LETTERS

Stoichiometric control of organic carbon–nitrate relationships from soils to the sea

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The production of artificial fertilizers, fossil fuel use and leguminous agriculture worldwide has increased the amount of reactive nitrogen in the natural environment by an order of magnitude since the Industrial Revolution[1]. This reorganization of the nitrogen cycle has led to an increase in food production[2], but increasingly causes a number of environmental problems[1,3]. One such problem is the accumulation of nitrate in both freshwater and coastal marine ecosystems. Here we establish that ecosystem nitrate accrual exhibits consistent and negative nonlinear correlations with organic carbon availability along a hydrologic continuum from soils, through freshwater systems and coastal margins, to the open ocean. The trend also prevails in ecosystems subject to substantial human alteration. Across this diversity of environments, we find evidence that resource stoichiometry (organic carbon:nitrate) strongly influences nitrate accumulation by regulating a suite of microbial processes that couple dissolved organic carbon and nitrate cycling. With the help of a meta-analysis we show that heterotrophic microbes maintain low nitrate concentrations when organic carbon:nitrate ratios match the stoichiometric demands of microbial anabolism. When resource ratios drop below the minimum carbon:nitrogen ratio of microbial biomass[4], however, the onset of carbon limitation appears to drive rapid nitrate accrual, which may then be further enhanced by nitrification. At low organic carbon:nitrate ratios, denitrification appears to constrain the extent of nitrate accretion, once organic carbon and nitrate availability approach the 1:1 stoichiometry[5] of this catabolic process. Collectively, these microbial processes express themselves on local to global scales by restricting the threshold ratios underlying nitrate accrual to a constrained stoichiometric window. Our findings indicate that ecological stoichiometry can help explain the fate of nitrate across disparate environments and in the face of human disturbance.

Reactive nitrogen (N) refers to inorganic and organic forms of N that are biologically, photochemically and/or radiatively active, in contrast to the vast but inert atmospheric N_2 pool[1]. In the absence of human disturbance, relatively low reactive N availability constrains both the structure and function of a wide variety of ecosystems[6]. However, the rapid expansion of the global economy from the Industrial Revolution onward, fuelled by fossil fuel combustion, creation of synthetic fertilizer, widespread land conversion and accelerating global trade, has quickly increased reactive N in the environment[1]. Many environmental threats, including air pollution, eutrophication, soil acidification, losses of biodiversity and climate change[1,3], stem from the diverse fates of newly created reactive N. Given the environmental and social importance of managing a changing N cycle, there is growing demand for conceptual and analytical models[7–10] that can help to predict the fate of reactive N across multiple environments.

Generally, efforts to understand the sources and sinks of nitrate (NO_3^-) in ecosystems have focused on the roles of resource quantity and quality. As with any biogeochemical species, both kinetic and energetic controls will affect NO_3^- cycling, and models rooted in the principles of Michaelis–Menten uptake kinetics have improved our predictive ability of NO_3^- dynamics in streams[7–10]. However, one challenge to such efforts arises from the fact that N does not cycle independently of other elements. Instead, transformations of reactive N in the environment are closely linked with several other major biogeochemical cycles, perhaps most notably that of carbon (C)[9–16]. Thus, understanding human disruptions to either the N or C cycle is often not possible without a multi-element perspective.

Here, we show that consistent and negative nonlinear relationships between NO_3^- and dissolved or particulate organic C (DOC or POC) occur along a hydrologic continuum from soils, to streams and lakes, and on to estuaries and the open ocean (Fig. 1). Notably, the pattern remains robust even in human-disturbed streams and rivers (Fig. 1c). The consistency of the pattern across a wide range of environments and disturbance regimes suggests the potential for common underlying controls. Past studies in streams and groundwater have proposed several explanations for this pattern[13–17], with some recent discussions focusing on increased DOC leaching from ecosystems rehabilitating from acid deposition[17]. However, acid deposition cannot account for the widespread coherence shown in Fig. 1, nor do kinetic models alone seem to offer a good explanation, given the frequently low NO_3^- values even in regions with high N loading to watersheds (Fig. 1c).

