Global nutrient transport in a world of giants

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The past was a world of giants, with abundant whales in the sea and large animals roaming the land. However, that world came to an end following massive late-Quaternary megafauna extinctions on land and widespread population reductions in great whale populations over the past few centuries. These losses are likely to have had important consequences for broad-scale nutrient cycling, because recent literature suggests that large animals disproportionately drive nutrient movement. We estimate that the capacity of animals to move nutrients away from concentration patches has decreased to about 8% of the preextinction value on land and about 5% of historic values in oceans. For phosphorus (P), a key nutrient, upward movement in the ocean by marine mammals is about 23% of its former capacity (previously about 340 million kg of P per year). Movements by seabirds and anadromous fish provide important transfer of nutrients from the sea to land, totalling ~150 million kg of P per year globally in the past, a transfer that has declined to less than 4% of this value as a result of the decimation of seabird colonies and anadromous fish populations. We propose that in the past, marine mammals, seabirds, anadromous fish, and terrestrial animals likely formed an interlinked system recycling nutrients from the ocean depths to the continental interiors, with marine mammals moving nutrients from the deep sea to surface waters, seabirds and anadromous fish moving nutrients from the ocean to land, and large animals moving nutrients away from hotspots into the continental interior.

biogeochemical cycling | extinctions | megafauna | whales | anadromous fish

> There were giants in the world in those days.
>
> Genesis 6:4, King James version

The past was a world of giants, with abundant whales in the oceans and terrestrial ecosystems teeming with large animals. However, most ecosystems lost their large animals, with around 150 mammal megafaunal (here, defined as ≥44 kg of body mass) species going extinct in the late Pleistocene and early Holocene (1, 2). These extinctions and range declines continued up through historical times and, in many cases, into the present (3). No global extinctions are known for any marine whales, but whale densities might have declined between 66% and 99% (4–6). Some of the largest species have experienced severe declines; for example, in the Southern Hemisphere, blue whales (*Balaenoptera musculus*) have been reduced to 1% of their historical numbers as a result of commercial whaling (4). Much effort has been devoted to determining the cause of the extinctions and declines, with less effort focusing on the ecological impacts of the extinctions. Here, we focus on the ecological impacts, with a specific focus on how nutrient dynamics may have changed on land following the late-Quaternary megafauna extinctions, and in the sea and air following historical hunting pressures.

Most biogeochemists studying nutrient cycling focus on in situ production, such as weathering or biological nitrogen (N) fixation, largely ignoring lateral fluxes by animals because they are considered of secondary importance (3). The traditional understanding of biogeochemistry is that "rock-derived" nutrients originate with the weathering of primary rock. These nutrients are then lost to the hydrosphere by leaching or runoff or to the atmosphere by dust, fire, or volatilization. These nutrients slowly make their way to the oceans, where they are buried at the bottom of the sea. Eventually, these sediments are subducted, transformed to metamorphic or igneous rock, and uplifted to be weathered once again. We are left with an impression that nutrient cycling in adjacent landscapes or gyres is disconnected except through the atmosphere or hydrosphere, and that animals play only a passive role as consumers of nutrients. However, this notion may be a peculiar world view that comes from living in an age where the number and size of animals have been drastically reduced from their former bounty. We must wonder: What role do animals play in transporting nutrients laterally across ecosystems on land, vertically through the ocean, or across the ocean land divide?

Animal digestion accelerates cycling of nutrients from more recalcitrant forms in decomposing plant matter to more labile forms in excreta after (wild or domestic) herbivore consumption on land (7). For instance, nutrients can be locked in slowly decomposing plant matter until they are liberated for use through animal consumption, digestion, and defecation. This process has been theorized to have played a large role in the Pleistocene steppes of Siberia. Abundant large herbivores ate plants that were rapidly decomposed in their warm guts, liberating the nutrients to be reused. However, following extinctions of these animals, nutrients were hypothesized to have been locked into plant matter that is decomposing only slowly, making the entire ecosystem more nutrient-poor (8). Similarly, at present times, large herbivores enhance nutrient cycling in the grazing lawns of the Serengeti (9).

What role do animals play in the spatial movement of nutrients? This question is especially pertinent because animals are most likely to influence the flow of nutrients that are in short supply. There are now a large number of site-level studies that have demonstrated how

Significance

Animals play an important role in the transport of nutrients, but this role has diminished because many of the largest animals have gone extinct or experienced massive population declines. Here, we quantify the movement of nutrients by animals in the land, sea, rivers, and air both now and prior to their widespread reductions. The capacity to move nutrients away from hotspots decreased to 6% of past values across land and ocean. The vertical movement of phosphorus (P) by marine mammals was reduced by 77% and movement of P from sea to land by seabirds and anadromous fish was reduced by 96%, effectively disrupting an efficient nutrient distribution pump that once existed from the deep sea to the continental interiors.

