	(2) + (3) + (5)	3,030	±	1,090	144	-435 ± 160	
(2)	Leaf and wood R	26% of GPP _*	0.26 x (1)	790	±	280	144	115 ± 40	
(3)	Root R	t	ref. 61,62	1,070	±	670	93	100 ± 60	
(4)	Plant R	Leaf R + wood R + root R	(2) + (3)	1,860	±	730	144	270 ± 105	
(5)	NPP	Wood P + Litter fall ‡	ref. 14	1,170	±	452	144	-170 ± 65	
(6)	Litter Fall	§	ref. 14	415	±	140	144	-60 ± 20	
(7)	Wood P	П	ref. 14	530	±	200	144	-75 ± 30	
(8)	Export to water	Area-weighed root R + Litter fall ¶	(3) + (6) ¶	1,100	±	455	-	-160 ± 65	
								36% of GPP	
Floa	ating macrophytes								
(9)	GPP	NPP + leaf R + root R	(12) + (13)	6,035	±	3,450	30	-180 ± 60	
(10)	Leaf R	#	ref. 67	1,175	±	500	30	35 ± 15	
(11)	Root R	0	ref. 16	660	±	300	30	20 ± 10	
(12)	Plant R	Leaf R + root R	(10) + (11)	1,835	±	580	30	55 ± 15	
(13)	NPP	жж	ref. 15,27,68	4,200	±	3,400	30	- 125 ± 100	
(14)	Export to water	NPP + root R	(11) + (13)	4,860	±	3,415	30	- 145 ± 100	
								80% of GPP	
(15)	Total GPP		(1) + (9)					- 615 ± 160	
(15) Total wetland ex	Total wetland exp	ort to waters	(8) + (14)					- 305 ± 120	
								50% of GPP	
(16)	Outgassing	††	ref. 8	830	±	240	253	210 ± 60	
(17)	NEE	‡ ‡	(15) - (16)					-95 ± 130	

Negative signs refer to uptake of atmospheric CO₂.

* Leaf and wood respiration were estimated using a fraction of 26% of gross primary production as reported in ref. 59 for Amazonian *terra firma* forest, that is, 13.5% of gross primary production for leaf respiration plus 12.8% for wood respiration (stem and branches). The value based on terrestrial forest is probably a lower estimate, because the stress caused by flooding may enhance leaf and wood respiration⁶⁰.

[†] The limited data available for submerged root respiration provides an average value of 40 ± 25 µl per gram fresh weight of root per hour during the first 100 days of flooding⁶¹. We converted this rate into a carbon flux by applying a 30% moisture content for the roots and a root density of 40 Mg ha⁻¹ (that is, 4,000 Mg km⁻²) derived from ref. 62. Because this flux occurs only during flooding periods, the rate was applied to a surface area of 92,000 km², that is, the average surface area of flooded forest between high water and low water.

[‡] The NPP rates of flooded forest were computed as the sum of litter fall and wood production¹⁴; this flux is an underestimate, because it does not include herbivory¹⁴, seasonal fine root production⁶³ and the exudation during flooding of fermentation products such as ethanol^{64,65}.

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Sequestration in above-ground wood occurs mostly during the terrestrial phase in the forest; in fact, it is believed that the carbon stock in the aboveground biomass of the entire floodable forest ecosystem is more or less balanced because the carbon sequestrated during the first 50–100 years of primary succession is lost by natural tree mortality and forest destruction due to lateral erosion by the river and channel migration^{14,66}.

The rates of litter fall and root respiration have been weighted by their respective surface areas; all the litter was assumed to fall into the water (or to be rapidly mobilized by flooding), whereas root respiration releases CO₂ into waters only during the aquatic phase. This export to water by flooded trees is conservative, as it does not include seasonal dead fine root decomposition⁶³ or the exudation of biodegradable fermentation products by tree roots^{64,65}.

#The respiration rates of macrophytes in the floodplain were assumed to be the night-time CO₂ fluxes measured by eddy covariance during the dry season, when macrophytes were growing on dry sediments⁶⁷. This value was 30% of that measured under the same conditions at high water, when both above-water leaves and outgassing contributed to the CO₂ flux.

*A root respiration value equivalent to 30% of the CO2 flux from the macrophyte meadows was applied¹⁶.