Here we develop and test a model (Supplementary Fig. 1) that describes how shifts in elemental limitation may drive organic C–NO_3^- patterns by governing the relative rates of key microbial processes that couple dissolved C and N cycling. All organisms require energy and nutritional resources in characteristic stoichiometric ratios[4], which couple the global N cycle to other biogeochemical cycles in predictable ways[4,11,18–21]. The point at which growth limitation shifts from one element to another owing to inadequate supply of an energy or nutritional resource is known as the threshold elemental ratio[4,21]. Critical thresholds can underlie ecological processes when organisms that encounter nutritionally imbalanced resources maintain stoichiometric homeostasis by recycling or avoiding the element in excess[4,12,21]. For example, critical threshold ratios are known to prompt phosphorus and N accrual in aquatic and soil systems, respectively, when resource organic C:nutrient ratios fall below the requisite ratios of biomass construction.

C:N ratios of microbial biomass vary widely, from a low of ~3 to a high of ~20 (refs 4, 18, 20). In addition, critical supply ratios are higher than microbial C:N tissue quotients because heterotrophic microbes use some of their organic C resource for energy production and building new cellular material. However, such bacterial growth efficiency varies widely, often in response to the trophic state of the ecosystem[22–24]. In oligotrophic conditions, with high resource C:N ratios and relatively low C lability, bacterial growth efficiency tends to

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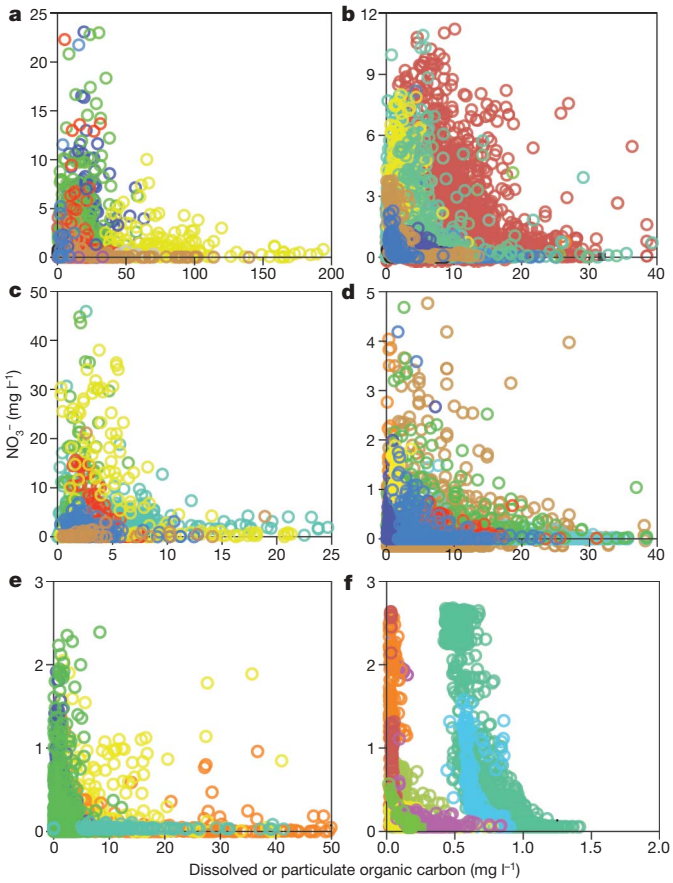

Figure 1 | NO_3^- concentration as a function of DOC or POC concentration among Earth's major ecosystems. Data were gathered from ecosystems in tropical, temperate, boreal and arctic regions, and include data sets collected on local, watershed, regional, national and global scales. **a**, Soils. **b**, Groundwaters, streams and rivers. **c**, Human-disturbed streams and rivers are waterways within the USA, which are predominantly influenced by agricultural activities. **d**, Lakes, ponds and wetlands. **e**, Estuaries, bays and coastal margins. **f**, Seas and oceans: the separation of the pattern reflects biogeochemical differences in C richness among distinct ocean provinces. See Table 1 for statistical analyses and Supplementary Table 1 for references used. Axes are truncated for best observation of data.

range between 5% and 20% (refs 22–24). In contrast, bacterial growth efficiency values in nutrient-rich systems are much higher and typically range between 40% and 80% (refs 22, 24). Moreover, bacteria exhibiting compositional plasticity can modify threshold ratios because biomass C:N can shift in concert with changes in resource C:N ratios[25]. Such capability can shift the point at which N is in excess relative to heterotrophic demand. We note that microbial C:N ratios tend to decline as N supply increases relative to C[25]. This, coupled with data showing that bacterial growth efficiencies reach their peak in nutrient-rich conditions, suggests that the critical ratio determining a switch from N to C limitation of microbial anabolism—and thus the point at which NO_3^- concentrations may rise sharply—should approach the low end of the microbial C:N tissue quotient range. Hence, the flexibility inherent in both bacterial growth efficiency and tissue stoichiometry probably underlies the variation in threshold ratios seen in Fig. 1 (see Supplementary Discussion).