animals move nutrients from one site to another or across ecosystem boundaries. For example, moose (*Alces americanus*) transfer significant amounts of aquatic-derived N to terrestrial systems, which likely increases terrestrial N availability in riparian zones (10). Terrestrial predators (e.g., bears, otters, and eagles) feeding on anadromous fish that move from the ocean to freshwater to spawn can transport ocean-derived nutrients to terrestrial ecosystems, a process that has been verified by isotopic analysis (11). Hippopotamuses (*Hippopotamus amphibius*) supplement aquatic systems with terrestrial-derived nutrients, which strongly enhance aquatic productivity (12). Seabirds transport nutrients from the sea to their breeding colonies onshore (13, 14). Studies have documented increases of soil phosphorus (P) concentrations on seabird islands compared with non-seabird islands that were much stronger than for soil %N and present in soils for up to thousands of years (14). In some sites, increased soil P more than doubled plant P concentrations, but this concentration varied substantially from site to site (14). Furthermore, seabirds and marine mammals play an important role as nutrient vectors aiding in the redistribution of micronutrients, such as iron (Fe) (15). Despite their vastly decreased numbers, the important role of whales in distributing nutrients is just now coming to light. Whales transport nutrients laterally, in moving between feeding and breeding areas, and vertically, by transporting nutrients from nutrient-rich deep waters to surface waters via fecal plumes and urine (16–18). Studies in the Gulf of Maine show that cetaceans and other marine mammals deliver large amounts of N to the photic zone by feeding at or below the thermocline and then excreting urea and metabolic fecal N near the surface (17).

More recently, studies have demonstrated that animals can diffuse significant quantities of nutrients from areas of high nutrient concentration to areas of lower nutrient concentration even without mass flow of feces out of the fertile area. For instance, woolly monkeys (*Lagothrix lagotricha*) in Amazonia transported more P than arrives from dust inputs across a floodplain concentration gradient, without preferentially defecating in the less fertile area, merely by eating and defecating back and forth across the nutrient concentration gradient (19). If a small single species can transport such significant quantities of P, what is the role of all animals in an ecosystem over long periods of time? Two recent studies compiled size relationship data for terrestrial mammals within a random-walk mathematical framework and found that the distribution of nutrients away from a concentration gradient is size-dependent, with larger animals having disproportionally greater importance to this flow of nutrients than smaller animals (20, 21). For the Amazon basin, it was estimated that the extinction of the megafauna may have led to a >98% reduction in the lateral transfer flux of the limiting nutrient P, with large impacts on ecosystem P concentrations in regions outside of the fertile floodplains (20, 21).

If large animals are of disproportionate importance, then the obvious question is: What was this nutrient movement like in the past, in a world of giants, when mean animal size was much greater on land and at sea? Furthermore, what was the role of animals in returning nutrients from sea to land, against the passive diffusion gradients? Seabirds and anadromous fish are two important animal groups for the transport of nutrients from sea to land. Both groups are also facing pressure, and 27% of all seabirds are classified as threatened (critically endangered, endangered, or vulnerable), and the largest of all seabirds, the albatross, is the most endangered, with up to 75% of albatross species considered threatened or endangered (22–24)]. Likewise, populations of anadromous fish have declined to less than 10% of their historical numbers in the Pacific Northwest (25) and both the northeastern and northwestern Atlantic (26, 27). There have been many individual site-level studies showing the importance of animals in distributing nutrients, but as far as we are aware, no previous study has attempted to estimate at a global scale how this distribution has changed from the time before human-caused extinctions and exploitation up to today in the oceans, air, rivers, and land. In this study, we aim to estimate three things: (*i*) the lateral nutrient distribution capacity of terrestrial and marine megafauna, (*ii*) the global vertical flux of nutrients to surface waters by marine megafauna, and (*iii*) the global flux of nutrients by seabirds and anadromous fish from the sea to land.

Results

Lateral Nutrient Distribution Capacity by Terrestrial Mammals and Whales. We used a "random walk" mathematical formulation (28) (mathematically formulated in Eq. **1** in *Methods* and *SI Appendix*) to calculate a global per pixel nutrient diffusivity in units of square kilometers per year (these units are of diffusivity and signify the ability of nutrients to move away from a nutrient concentration gradient, just like thermal diffusivity indicates the ability of a surface to move heat away from a hot area). We estimate that the global mean nutrient distribution capacity before the late-Quaternary extinctions averaged 180,000 $km^2 \cdot y^{-1}$ on the land surface and that it is currently 16,000 $km^2 \cdot y^{-1}$, ~8% of its former value (Table 1; detailed methodology is provided in *Methods* and *SI Appendix*). However, there is much regional variation. For example, in parts of Africa, such as Kruger National Park in South Africa, capacity is still close to 100% of what it once was in the Late Pleistocene, whereas other regions, such as southern South America, are at less than 0.01% of previous values (Fig. 1). Before the extinctions, nutrient distribution capacity was much more evenly spread than it is currently, with most of the current capacity only in Africa, where extensive megafauna remain. Every continent outside Africa (Africa is at 46% of its late-Quaternary value) is at less than 5% of the original value, with the largest change in South America (~1% of the original value; Table 1). Historical range reduction of species also played an important role in the decrease of the lateral nutrient flux, and we estimate that without the range reduction of large species (excluding all extinctions) the capacity would be 37% higher compared with today's baseline. Each estimated value is based on a number of assumptions that we explore in a sensitivity study (*SI Appendix,* Tables 1 and 2).