**The NPP of floating grasses shows large spatial variability that has been relatively well documented^{15,58,68,69}. As the water level rises and plants grow, the above-water biomass is transferred to the water, where it almost totally decomposes annually^{15,59}. No sedimentary evidence was found for significant burial of macrophyte biomass⁷⁰. Consequently, the litter fall of macrophytes was assumed to be equal to the NPP. However, it is not clear whether the applied methods for NPP quantification adequately account for the carbon lost from the submerged parts of the plants as they grow⁶⁹. We used the average of 11 NPP values reported in 6 studies for 5 different floating macrophyte species in the Amazon floodplain^{15,56,66,69}.

†† Carbon dioxide outgassing was reported for the entire river and wetlands in the central Amazon reference quadrant⁸.

the net ecosystem exchange with the atmosphere is the balance between the wetland carbon export to water and outgassing from water. The net ecosystem exchange was not significantly different from zero, which suggests an almost balanced CO₂ budget for the central Amazon River and wetlands. References are in the Methods.

S1. Lessons from high-resolution pCO₂ records

The recorded pCO_2 in the Amazonian rivers and floodplains was related to the connectivity of the waters with vegetation at all spatial and temporal scales (Fig. 3). In the main channels of the rivers, pCO_2 followed a seasonal pattern that was well-synchronised with the hydrological cycle⁸ (Extended Data Table 2) and with the total surface area of flooded forest; the pCO_2 in the channel also decreased downstream, as did the amount of vegetation occupying the floodplain (Extended Data Fig. 2&3). In the floodplain lakes, the connection between pCO_2 and wetland vegetation was even more pronounced at all scales (Fig. 3).

A typical example of the large-scale connection between high pCO_2 and floodplain vegetation occurred during a high water period in June 2009, when the Amazon River flowed over the banks of all of its floodplains. During this cruise, the water pCO_2 distribution (Extended Data Fig. 2), and the balance between water column respiration and CO_2 outgassing perfectly illustrated how wetlands, particularly flooded forests, fuel CO₂ outgassing to surrounding waters. Downstream on the Amazon River, where flooded forest is scarce (Extended Data Fig. 2, right), the pCO₂ in Curuai Lake decreased from the main channel value of $\sim 6,000$ ppmv on the day we entered the floodplain to a value of $\sim 2,000$ ppmv after four days of very stormy weather that greatly enhanced gas transfer (the computed average k_{600} was 11 cm h⁻¹). We returned the next day to the main channel of the Amazon and again observed the same initial value of 6,000 ppmv (Extended Data Fig. 2, right). Such a contrast in the channel to floodplain pCO₂ in chlorophyll-poor waters (Extended Data Table 2) could be explained by the lower depth-integrated respiration rates (or net heterotrophy during this unproductive period) in the 6-m-deep Curuai Lake relative to the 48-m-deep Amazon channel. In the lake, respiration was 87 ± 33 mmol m⁻² d⁻¹ and accounted for only 19% of the CO₂ outgassing flux $(464\pm117 \text{ mmol m}^{-2} \text{ d}^{-1} \text{ for a } k_{600} \text{ of } 11 \text{ cm h}^{-1} \text{ because of the heavy storm}); in contrast, in the$ Amazon channel, net heterotrophy was $570\pm87 \text{ mmol m}^{-2} \text{ d}^{-1}$ and was not significantly different from CO₂ outgassing (466±56 mmol m⁻² d⁻¹ for a k_{600} of 8.2 cm h⁻¹). Although

respiration of the organic matter carried from upstream appeared to be able to sustain outgassing in the deep Amazon channel at the farthest downstream location, it was not able to sustain outgassing in the shallow Curuai Lake, where CO₂ was mainly advected with the river flood, because of the modest local connectivity with the flooded forest even at this high water level.

During the same season, in the upstream reach of the Solimões River where flooded forest was extensive and connectivity to the wetland was maximal (Extended Data Table 1), the pCO₂ in the 5-7-m-deep Cabaliana and Janauaca Lakes was similar to or even higher than that in the 30-m-deep Solimões channel (Extended Data Fig. 2, left). In this region, respiration did not account for outgassing in the floodplain or in the channel. Depth-integrated respiration was 220±43 mmol m⁻² d⁻¹ in the Solimões channel and accounted for 30% of the outgassing (727±68 mmol m⁻² d⁻¹ for a k_{600} of 8.2 cm h⁻¹) and was 88±25 mmol m⁻² d⁻¹ in Cabaliana Lake, where it accounted for less than 20% of the outgassing flux (455±130 mmol m⁻² d⁻¹ for a k_{600} of 5 cm h⁻¹). These discrepancies between outgassing fluxes and respiration, as a measure of the net heterotrophy in these unproductive waters, are consistent with previous reports^{20,S1}. These numbers imply CO₂ input from the surrounding wetlands, and particularly from the flooded forests, which cover 75% of the Cabaliana floodplain in this season (Extended data Table 1c).