We first tested this notion by comparing rates of microbial NO_3^- assimilation to POC:NO_3^- ratios in marine biomes, for which data on gross rates NO_3^- assimilation are most widely available. We use POC as the organic C resource because it reflects the bioavailable pool of marine organic C better than does DOC, which is typically comprised of older and more recalcitrant material[18]. We found POC:NO_3^- breakpoint ratios between 4 and 14 across three distinct ocean biomes, as

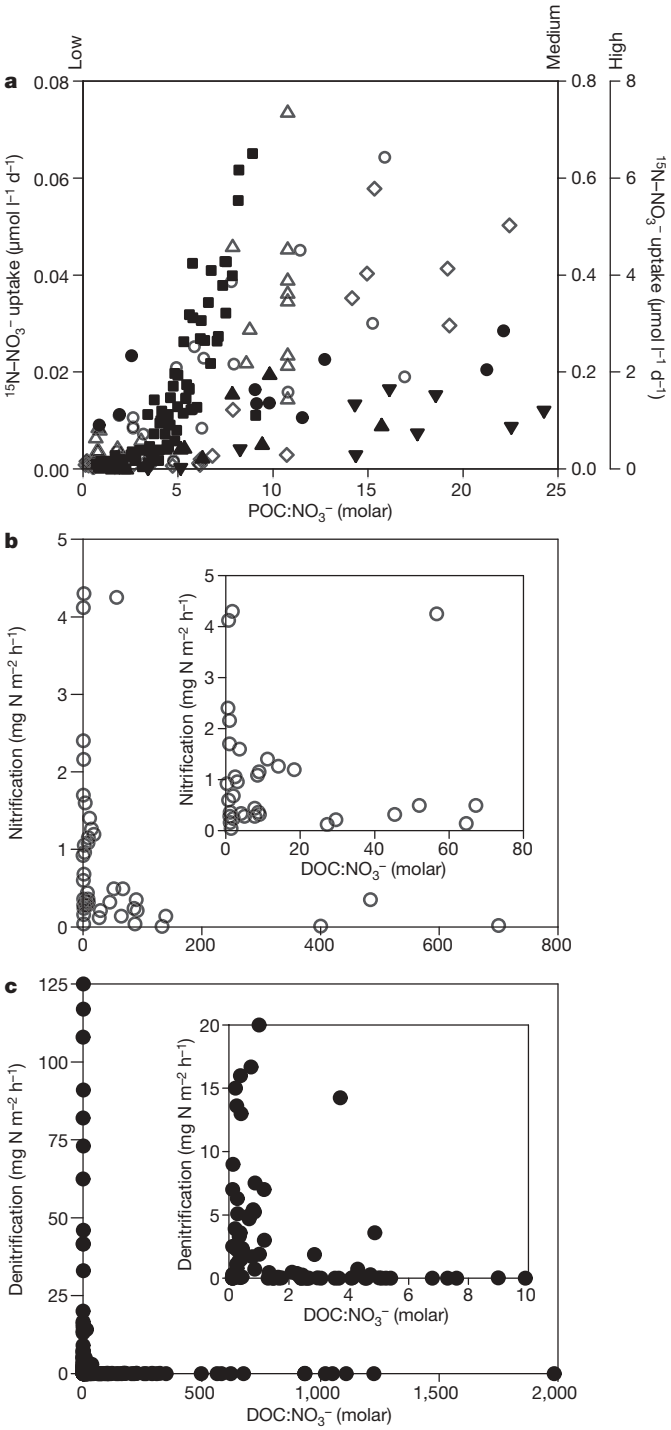

Figure 2 | Resource stoichiometry controls on microbial NO_3^- processing. a, Regression of planktonic isotopically labelled ^{15}N-NO_3^- uptake on oceanic POC:NO_3^- ratios. Low uptake rates occur in the Atlantic (white diamonds) and Lake Superior (inverted black triangles). Medium uptake rates occur in the Equatorial Pacific (white triangles), Southern Ocean (black squares), the English Channel (black triangles) and the Pacific upwellings (black diamonds). High uptake rates occur in the Scheldt Estuary (white circles) and Rio de Ferrol (black circles). Medium and high uptake rates are shown on the right *y*-axis in the same units. See Supplementary Discussion for details on data assembly and Supplementary Table 2 for statistical analysis. **b**, **c**, Regression of in-stream nitrification and denitrification on DOC:NO_3^- ratios, respectively. The inset panels in **b** and **c** simply show the low values more clearly.