Nutrient Movement by Marine Mammals. We calculated lateral diffusion capacity for 13 species of great whales (*SI Appendix*, Table 3) and estimated that the capacity in the Southern Ocean is 2% of its historical value, with slightly higher values in the North Pacific (10%) and the North Atlantic (14%) (Fig. 2 *A–C* and Table 1). Mean nutrient diffusion capacity is larger for the great whales than for terrestrial animals at natural capacity (640,000 $km^2 \cdot y^{-1}$ for great whales vs. 180,000 $km^2 \cdot y^{-1}$ for terrestrial mammals). Because of their enormous size and high mobility (and despite having many fewer species), great whales might have once transported nutrients away from concentration gradients more efficiently than terrestrial mammals.

Marine mammals can also distribute nutrients vertically in oceans (Fig. 2 *D–F*). We calculate nutrient fluxes caused by animals in terms of the frequently limiting nutrient, P, which serves as a proxy for other limiting elements, such as N and Fe. We calculate this vertical distribution of nutrients for nine marine mammals (*SI Appendix*, Table 4) and find that they moved a global total of ~340 million (260–430 million; *SI Appendix*, Table 2) kg of P per year from the depth to the surface waters before widespread hunting and that they now move ~75 million (54–110 million; *SI Appendix*, Table 2) kg of P per year, representing a decrease to 23% of original capacity (Fig. 2 *D–F* and Table 1). We also found vast regional differences: Vertical transport capacity in the Southern Ocean is now ~16% of its historical value, but there are higher values in the North Pacific (34%) and the North Atlantic (28%). We compare our estimates of P movement at natural capacity by marine mammals with quantities of ocean P concentrations that were measured by the Ocean Climate Laboratory (details are provided in *SI Appendix*) and estimate that on a yearly basis, in the past, marine mammals could have increased surface concentrations by up to 1% per year in the Southern Ocean [2.5 $kg \cdot km^{-2} \cdot y^{-1}$ added to a mean concentration of 248 $kg \cdot km^{-2}$, although other calculations have suggested that the effect on trace elements could be even higher (29)], which could result in considerable stock changes in surface P over time.

Nutrient Distribution from the Ocean to Land by Seabirds and Anadromous Fish. Based on global range maps of seabirds and their body masses, we calculate coastal consumption by seabirds and assume 20% (5 to 35%) of guano reaches land (methods on

Table 1. Average global and regional estimates of nutrient distribution capacity (km^2·y^{-1}) for terrestrial mammals and whales, and global and regional estimates of vertical nutrient movement of P (kg·y^{-1}) by all diving marine mammals and sea-to-land total P movement (kg·y^{-1}) by seabirds and anadromous fish

Units	Total land average	Total ocean average	Africa	Australia	Eurasia	North America	South America	Southern Ocean	North Atlantic	North Pacific
					Nutrient distribution capacity					
Past mean, km^2·y^{-1}	Land mammals 1.8e5	Great whales 6.4e5	Land mammals 1.28e5	Land mammals 0.15e5	Land mammals 2.77e5	Land mammals 2.39e5	Land mammals 1.53e5	Great whales 11e5	Great whales 4.0e5	Great whales 2.7e5
Current mean, km^2·y^{-1}	1.6e4	3.2e4	6.67e4	467	1.13e4	0.42e4	0.17e4	0.22e5	0.57e5	0.25e5
%	8%	5%	46%	3%	4%	2%	1%	2%	14%	10%
					P movement					
Past total, kg P·y^{-1}	A. fish 1.4e8 kg·y^{-1} Seabirds 6.3e6 ± 5e6	Marine mammals 3.4e8 kg·y^{-1}	A. fish 1.9e6 kg·y^{-1} Seabirds 0.89e6 ± 0.66e6	A. fish 0.4e6 kg·y^{-1} Seabirds 0.79e6 ± 0.6e6	A. fish 69e6 kg·y^{-1} Seabirds 2.4e6 ± 1.8e6	A. fish 51e6 kg·y^{-1} Seabirds 0.99e6 ± 0.7e6	A. fish 0.5e6 kg·y^{-1} Seabirds 0.89e6 ± 0.6e6	Marine mammals 1.7e8	Marine mammals 0.9e8	Marine mammals 0.7e8
Current total, kg P·y^{-1}	A. fish 5.6e6	Marine mammals 7.9e7 kg·y^{-1}	A. fish 0.1e6	A. fish 0.01e6	A. fish 3.2e6	A. fish 2.3e6	A. fish 0.02e6	2.8e7	2.6e7	2.4e7
%	4%	23%	NA	NA	NA	NA	NA	16%	28%	34%

(*Top*) Average global and regional estimates of nutrient distribution capacity (km^2·y^{-1}) based on Eq. **1** for terrestrial mammals and for whales (*SI Appendix,* Table 3). Percentages are the current value divided by the past value. (*Bottom*) Global and regional estimates of vertical nutrient movement of P (kg·y^{-1}) by all diving marine mammals (*SI Appendix,* Table 4) and sea-to-land total P movement (kg·y^{-1}) by seabirds and anadromous (A.) fish (*SI Appendix,* Table 5). We assume that 20% (ranging between 5% and 35%) of seabird guano produced arrives on coastal land. We assume our calculations for seabird populations are representative of past, not current, populations because they are based on theoretical population densities (43). NA (not available) represents regions where there are not sufficient data for an estimate. A sensitivity study for each number is provided in *SI Appendix,* Tables 1 and 2.