Another coincidence between high water pCO_2 and connectivity to vegetation was observed for lake isolation when pCO_2 was much lower in the floodplain lakes than in the main stem, for instance, at low water in October 2009 (Extended Data Fig. 3) and at falling water in September 2010 (Extended Data Table 2). The phytoplankton biomass was high in these seasons (Extended Data Table 2, Ref S2), and during the daytime, the phytoplankton decreased the pCO_2 below the atmospheric equilibrium in all of the floodplain lakes except

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Cabaliana on the Solimões (Extended Data Fig. 3, left), which remained connected to the flooded forest even at this low water stage (Extended Data Table 1). Additional carbon was apparently supplied by the wetland to maintain a high pCO_2 in the water.

Extremely low pCO₂ occurred in lakes disconnected from flooded forest at intermediate and low water stages, and low pCO₂ was associated with a high phytoplankton biomass (Extended Data Table 2). For instance, occasional undersaturation of the water relative to atmospheric CO₂ occurred in four of the five floodplain lakes studied in October, 2009 (Extended Data Fig. 3). In contrast to the deep and well-mixed channel, the shallow depth, thermal stratification, and partial sedimentation of particles in the floodplain lakes created the light conditions for a positive phytoplankton carbon balance^{S3}. The 18 ppmv pCO₂ value from September 2010 in Curuai Lake is the lowest ever directly measured in an aquatic system. Diurnal variation of pCO₂ was important within these blooms, and the lakes generally became a CO₂ source at the end of the night (not shown). Meteorological conditions and associated stratification, sedimentation, and resuspension as well as adaptation of phytoplankton to light conditions also greatly affect pCO₂ in these shallow, turbid waters. The phytoplankton biomass in lakes often followed a trend opposed to that of pCO₂ and increased from the forested floodplains upstream to the open floodplains downstream, as seen in September, 2010 (Extended Data Table 2, see Chl *a*).

However, CO_2 uptake by phytoplankton was too restricted in time and space to significantly affect the CO_2 budget of the Amazon River. Although very active locally, phytoplankton production has a limited impact on the carbon balance of the Amazon River for several reasons: (1) although open lakes represent 34% of the wetland in Quadrant-c, they occupy less than 4% of the central Amazon flooded area in Quadrant-b¹²; (2) strong CO_2 depletion and dense phytoplankton blooms occur only in lakes disconnected from the vegetated areas in the more downstream part of Quadrant-c (Extended Data Table 2), and (3) most of the phytoplanktonic organic material will be further mineralised or exported rather than buried in sediments⁷⁰ and thus does not constitute a significant C sink. Phytoplankton is also exported from the floodplains to the main channels^{21,22} and seasonally contributes to river respiration²⁰. Although phytoplankton contributed to pCO₂ gradients among lakes and seasons, the dominant driver of the CO₂ gradients was connectivity with semi-aquatic vegetation in the wetland, including floating grasses and flooded forests (Fig. 3).

S2. Modelling CO₂ export from wetlands

When CO₂ is dissolved in water, it is partly outgassed to the atmosphere and partly transported downstream with water movement; both processes can be modelled easily. In rivers and floodplains, water movement is fast enough relative to gas exchange to generate a lateral CO₂ flux with the water mass (e.g., ref. 4), and this flux should be taken into account in the interpretation of the spatial and temporal patterns of CO₂ outgassing. By computing the gas exchange and water velocity, theoretical curves for CO₂ dispersion can be generated from a point source to give the potential extent of pCO₂ saturation that can be maintained without respiration. We assessed the potential for lateral CO₂ transport in rivers and floodplains using a simple 1D model that simultaneously calculates the CO₂ lost by outgassing and the CO₂ that remains dissolved in water and is transported downstream by the currents (Extended Data Fig. 5). We start from a point source in the wetland at 12,000 ppmv, which is a typical value observed in the vicinity of a floodel forest (Extended Data Fig. 2). The iteration time was 1 min. In the model, FCO₂ is calculated from pCO₂, using representative values of k_{600} . The quantity of CO₂ lost to the atmosphere during one iteration time is subtracted from the initial CO₂ quantity present in a column of water of a determined depth.