well as coastal, estuarine, riverine and lacustrine ecosystems (Fig. 2a; see Methods). Commonly available ^{15}N–NO_3^- uptake data do not distinguish between phytoplankton and bacterial N assimilation.

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However, using data from three marine systems, we found that strong increases in bacterial production track the rise in threshold ratios seen for N uptake across a gradient of eutrophic to oligotrophic conditions (Fig. 2a; Supplementary Figs 2 and 3; Supplementary Table 3). In contrast, we found that autotrophy was largely unrelated to C:N breakpoints (Supplementary Fig. 2c, d; Supplementary Table 3, Supplementary Discussion).

Thus, we believe these patterns may reflect a contemporary view of marine N cycling, in which bacterioplankton significantly contribute to NO_3^- uptake, regeneration and nitrification[26]. This pattern suggests that high N assimilation by heterotrophs activates only when resources and theoretical consumer stoichiometry come into balance. As POC:NO_3^- ratios rise above minimal ratios near to 4, resource C:N composition becomes increasingly N-poor relative to the microbial N assimilation stoichiometry for anabolism, and NO_3^- concentrations remain consistently low. Most notably, declines below a POC:NO_3^- ratio of 4 probably reflect increasing C limitation of microbial anabolism, suggesting that stoichiometric controls over heterotrophic activity regulate NO_3^- build-up.

Of course, NO_3^- is not the only potential N source for microbial activity in these environments. However, in both freshwater and marine ecosystems, inorganic N pools tend to be dominated by NO_3^- (refs 7, 9, 27), and using a subset of representative sites from oceans and streams, we find that including ammonium (NH_4^+) does not alter inverse relationships (Supplementary Fig. 4a, c and Supplementary Table 4). In contrast, dissolved and particulate organic forms of N display positive correlations with their organic C counterparts (DOC and POC; Supplementary Fig. 4b, d), but this is expected given that the vast majority of organic matter in ecological environments contains both C and N in fairly constrained ratios[4,18–20].

NO_3^- accumulation may also be driven by nitrification, which could be enhanced as a consequence of C limitation of heterotrophic N assimilation. Heterotrophic organisms often out-compete nitrifying organisms for NH_4^+, but that effect will be strongest when N supply limits metabolism. Consequently, when N assimilation is C-limited at low DOC:NO_3^- ratios, enhanced NH_4^+ availability may promote nitrification. Indeed, we find that across streams with wide variation in adjacent land-use and underlying biome-scale differences, resource controls on nitrification are more complex than basic concentration-dependent uptake kinetics (Supplementary Fig. 5e, f and Supplementary Table 5). Instead, nitrification rapidly increases at resource ratios below the minimum supply C:N ratios for heterotrophic microbes (Fig. 2b).

As with heterotrophic assimilation and nitrification (Supplementary Fig. 5a, b, e, f), the availability of both organic C and NO_3^- regulates denitrification (as emphasized by Supplementary Fig. 5c, d). Unlike the anabolic process of NO_3^- uptake explored above, denitrification is a catabolic process that requires organic C and NO_3^- in an approximately 1:1 ratio (when biomass synthesis is ignored). Our meta-analysis revealed that denitrification activity abruptly responds with increases up to 125-fold at DOC:NO_3^- ratios that are in line with the stoichiometric requirements (Fig. 2c). For systems in which NO_3^- accumulation continues at very low organic C:NO_3^- ratios, other environmental factors (for example, oxic conditions) may constrain denitrification activity.