how 20% was calculated are provided in *SI Appendix*). Therefore global averaged sea-to-land movement of P is 0.19 ± 0.15 kg of P km^{-2}·y^{-1} in coastal regions, but varies by an order of magnitude throughout the planet, with peaks in the Southern Hemisphere (Fig. 3 and Table 1). These estimates are calculated based on theoretical population densities (30), and it is probably closer to theoretical historical values than to actual values today. When averaged by coastal continental area, we find a maximum in Oceania, with 0.31 ± 0.23 kg of P km^{-2}·y^{-1}, and lower values in North America, with 0.16 ± 0.12 kg of P km^2·y^{-1}. We calculate a global flux of 6.3 million (1.5–16 million; *SI Appendix,* Table 2) kg km^{-2}·y^{-1} of P from sea to land by the seabirds, with almost half moving onto the Eurasian landmass (Table 1).
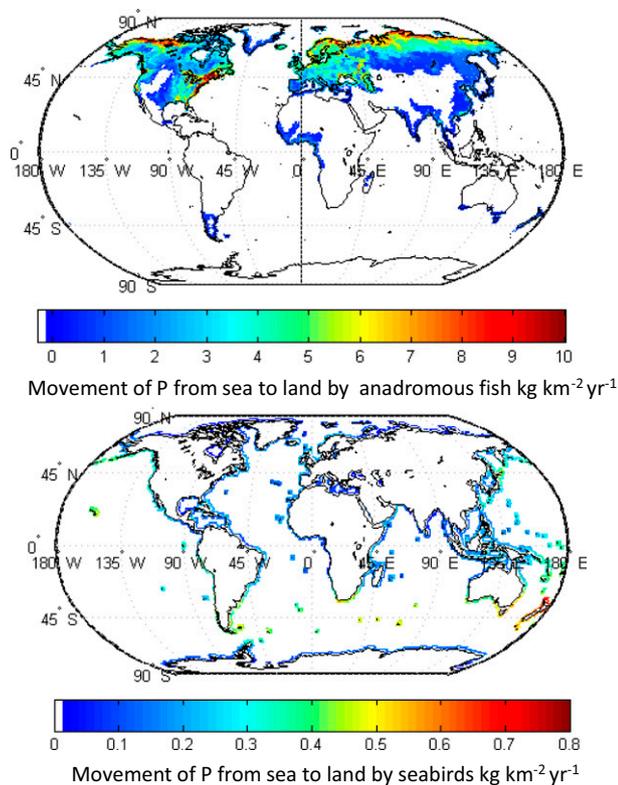
It is estimated that there are 110 species of anadromous fish, such as salmon, that migrate from oceans to rivers to breed and eventually die (*SI Appendix,* Table 5) (31). Using range maps for 42 of these species, and an additional 47 closely related species as proxies for the missing range maps, we estimate that, historically, anadromous fish may have moved at least an order of magnitude more P from ocean to land [140 million (71–430 million) km^2·y^{-1}; *SI Appendix,* Table 2] than seabirds [6.3 million (1.5–16 million) km^2·y^{-1}; *SI Appendix,* Table 2], but this estimated value has decreased to ~4% (5.6 million km^2·y^{-1}) of the original value. These values are not evenly distributed, and there are much higher values in the Northern Hemisphere and at high latitudes than in more tropical latitudes. Each value has many uncertainties involved in its calculation, which we explore in a sensitivity study (*SI Appendix,* Tables 1 and 2).

Discussion

We estimate that the decimation of terrestrial megafauna and whales has reduced the ability of animals to distribute nutrients away from regions of nutrient abundance to ~6% of global natural capacity. Did this change make the planet less fertile? We do not calculate changes to fertility from lateral diffusivity declines because accurate global maps of nutrient hotspots necessary for such a calculation do not exist at the necessary resolution. Previous experimental studies, however, have found that animals move significant quantities of nutrients across concentration gradients despite not necessarily moving dung from fertile to nonfertile areas (11, 14, 19). Regional models found that the transfer of P away from the Amazonian floodplains may have dropped by more than 50% following the extinction of the Amazonian megafauna (20, 21). We hypothesize that such a drop in nutrient diffusion capacity would have decreased nutrient concentrations in regions that are distant from their abiotic sources (deposited by either wind or water), resulting in broad global regions being less fertile.