The distance dx (m) travelled by the water mass during an iteration dt (sec) is given by: dx=wdt

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where w is the water velocity in m s⁻¹. The CO₂ degassing flux F(x) (mol m⁻² sec⁻¹) of a water body located between positions x and x+dx is written as:

$$F(x) = k\alpha[pCO_2(x)-pCO_2(air)]$$

where k is the gas transfer velocity deduced from k_{600} , α is the solubility coefficient of CO₂ (mol kg⁻¹ atm⁻¹), pCO₂(x) is the water pCO₂ between position x, and x+dx and pCO₂(air) is the pCO₂ in the air. The change of CO₂ concentration in the water d[CO₂] (mol m⁻³) induced by gas exchange between positions x and x+dx is given by:

$$d[CO_2] = -F(x) H^{-1} dt = -F(x) H^{-1} dx w^{-1} = -k \alpha [pCO_2(x)-pCO_2(air)] H^{-1} dx w^{-1}$$

where H is the water height (m). Because the pH was below 7 and the alkalinity was below $0.5 \text{ mmol } \text{L}^{-1}$ in these CO₂-rich waters, we could neglect the buffering capacity of the carbonate system on CO₂ exchange^{S5,S6}. Note that in basic and alkaline waters, gas exchange would induce significant modification of the HCO₃ and CO₃²⁻ forms as well, and it would be necessary to account for changes in the whole dissolved inorganic carbon (DIC) pool^{S6}. The change in pCO₂, noted as dpCO₂(x), can then be written as:

 $dpCO_2(x) = d[CO_2] \alpha^{-1} = -k [pCO_2(x)-pCO_{2air}] H^{-1} dx w^{-1}$

$$\frac{dpCO_2(x)}{pCO_2(x) - pCO_2(air)} = -\frac{k}{wH}dx$$

Integrated, this equation gives a one-phase exponential decay function:

$$pCO_2(x) = [pCO_2(wetland) - pCO_2(air)]e^{\left(-\frac{k}{wH}x\right)} + pCO_2(air)$$

From this model, we compute the theoretical curves for pCO₂ export using representative values of the gas transfer velocity, water depths, and current velocities for floodplains and rivers (Fig. 2b). In the floodplain lakes, we used k_{600} values between 2 and 12 cm h⁻¹, which correspond to the case of tropical low wind speed conditions without thermal enhancement of gas exchange⁴⁸ and with thermally enhanced gas exchange^{17,53}, respectively. We used typical floodplain water current velocities between 5 and 40 cm s⁻¹, and water depths between 2 and 8 m. For the river channels, we used k_{600} values between 15 cm h⁻¹, the average value obtained

for the Amazon with floating chambers⁵⁸, and 30 cm h⁻¹, as deduced from ²²²Rn mass balance^{S1}. Selected water current velocities in river channels were between 50 and 150 cm s⁻¹ ^{S7}, and the water depths were between 8 and 40 m. We deliberately did not apply the maximum depth of 60 m in the Amazon River main channel because we do not have information on the vertical distribution of pCO_2 as a function of water depth. On many cruises, and particularly while sailing in the Solimões River at high water (May 2008 in Fig. 2, and June 2009 in Extended Data Fig. 2), we observed much higher surface water pCO_2 close to the banks and to the flooded forest; indeed, it is very likely that the warmer and CO₂enriched water masses from the wetlands could form plumes that preferentially degas CO_2 in the surface layers of the river channels. In this case, CO_2 advection should be modelled using the height of the surface layer flowing from the wetland and not using the total water depth. Alternatively, when vertical mixing of the water column occurs, the CO₂-enriched surface waters from the wetlands would be diluted by water from the river bottom, and this dilution would temporally limit degassing to the atmosphere and favour longitudinal transport downstream. The observed pCO₂ (Extended Data Fig. 2,3) in the Amazon River-Floodplain system and those computed with the 1D advection model (Fig. 2b) indicate that a large supersaturation can be maintained over dozens to hundred of km in open waters downstream of wetlands without any respiration necessarily occurring in the water itself.