Taken as a whole, the above analyses of marine and stream ecosystems suggest that N assimilation, nitrification and denitrification probably all contribute to the comparative uniformity of the patterns in Fig. 1. Thus, we explored whether organic C:NO_3^- ratios at the inflection point of each exponential model (Table 1) to see whether the threshold C:N ratios for each major environment align with the breakpoints found in Fig. 2. We focused on DOC:NO_3^- ratios in all systems except oceans because POC in non-pelagic systems may encompass a greater proportion of terrigenous, recalcitrant C[28,29], which would explain the higher POC:NO_3^- ratios for those systems (Table 1). We find that despite wide variation in pools of organic C and NO_3^- among the Earth's ecosystems (Fig. 1), the DOC:NO_3^- ratio at the inflection point averages 3.5 across all systems and is constrained between 2.2 and 5.2 (Table 1). At the global scale, threshold ratios are greater for lakes and ocean margins when POC is used in the numerator (Table 1), as well as for several system-specific scenarios (Supplementary Fig. 6; Supplementary Table 6). These higher ratios rest within the expected stoichiometric window for NO_3^- accretion, and probably reflect the response of bacterial compositional plasticity and growth efficiency to organic C bioavailability (see Supplementary Discussion). When viewed across all systems and scales of observation, NO_3^- tends to rise sharply at organic C:NO_3^- requirements between those of heterotrophic assimilation and those of denitrification, a pattern which may arise from both an alleviation of N limitation to many heterotrophs and an increase in nitrification rates.

Finally, we believe the increase in the exponential decay constant k from soils to the sea reveals a systematic (Table 1) decline in energetic constraints over NO_3^- cycling along the hydrologic continuum. Where terrestrial plant derivatives dominate DOC pools, more chemically complex, decay-resistant compounds are more prevalent than in systems where aquatic sources prevail[28,29]. In fact, k for human-disturbed rivers and streams is more similar to k for soils than to k for undisturbed rivers and streams (Table 1), which suggests increased terrestrial DOC inputs to freshwater systems in landscapes susceptible to anthropogenic run-off. Also, the concurrent decline in unexplained variation in DOC–NO_3^- relationships from soils to the sea (Table 1) may support a weakening influence of C quality on the expression of resource–consumer imbalance as organic C supply shifts from terrestrial to aquatic sources. Taken together, these trends might signal a progressive shift towards increasingly pure stoichiometric control in marine environments versus freshwaters with substantial allochthonous sources of C.

In this paper, we have attempted to link stoichiometric and metabolic theories of ecology[30] to develop a new context in which to understand

Table 1 | Analysis of global organic C–NO_3^- trends

Global system	DOC observations (%)	Modelled parameters ($y = a + b^{-k(x)}$)			Model fit (r^2)	Molar C:NO_3^- at inflection point (x, y)
		a	b	k		
Soils	100	0.85	1.72	0.13	0.25	5.22 (7.03,1.56)
Streams/rivers	45	0.94	1.67	0.32	0.26	4.79 (10.12, 2.41)
Streams/rivers	100	1.20	1.51	0.40	0.28	3.12 (4.04,1.50)
Human-disturbed streams/rivers	100	2.95	2.61	0.14	0.24	3.29 (10.42, 3.67)
Lakes/wetlands	26	0.05	1.25	1.39	0.35	15.7 (1.97, 0.13)
Lakes/wetlands	100	1.19	1.51	0.31	0.42	4.76 (0.76, 0.16)
Ocean margins	31	0.02	2.11	1.38	0.44	16.7 (2.02, 0.14)
Ocean margins	100	0.12	0.43	3.55	0.39	2.19 (3.68, 1.68)
Oceans (high C)	0	0.33	26.21	4.86	0.50	3.79 (0.20, 0.06)
Oceans (low C)	0	0.19	0.78	8.15	0.47	2.67 (0.76, 0.33)

'Human-disturbed streams and rivers' includes systems in agricultural and urban landscapes (see Supplementary Notes). Assembled databases contained paired NO_3^- with DOC, POC or total organic carbon observations. For 'Streams/rivers', 'Lakes/wetlands' and 'Ocean margins', exponential models were fitted to data using DOC, POC and total organic carbon observations together (first row of each pair) and DOC only (second row of each pair). (We separated organic carbon observations for reasons described in the text.) An exponential model with three estimated parameters was chosen based on root-mean-squared error comparisons with one- and two-parameter exponential models. Parameters a, b and k were optimized using the root-mean-squared error criterion (versus regression coefficient) with a ''trust-region'' least-squares curve-fitting procedure. All exponential models are significant at $P < 0.001$. We used the second derivative of the exponential model to find the x, y coordinate at the inflection point of each exponential model to determine the molar C:N ratio for organic C:NO_3^- in each environment. The organic C:NO_3^- is reported molar whereas x, y coordinates are mass based (mg l^{-1}) for visual comparison with Fig. 1.