On land, large disparities in animal sizes and total animal numbers led to differences in nutrient distribution capacity both before and following the extinctions due to regional disparities in extinctions. For instance, South America once had the largest nutrient distribution capacity, but following the Late-Pleistocene extinctions, it experienced the largest drop, to ~1% of its original continent-wide capacity. With accurate megafauna range maps, we can pinpoint regions with especially large drops. For instance, southern South America once had the largest number of megaherbivores (>1,000 kg, n = 15), all of which went extinct (32). This large number of megaherbivores gave it, before the extinctions, the largest estimated present natural lateral diffusion capacity of

Fig. 1. Lateral nutrient distribution capacity (km²·y⁻¹) by terrestrial mammals. Lateral diffusion capacity (Φ; Eq. **1**) of nutrients by all mammals as it would have been without the end-Pleistocene and Holocene megafauna extinctions and extirpations (*Top*), as it is currently (*Middle*), and as the percentage of the original value (*Bottom*).

their often single-cellular nature, and due to this faster turnover time, nutrients, especially limiting nutrients, should be converted to primary producer biomass more quickly in the oceans. Furthermore, a much larger share of primary production in oceans (algae) is consumed compared with terrestrial primary producers (35). The nutrients transported by whales, or as a consequence of whale activity, should be assimilated more rapidly, and contribute to system productivity more directly than on land. Also, whales and their prey may help in retaining limiting nutrients (N, P, and Fe) in the surface layer and releasing these nutrients slowly into the water (18).

Seabirds may act as a link connecting nutrient concentrations in the oceans with nutrient concentrations on the land. Here, we have estimated that seabirds can increase P concentrations in coastal environments globally by ~6 million kg·y⁻¹ through the deposition of guano. Guano is generally deposited on steep cliffs or offshore islands generally inaccessible to most terrestrial animals. However, over long time scales, these nutrients may become accessible to terrestrial fauna as sea levels drop during the ice ages and sea cliffs erode. This flux of nutrients has almost certainly decreased through time as seabird populations have decreased [27% of seabirds are classified as threatened (22)] or gone extinct (e.g., the great auk, *Pinguinus impennis*) often due to, for instance, invasive mammal predators decimating seabird colonies (36). In the past, scavenging birds, such as condors, may also have acted as vectors of nutrients from the sea to the land. For example, during the Pleistocene, isotope data suggest that California condors (*Gymnogyps californianus*) fed on both terrestrial megafauna and marine mammals, but by the late 1700s, condor diets had shifted predominantly to terrestrial animals because there were fewer marine mammals to be harvested after likely having subsisted on marine carcasses across the Holocene, with inland populations going extinct at the end of the Pleistocene (37). This flux has certainly greatly decreased as both marine mammals and large scavengers have seen their numbers drop substantially (38).

Possibly, a more important form of sea-to-land nutrient transport comes from the migratory behavior of anadromous fish, which we estimate to bring at least an order of magnitude more nutrients from oceans to land than do seabirds. However, they have also experienced drastic population losses (25–27), and we estimate that the current nutrient flux is less than 4% of historic values, before overfishing and habitat modification, such as damming of rivers. Anadromous fish seem to be especially important vectors of nutrients

anywhere in the world. However, currently, with the largest animals in South America only weighing up to ~300 kg, continental nutrient distribution capacity has dropped to ~0.01% of its original value in some regions. However, in some regions, exotic and mainly domesticated ungulates may have partially taken over this role (33). Therefore, because southern South America had the largest change in capacity by animals to move nutrients away from abiotic sources, it may be a good test region to look for such changes in long-term nutrient deposition.

Marine mammals have seen broad population reductions due to widespread hunting over the past few hundred years (34). Such population decreases reduced the lateral distribution capacity and perhaps reduced the vertical distribution, allowing more nutrients to drop below the photic zone. This ability to spread nutrients vertically may be especially important, because once nutrients drop below the photic zone and into the deep ocean sediments, they are generally considered to be lost to the surface biota, and only tectonic movements and limited regions where water is uplifted, will further recycle them (16). Aquatic algae, which conduct most of the ocean's photosynthesis, have a much faster turnover time than land plants due to

Fig. 2. Horizontal and vertical nutrient distribution capacity by great whales. Lateral movement capacity (Φ, km²·y⁻¹; Eq. **1**) by great whales (listed in *SI Appendix*, Table 3) for past whale densities before widespread human hunting (*A*), current whale densities (*B*), and the percentage of the original value (i.e., current values divided by past values) (*C*). Vertical movement of nutrients by marine mammals (listed in *SI Appendix*, Table 4), log₁₀ kilograms of P per square kilometer per year (kg·Pkm⁻²·y⁻¹), for past marine mammal densities before widespread human hunting (*D*), current marine mammal densities (*E*), and the percentage of the original value (*F*).

Fig. 3. Nutrient movement of P from ocean to land by anadromous fish and seabirds. (*Top*) Global estimates of historical P (kg·km⁻²·y⁻¹) moved by the bodies of anadromous fish in the past. Nutrient movement by anadromous fish may be underestimated in tropical regions due to a lack of data. (*Bottom*) Global estimates of guano movement to coastal land by all seabirds, assuming 20% of the guano arrives on land (measured in kg·km⁻²·y⁻¹) and assuming theoretical population densities of seabirds based on body mass population density scaling relationships (43).

because they travel much further inland than seabirds (Fig. 3). It is uncertain what quantity of nutrients transported inland by the fish arrives onto *terra firma*, but it is clearly a function of river size, distance transported inland, and consumption of the fish by scavengers and predators. However, isotopic evidence indicates that significant quantities of ocean-derived nutrients from anadromous fish do enter terrestrial ecosystems (11). This loss of nutrients to these ecosystems from historic highs may have affected the entire ecosystem, including the fish themselves, and "contributed to the downward spiral of salmonid abundance and diversity in general" (25). We estimate the total flux of P from sea to land by anadromous fish and seabirds in the past (146 million kg of P per year) is still much less than the total P consumed by humans for fertilizers each year [48,500 million kg of phosphoric acid (as P₂O₅) in 2010 and growing at 1.9% per year (39)].