To further characterise the CO₂ advection, we define the half evasion distance, D¹/₂ in km, as the theoretical distance the water mass travels before outgassing half of its initial excess CO₂: $D^{1}/_{2} = w H \ln(2) k^{-1}$,

and the corresponding travelling half-time of CO₂ evasion is

 $T_{2}^{1/2} = D_{2}^{1/2} w^{-1} = H \ln(2) k^{-1}$.

Typical D¹/₂ values vary from less than 1 km in a shallow, stagnant, wind- and heat-protected lake to more than 300 km in a deep and fast flowing river (Extended Data Fig. 5). This

illustrates, on the one hand, how far wetland CO_2 can be exported downstream, and on the other hand, the large heterogeneity of the transport process in the river-floodplain complex. The high water period, when the river flows over the floodplain at the fastest velocity, is the most favourable period for CO_2 export from the wetlands and occurs concomitantly with the largest CO_2 outgassing in the central Amazon⁸.

S3. Net CO₂ exchange of the Central Amazon River-Floodplain ecosystem

S3.1. Conceptualisation of carbon fluxes

Our observations call for a re-conceptualisation of the carbon fluxes among upland Terra Firme, the Central Amazon River-Floodplain system, and the atmosphere. This reconceptualisation must integrate the carbon export from Amazonian wetlands, as was first described by W.J. Junk^{S8}; however, at that time, only the export as particulate organic carbon had been considered. In fact, carbon is transported in the Amazon River in three major chemical forms. Alkalinity (mainly HCO₃⁻) generated upland by weathering^{S9} is the only form that is relatively conserved across rivers and floodplains. The two other forms, i.e., organic carbon (OC) and dissolved CO₂, are greatly affected by biological processes that occur in floodplains and rivers and that are directly related to exchange with the atmosphere (Extended Data Fig. 4).

In flooded forests, aerial primary production absorbs CO_2 from the atmosphere and sequesters part of this carbon in wood^{14,26,S10}. Tree rings indicate a dormancy period during flooding; most of the sequestration of carbon in wood occurs during the terrestrial phase²⁶. In contrast, litter fall primarily occurs during flooding and constitutes a significant OC input to the water^{14,64}. Below water, the respiration of flooded trees is poorly documented; extremely high CO_2 release from standing living stems was observed just above the water table at the onset of flooding, which suggests an upward flux of carbon dioxide within the wood⁶⁰; this upward flux suggests high CO₂ release below the water surface. With the establishment of anoxic conditions in forest soils, tree metabolism deviates to an anaerobic pathway that generates fermentation products such as ethanol, which is released directly from the roots into the surrounding water^{55,65}. Large carbon losses from the forest to the water are also expected from the observed contrast between low wood production and high net primary productivity of trees during flooding^{26,65}. Indeed, the water in the vicinity of flooded forest was largely supersaturated with CO₂ (Fig. 2).

The net primary production of macrophytes is even higher than that of the forest, and this material is almost completely recycled annually^{15,27,S8}. For instance, when CO₂ fluxes were measured directly by the eddy covariance technique, floating meadows of macrophytes were a sink of atmospheric carbon⁶⁷. Therefore on a daily basis, the aerial NPP was greater than the sum of outgassing from the waters below the meadows and the respiration of the emerged leaves at night. This carbon uptake provides great potential for export to the surrounding waters. Floating plants in the Amazon have life cycles that are well adapted to the flood pulse; they grow above the water level to perform aerial photosynthesis, and as the water level progressively rises, the biomass is recycled and decomposes underwater^{S11}. Root respiration of macrophytes is also an important source of CO₂ for floodplain waters¹⁶. We measured pCO₂ values of 4,000-12,000 ppm in live floating meadows and greater than 20,000 ppm in a decomposing, sulphide-rich, meadow in Cabaliana Lake in February, 2011 (Extended Data Table 2; note that 20,000 ppmv is the saturation value of the gas analyser, so the actual water pCO_2 was even higher). In this latter case, the extension of macrophytes in the floodplain was favoured by the severe 2010 drought a few months before, and the floating meadows had been pushed by the wind and were concentrated at the western end of the lake.

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Carbon flux between the Amazonian wetlands and rivers thus occurs through two distinct pathways. CO_2 export from the wetlands is derived from root and sediment respiration within the wetlands, whereas OC export from the wetlands is derived from litterfall, plant exudation, and fermentative products released by roots. If we consider the whole floodplain, the phytoplankton biomass produced in open lakes is an additional source of OC for the river^{21,22} (Extended Data Fig. 4). Note that phytoplankton uses CO_2 dissolved in water (that is primarily derived from the surrounding wetland vegetation) and infrequently uses atmospheric CO_2 because the lakes were rarely net CO_2 sinks on a daily basis (Fig. 3; Extended Data Table 2).