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coupled organic C and NO_3^- cycling from local to global scales. We believe the framework presented here may aid a variety of reactive N-related management challenges. For instance, downscaling from our global analysis to a variety of system-specific scenarios shows that DOC–NO_3^- relationships become stronger (Supplementary Fig. 6 and Supplementary Table 6). Such analyses, when done at management-related scales, could allow management strategies that focus on a subset of conditions to direct the fate of NO_3^-. For example, resource ratios could be strategically regulated to optimize heterotrophic NO_3^- assimilation, where high NO_3^- accumulation rarely occurs.

That said, we do not advocate a stoichiometric perspective to the exclusion of kinetic, thermodynamic and mass-balance approaches. Indeed, substantial variation in organic C–NO_3^- relations suggests the importance of environmental factors in addition to stoichiometric controls. Thus, we believe that better integration of established applications with the first principles of ecological stoichiometry would improve a range of diagnostic and prognostic models of water quality. Achieving this goal will require continued evaluation of the mechanisms that underlie inverse organic C–NO_3^- patterns. Furthermore, additional research should resolve key uncertainties in what determines C–NO_3^- thresholds; we believe a focus on the controls over microbial compositional plasticity and growth efficiency is particularly important. Nonetheless, the results presented here provide a testable framework for further unravelling the controls over NO_3^- accumulation in ecosystems worldwide.

METHODS SUMMARY

All references to NO_3^- in the above text, as well as all analyses, refer to the atomic portion of N in nitrate, and organic C:NO_3^- ratios refer to the molar C:N ratio of the two constituents. Databases are available via online data repositories and published literature (see Supplementary Notes). Colour distinctions for data sets used in Fig. 1 are listed in Supplementary Table 1. Oceanic databases were downloaded from the Biological and Chemical Oceanography Data Management Office (we used the Woods Hole Oceanographic Institution data portal, http://www.whoi.edu/page.do?pid=7140). Databases from the CARIACO, EDDIES, Arabian Sea, Equatorial Pacific, Ocean Margins, North Atlantic Bloom Experiment, Southern Ocean, Bermuda Atlantic Time-Series Study and Hawaii Ocean Time-Series projects were used. The US EPA monitoring and assessment program (http://www.epa.gov/emap/) provided estuary, wetland, lake and stream ecosystems, including data from the Chesapeake Bay, the Mid-Atlantic Integrated Assessment, the Western Lakes Survey, the Eastern Lakes Survey, the EMAP Lakes and Streams Survey and the National Surface Water Survey. The NSF-sponsored Long-term Ecological Research program data network (http://metacat.lternet.edu/knb/) also served as a data source for estuarine, lacustrine, soil solution and stream chemistry from the Florida Coastal Everglades, Plum Island Ecosystem, Northern Temperate Lakes, Niwot Ridge, Bonanza Creek, Luquillo, Coweeta, Andrews, Virginia Coastal Reserve and Hubbard Brook LTERs. The European Environment Agency (http://dataservice.eea.europa.eu/dataservice/) served as the source for stream, river and lake water-quality data. Additional stream chemistry data was accessed through the Pan-Arctic River Transport of Nutrients, Organic Matter, and Suspended Sediments (http://ecosystems.mbl.edu/partners/data.html) programme, the Brazil Streams project at the Woods Hole Ecosystems Center (http://ecosystems.mbl.edu/brazilstreams/), and a large-scale and long-term Amazon River project, CAMREX (http://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=904). In the Supplementary Notes, references 31–58 were used to compile data for Fig. 2 and Supplementary Figs 4 and 5. Data for Supplementary Fig. 2a and b was obtained from the US Joint Global Ocean Flux Study database for the North Atlantic, Equatorial Pacific and Southern Ocean. Supplementary references 58–83 were used in Fig. 1.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions P.G.T. conceived the project, gathered the requisite data, and performed statistical analyses. P.G.T and A.R.T. developed the conceptual model, interpreted the empirical findings, and wrote the manuscript.

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