Before the widespread extinction of megafauna and hunting of whales, an interlinked system for the recycling of nutrients may have existed, where nutrients flowed against entropy from the ocean depths to continental interiors (Fig. 4). Marine mammals moved nutrients vertically to the surface, increasing productivity. This increased surface productivity increased available food for seabirds and anadromous fish, potentially increasing the flux of nutrients from sea to land. Finally, on longer time scales, coastal seabird island nutrient hotspots may become exposed to terrestrial fauna and spread toward continental interiors. For instance, most seabird islands are on the continental shelves, which became connected to the continent during interglacial periods, thus exposing the nutrient hotspots to terrestrial animals. Each step is potentially a nonlinear positive feedback of increasing productivity. Examples of such nonlinear feedbacks include shifts in plant productivity on islands where

foxes were removed and seabirds returned (40) and higher abundance of arthropods on bird islands with greater nutrient concentrations than on bird-free islands (41). Given these and many other connections, it is clear that although we can calculate each of these fluxes (marine mammals, seabirds, anadromous fish, and megafauna) separately, the net increase in global productivity is likely more than the sum that we have calculated of the four systems together.

Have domestic animals taken over the nutrient distribution roles of the now-extinct terrestrial megafauna? Although the biomass of domestic animals is now much greater than the total biomass of the extinct large terrestrial animals (42), there are two reasons why it is unlikely that they distribute nutrients in the manner that we believe existed in the world of giant megafauna. First, most domestic animals in the industrialized world are fenced in (or indoors), and fences constrain movement, thus stopping the diffusion of nutrients (fences are less common in the nonindustrialized world, although the animals may be fenced in at night). Second, most pastures have only a single animal type, such as cattle. A single species is more likely to have consistent behavior, eating in one place, defecating in another, and concentrating nutrients instead of dispersing them across gradients. By contrast, multiple species have different eating and defecating patterns and are more likely to diffuse nutrients across gradients. To restore this pattern, future pastures could be set up with fewer fences and with a wider range of species to simulate natural pastures; such mixed pastoral systems, with communally held unfenced ranges supporting mixed livestock, such as cattle, sheep, horses, goats, and camels, that are still in use in parts of the world. Free-ranging wild herbivores could also be restored to areas where they have long been absent; wildlife comebacks have been observed in some global regions, although the overall decline in biodiversity continues (43). In the oceans, there are fewer space constraints. The restoration of whale populations could increase productivity by transferring nutrients to oligotrophic areas and enhancing Fe and N at the ocean surface. These processes can regulate atmospheric CO₂ levels through the stimulation of new primary production and consequent export of carbon to the deep ocean (16, 44).

At current rates of use, the known global stocks of phosphate rock are estimated to run out in as little as 50 y (45). How might civilization sustain agricultural productivity once those supplies are exhausted? Can animals, as rapid recyclers, be used to enhance the residence time of P in ecosystems? P is not well
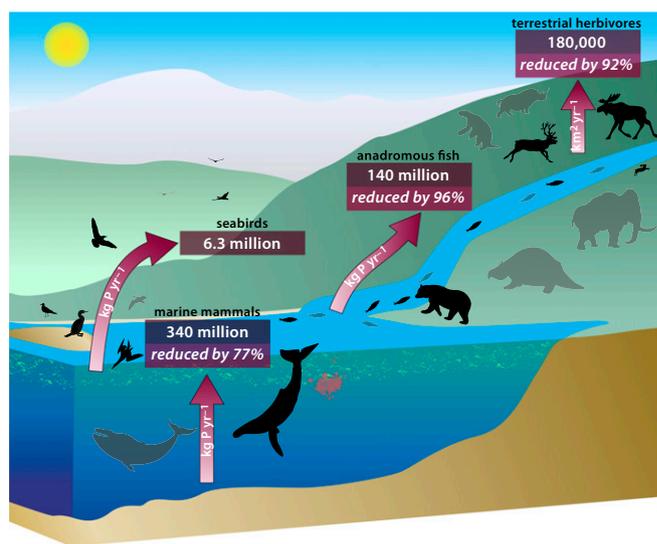
Fig. 4. Potential interlinked system of recycling nutrients. The diagram shows a potential route of nutrient transport of the planet in the past. Red arrows show the estimated fluxes or diffusion capacity of nutrients listed in Table 1. Grey animals represent extinct or reduced population densities of animals.

distributed, and it causes eutrophication in some areas, whereas P deficits still affect almost 30% of the global cropland area (46, 47). Therefore, a redistribution of P from areas where it is currently found in excess to areas where the soil is naturally P-poor may simultaneously boost global crop production and reduce eutrophication (47). Animals play a key role in nutrient movement on the land and in the sea, rivers, and air. Although the numbers we have calculated in this paper are exploratory (we explore this uncertainty in *SI Appendix*, Tables 1 and 2) and subject to further research and quantification, we have demonstrated the plausibility of an animal-mediated chain of nutrient transfer that connects the deep ocean to the continental interiors. We have shown that a world teeming with large animals may have had an efficient system of redistributing P. Some restoration of this important process could be aided with fenceless pastures with greater livestock biodiversity, restoration of great whales to their historic numbers, and restoration of seabird colonies and anadromous fish populations.