The CO_2 and OC pathways may be difficult to differentiate because they generally occur concomitantly, and they are interconnected by microbial respiration, which converts OC to CO_2 in all waters, and by phytoplankton production in lakes, which converts some of the CO_2 originating in the wetlands to OC. In addition, there is no unequivocal isotopic or molecular tracer for carbon that originates from the floodplains because this carbon is derived from phytoplankton, C4 plants, and many C3 woody species that are common to both the floodplain and the *terra firme* forest^{S8}. The variations in the OC and CO₂ pathways throughout the year may depend on the flood pulse and the coupling between biological production and hydrology^{S11}. At rising water, river waters with relatively low pCO₂ (Extended Data Table 2) begin to fill the floodplains through paranás to flood most of the proximal forest and some young macrophyte vegetation that begins to float. River water carries small amounts of relatively refractory terrestrial POC adsorbed onto fine suspended sediments^{S12}, which is partly buried in the floodplain sediments⁷⁰. During this rising period, the Amazon water is enriched in CO₂ and OC inside the wetlands. Some phytoplankton blooms also occur in open lakes, as shown by the Chl a concentrations in February 2011 (Extended Data Table 2). At high water, the river starts to flow over the floodplain^{S11}, thereby rapidly mobilising wetland waters enriched in OC and CO₂ and maximising the flooded wetland surfaces. This period corresponds to the highest and relatively homogeneous pCO_2 throughout the river and the floodplain continuum⁸ (Extended Data Fig. 2 & Table 2). At this time, most of the phytoplankton is flushed out of the floodplains (Extended Data Table 2) because environmental conditions such as residence time and water depth and destratification become less favourable for growth. At falling water, when the river no longer overflows its banks, the water residence time in the floodplains increases again, and contrasts between the water composition in the floodplains and that in the main stem become more pronounced^{22,S2}. First, as the connectivity with the wetlands progressively decreases with time and decreases more quickly along the biogeographic gradient, a decrease in pCO₂ is observed in the channels and lakes (Extended Data Fig. 3); second, the algal bloom in lakes becomes increasingly dense, reaching Chl a concentrations $> 30 \text{ µg L}^{-1}$ (Extended Data Table 2). As a result, pCO₂ decreases much more rapidly in the floodplain lakes than in the channels and reaches maximum contrast at low water. Water flowing out of the floodplains to the main stem through the paranás is thus enriched with OC produced in $situ^{21,22}$. Potentially, there are large differences in the nature and origin of the carbon exported from the floodplains at high water and at falling water^{21,S8}: Although the river flowing over the floodplain at high water may transport CO₂ and OC mainly from the flooded forest and floating vegetation, at falling water, the paranás export progressively less CO₂ because the CO₂ is consumed in the lakes by phytoplankton, and more macrophyte and algal material is exported^{21,22}. This trend explains why a large phytoplankton contribution to respiration was observed during the falling water season in the main channel²⁰. Regardless of the season, CO₂ outgassing from the river channel is composed of young carbon²⁵.