Methods

Lateral nutrient distribution capacity was mathematically formulated and found to be strongly size-dependent in two previous papers (20, 21), and this mathematical framework is reformulated in *SI Appendix*. We now use this framework to calculate how the ability of land mammals and great whales to diffuse nutrients away from hotspots may have changed following the widespread extinctions of

megafauna and hunting of whales. We estimate the total capability of animals to distribute nutrients both now, with the current International Union for Conservation of Nature (IUCN) species range maps and body mass, and in the past for the now-extinct Pleistocene megafauna, using a dataset of the ranges and body masses of extinct megafauna (48, 49). We use the following equation to estimate diffusion capacity (completely described in *SI Appendix*) based on mass (M) and the scaling parameters of day range (DD), metabolic rate (MR), population density (PD), and food passage time (PR) (this equation differs slightly from our previous formulation by excluding parameters not dependent on animal mass):

$$\Phi = MR * PD * \frac{(DD * PR)^2}{2 * PR} = 0.78 * 0.05 * M^{1.17}. \qquad [1]$$

We estimate vertical movement of nutrients by marine mammals and sea-to-land nutrient flux by seabirds and anadromous fish based on IUCN species range maps, mean body size, and scaling relationships for metabolic consumption and population densities (detailed methodology is provided in *SI Appendix*).

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Supplementary Information

Detailed Methods

I - Lateral nutrient distribution

Terrestrial mammal lateral nutrient distribution

Lateral nutrient distribution capacity was mathematically formulated and found to be strongly size dependent in two previous papers (1, 2). We now use this framework to calculate how the ability of land mammals and great whales to diffuse nutrients away from hotspots may have changed following the widespread extinctions of megafauna and hunting of whales. We estimate the total capability of animals to distribute nutrients both now, with the current IUCN species range maps and body mass, and in the past for the now extinct Pleistocene megafauna, using a dataset of the ranges and body masses of extinct megafauna (3). We estimate the total capability of animals to distribute nutrients both now, with the current IUCN species range maps and body mass, and in the past for the now extinct Pleistocene megafauna, using a dataset of the ranges and body masses of extinct megafauna (3). All species with occurrence records from within the last 130,000 years (Late Pleistocene and Holocene) were included. The taxonomy for extinct species followed Faurby and Svenning (3). The present-natural distribution for all extant and extinct species were estimated, i.e., maps of where these species would have occurred today under natural conditions in the absence of human-driven extinctions and range changes. This dataset is based on historical information when available or alternatively based on a method similar to the co-existence approach to inferring paleoclimate based on co-occurring taxa (4). We combine this with the current IUCN mammal database to estimate total nutrient diffusion capacity and how that has changed since the extinctions. This methodology ignores barriers

such as deserts, mountains and major rivers and therefore may overestimate transport kinetics in continental interiors. We use equation 1 to estimate diffusion capacity (completely described below) based on mass (M) and the scaling parameters of day range (DD), metabolic rate (MR), population density (PD) and food passage time (PR) (this differs slightly from our previous formulation by excluding parameters not dependent on animal mass).

Marine mammal lateral nutrient distribution

To calculate nutrient movement in oceans we took two approaches, one for lateral distribution capacity, and one for vertical movement of nutrients. For lateral nutrient distribution, we created a table of estimated changes in regional populations (North Atlantic, North Pacific, and Southern Ocean) of all great whales prior to widespread hunting and post widespread hunting (SI Appendix Table 3). To estimate range, we used the datasets at the website http://seamap.env.duke.edu/ that gives data on all recorded sightings of whales as well as the IUCN species range database. For 80% of estimated populations, we divided each sighting by total estimated regional population to estimate population per pixel for each species. The remaining 20% were evenly divided in the IUCN species ranges in pixels where there were no recorded sightings in the seamap database. We then were able to estimate a per pixel pre-and post-hunting population density. We also used modified range maps of grey whales (*Eschrichtius robustus*) because it has been extirpated from large regions, with grey whales formerly occurring in the Atlantic (5). We then used scaling theory to estimate mean gut length and mean day range again based on the mean species size. There are much less data on scaling patterns with size among marine mammals than with terrestrial mammals, but evidence suggests size-related trends of some of the largest marine mammals are consistent with scaling trends of terrestrial mammals (6). Recent work shows marine mammals home ranges scale with mass, but with a higher exponent than terrestrial mammals (7). Therefore,

we use similar scaling theory for marine mammals to terrestrial mammals but recognize that this aspect of our work will need modification in the future when more scaling data become available for marine mammals.