S3.2. Quantitative evidence

The last argument in favour of river CO₂ outgassing primarily fuelled by wetlands comes from a quantitative analysis of the carbon fluxes in Ouadrant-b in light of the published metabolic rates within floodplain ecosystems (Extended Data Table 3). Due to the paucity of available data, these figures remain tentative and the carbon budget of the Amazon is far from being closed; however, these estimates allow the assessment of whether wetlands can potentially support CO₂ outgassing from waters in the central Amazon reference quadrant. Flooded forests (and some woodland and shrub areas) extend over 174 million km² at high waters and 67 million km² at low waters¹². Depending on their maturity, the annual net primary production of flooded forests varies between 670 and 1,590 MgC km⁻² yr⁻¹ and is composed of two dominant terms: aboveground wood biomass production (280-940 MgC km⁻ 2 yr⁻¹) and litterfall (320-680 MgC km⁻² yr⁻¹)¹⁴. During flooding, tree metabolism is greatly modified to adapt to anoxia, and this modification results in OC and CO₂ release from the vegetation to the water. Because litter fall primarily occurs during flooding^{14,64}, we can assume that the litter is completely transferred to the water by applying the litterfall yield to the 144 million km² maximum surface area of flooded forest only or to 80% of the maximum of flooded forest, woodland, and shrubs¹². Litterfall represents a flux of 60 ± 20 TgC yr⁻¹ (Extended Data Table 3). Carbon release through submerged roots is the second large input from the wetland vegetation to the water^{60,65}. The limited data available for submerged root respiration give an average value of $40\pm25 \ \mu L$ per fresh weight of root and per hour during the first 100 days of flooding²⁶. We converted this rate to a carbon flux by applying a 30%moisture content for the roots and a root density of 40 Mg ha⁻¹ (i.e., 4,000 Mg km⁻²) derived from a previous study⁶²; these values gave a yield of $1,070\pm670$ MgC km⁻² yr⁻¹ applied to a surface area of 92 million km² (the average surface area of flooded forest between high water and low water) and resulted in an additional flux of 100±60 TgC yr⁻¹. The latter flux from tree roots concerns only the CO_2 pathway and not the additional OC pathway, which arises from seasonal fine root production and associated dead root decomposition⁶³; it also does not include the exudation of biodegradable fermentation products such as ethanol^{64,65}. Consequently, the total flux of 160±65 TgC yr⁻¹ from flooded forest trees to waters must be considered to be a conservative estimate.

Floating vegetation covers only 12-26 million km² (Ref¹²) but potentially absorbs large amounts of atmospheric CO₂ through above-water NPP^{15,27,67}. As the water level rises and plants grow, the above-water biomass produced by macrophytes is transferred to the water, where it almost totally decomposes annually^{15,27}. The NPP of floating grasses shows a large spatial variability that has been relatively well documented^{15,27,68}. However, it is not clear whether the applied methods for NPP quantification adequately account for the carbon lost from the submerged parts of the plants as they grow⁶⁹. Here, we used the average of 11 NPP values reported in 6 studies for 5 different floating macrophytes species in the Amazon floodplain^{15,27,68}, i.e., 4,200±3,400 MgC km⁻² yr⁻¹, and a root respiration value equivalent to 30% of the CO₂ flux from the macrophyte meadows¹⁶, which is 660±300 MgC km⁻² yr⁻¹. The macrophytes thus provide a minimal carbon input of 145±100 TgC yr⁻¹ to the water.

In total, vegetation in the wetlands of Quadrant-b thus supplies a minimum of -305±120 TgC yr⁻¹ to the waters (Extended Data Table 3), which is not significantly different from the previously estimated outgassing flux of 210±60 TgC yr⁻¹ (Ref⁸). Consequently, the Amazonian waters receive as much atmospheric carbon from semi-aquatic plants as they release back to the atmosphere, and have a net atmospheric carbon balance of zero (Extended Data Table 3). C sequestration in wood in the flooded forest is 500±200 MgC km⁻² yr⁻¹ (Ref¹⁴), but this sequestration occurs mainly during the terrestrial phase²⁶. If the C storage in wood is applied, the net ecosystem exchange between the total water and wetland areas in

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Quadrant-b and the atmosphere would be -175 ± 140 Tg of C per year, which represents a net sink of atmospheric CO₂. However, it is believed that the carbon stock in the above-ground biomass of the entire várzea forest ecosystem is more or less balanced, because the carbon sequestrated during the first 50–100 years of primary succession is lost through natural tree mortality and forest destruction due to lateral erosion by the river and channel migration⁶⁶. Given the large uncertainties that remain in all of these numbers, the carbon budget of the Amazon is far from being closed. However, this quantitative analysis reveals that the amount of wetland carbon produced in the floodplain is sufficiently large to support all of the CO₂ outgassing from Amazonian waters.

S4. Synthesis and outlook

Our high-resolution water pCO_2 records show that the major source of CO_2 outgassing in the central Amazonian waters was vegetation that performs aerial photosynthesis in the flooded area itself. Thus, wetlands are different from permanent open waters because they function as sinks of atmospheric CO_2 in the aerial component and as sources of organic carbon and dissolved CO_2 in the aquatic component. They are also different from strictly terrestrial systems as they export the majority of their GPP to water (50% according to Extended Data Table 3) and this carbon is transported over long distance downstream before re-entering the atmosphere. Because the wetland-to-water carbon flux potentially offsets the water-to-air outgassing flux, the total flooded area in Quadrant-b is approximately neutral with respect to atmospheric CO_2 . Although remote sensing tools have considerably improved the quantification of wetland areas, errors associated with carbon fluxes remain large because of limited quantitative field data.

In the Amazon basin, interactions between deforestation, fire, and drought recently induced a transition to a disturbance-dominated regime that is characterised by losses of carbon storage

and changes in regional precipitation patterns and river discharge^{S13}. In such a context, our revision of the function of the river-floodplain system is crucial for predictions of future trends and also for recommendations for conservation. The fact that the Amazon floodplain potentially absorbs atmospheric CO_2 makes the floodplain a good candidate for conservation priority because conservation of the floodplain would simultaneously preserve carbon storage and biodiversity functions. However, these highly valuable environments are potentially vulnerable to alterations of the aquatic / terrestrial transition such as those induced by recent changes in the hydrological regime^{S14} or by the construction of hydropower projects^{S15,S16}.

Supplementary Information references

- S1- Devol, A. H., *et al.* Seasonal variation in chemical distributions in the Amazon (Solimões) River: a multiyear time series. *Glob. Biogeochem. Cycles* 9, 307–328. (1995)
- S2- Mortillaro J. M., *et al.* Fatty acid and stables isotopes (δ¹³C, δ¹⁵N) signatures of particulate organic matter in the Lower Amazon River: seasonal contrasts and connectivity between floodplain lakes and the mainstem. *Org. Geochem.* **42**, 1159–1168 (2011).
- S3- Cole J. J., Caraco, N. F., & Peierls, B. L. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnol. Oceanogr.* 37, 1608-1617 (1992)
- S4- Abril, G., Etcheber, H., Borges, A. V. & Frankignoulle, M. Excess atmospheric carbon dioxide transported by rivers into the Scheldt Estuary. *Comptes Rendus de l'Académie des Sciences, Série IIA* 330, 761-768. (2000)
- S5- Abril, G. Comment on: "Underwater measurements of carbon dioxide evolution in marine plant communities: A new method" by J. Silva et al. *Estuarine, Coastal and Shelf Science* 82, 357–360. (2009)
- S6- Polsenaere P. & Abril G. Modelling CO₂ degassing from small acidic rivers using water pCO₂, DIC and δ^{13} C-DIC data. *Geochimica et Cosmochimica Acta* **91**, 220–239 (2012)
- S7- Filizola, N., Guyot, J.-L., and Guimarães, V. Measuring the discharge of the Amazon River using Doppler technology (Manacapuru, Amazonas, Brazil). *Hydrol. Proc.* 23, 3151–3156. (2009)
- S8- Junk, W. J. in *Transport of carbon in the major World rivers*. (eds Degens E. T., Kempe,
 S., & Herrera, R.) 267-283 (Part 3. Mitt. Geol. Paläont. Inst. University Hamburg,
 SCOPE/UNEP Sonderbd. 58, 1985)
- S9- Moquet, J.S., et al. Chemical weathering and atmospheric/soil CO2 uptake in the Andean and foreland Amazon basins. Chemical Geology. 287. 1-26. (2011)

- S10- Malhi, Y. *et al.* (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Glob. Change Biol* 10, 563–591
- S11- Junk W.J. In *The central Amazon floodplain: ecology of a pulsing system*. (ed Junk W.J.) Springer, Berlin Heidelberg New York, 3-17. (1997)
- S12- Richey, J. E., et al. Biogeochemistry of carbon in the Amazon River. Limnol. Oceanogr. 35, 352-371. (1990)
- S13- Davidson E.A., *et al.* The Amazon basin in transition. *Nature* 481, 321-328.doi:10.1038/nature10717. (2012)
- S14- Espinoza. J. C. *et al.* From drought to flooding: understanding the abrupt 2010–2011
 hydrological annual cycle in the Amazonas River and tributaries. *Environ. Res. Lett.* 7, doi:10.1088/1748-9326/7/2/024008 (2012)
- S15- Abril, G., *et al.* Carbon dioxide and methane emissions and the carbon budget of a 10-year old tropical reservoir (Petit Saut, French Guiana), *Glob. Biogeochem. Cy* 19, GB4007, doi:10.1029/2005GB002457. (2005)
- S16- Fearnside, P. M. & Pueyo, S. Greenhouse-gas emissions from tropical dams. *Nature Climate Change* 2, 382–384. doi:10.1038/nclimate1540. (2012)