Formulation of equation 1

We estimate how land mammals and great whales may diffuse nutrients away from hotspots. We use a diffusion equation calculated previously based on mathematics and data from Doughty et al 2013 and Wolf et al. 2013 (1, 2) with the mathematics repeated below. It is based on a "random walk" model, which is a widely used methodology for simulating animal movement (8-11). Individual animals do not move randomly, but the net movement of all animals over long time periods (>1000 years) begins to approximate random motion. There is a large literature describing how different animal species overlap in space by consuming different foods and moving and sleeping in different patterns to avoid a variety of predators (12-14). Internal demographics of animal groups will also change which will lead to shifting ranges and boundaries of the group over time (15). Below, we show how we can calculate long term movement of nutrients by all animals in an ecosystem over long periods of time if the idea of approximate random motion of animals of all animals in an ecosystem over long periods of time is correct.

In diffusion, the flux is inversely proportional to the local concentration difference in material, with a constant of proportionality termed the "diffusivity" D (length^2/time). The equation that best incorporates the diffusive properties of animals is the following reaction diffusion equation:

SI-Eq. 1
$$\frac{dP}{dt} = D * \frac{\partial^2 P}{\partial x^2} - KP + G$$

where K is a first order loss rate and G is a gain rate. The diffusivity term D is based on the "random walk" whose form is demonstrated in the next sections.

Random walk

To calculate a diffusion term we estimate D based on the random walk with the form:

SI-Eq. 2
$$D = \frac{(\Delta x)^2}{2\Delta t}$$

Where Δx is a change in distance and Δt is a timestep of duration t. In general, a diffusivity can be derived from a random walk (9-11).

Estimate of $D_{excreta}$

Nutrients can be moved by animals through either their dung or flesh. Nutrients moved in dung will have different distance and time scales than those moved in the flesh. We therefore calculate D for each separately. Below we start with D for dung.

Δx is the daily displacement or day range (DD) of a single animal (DD; km), and Δt is a day. The length scale for diffusivity of ingestion and excretion is the day range multiplied by the average gut passage time (PT; fractions of a day). The time scale is again the food passage time (PT). Therefore, putting this in the framework of the random walk, we estimate that the diffusivity for transport of its dung is $D_{exreta} \sim= (DD*PT)^2/(2*PT)$, where the numerator is in km^2 and the denominator is in days.

Estimate of D_{body}

Next, we calculate a D term for nutrients incorporated into the animal's body. The diffusivity for nutrients in an animal's body mass, D_{bones}, is related to the lifetime of the animal L (days) and the residence time of these nutrients is L. The length scale is the home range (HR; km^2). The mean displacement over the lifetime of an animal is related to the range length (RL) and approximately $HR^{0.5}/2\pi$. Therefore, if HR is the range used

throughout an animal's lifetime, then $D_{body} \sim= RL^2/2L$ or $HR/(8\pi^2 L)$, where the numerator is in km^2 and the denominator is in days.

Consumption of nutrients

Next, we need to estimate the amount of food and nutrients consumed by a population of animals per area. $P(x,t)$ is the mass ($kgP\ km^{-2}$) of a nutrient. The mass of P at position x at time $t+\Delta t$ is given by:

SI-Eq. 3 $$P(x,t+\Delta t) = P(x,t) - losses + gains$$

The *losses* term is represented in Equation 9 by $\alpha p(x,t)$, the fraction of animals leaving x at time t. The loss of a nutrient in dry matter consumed and transported by a population of animals is

SI-Eq. 4

$$\alpha \frac{animals}{km^2} * \frac{kg\dfrac{DM}{\Delta t}}{animal} * \frac{kgP}{kgDM}(x,t)\Delta t = \alpha PD * MR * [P](x,t)\Delta t = \alpha Q[P](x,t)\Delta t$$

The loss rate of P ($kg\ DM\ km^{-2}$) is the population density of animals (PD; $\#/km^2$) consuming dry matter (DM) to fulfil their metabolic requirements (MR; $kg\ DM/animal/day$). The product of PD and MR is the population consumption rate of DM (denoted Q here), such that $Q\Delta t$ is the mass of DM consumed in Δt ($kg\ DM\ km^{-2}$). The consumption of the nutrient itself is then determined by $Q[P](x,t)$, which has units $kg\ P\ km^{-2}$, equivalent to P, the numerator on the left. Gains from adjacent regions will be represented as $Q[P](x+\Delta x, t)$ and $Q[P](x-\Delta x, t)$. A fraction ε of the consumed nutrient is incorporated into body mass, while the rest ($1-\varepsilon$) is excreted.

6

We estimate ε as 22.4% for megafauna based on the gross food assimilation efficiency of elephants (16). Incorporation of phosphorus into the body is, of course, more complicated with relative P fraction of biomass increasing with size due to the greater investment in bone growth in larger vertebrates (17). It also changes with animal age as full grown adult vertebrates need less P than immature growing animals. However, since we account for both the fraction in the biomass and the fraction excreted and there are no fates of the nutrient other than body mass or excrement, we use the simple value of 22.4%.

Consider the budget of just the fraction (1-ε) of consumed nutrient that will be excreted:

SI-Eq. 5

$$P(x,t+\Delta t) = P(x,t) - (1-\varepsilon)[\alpha Q[P](x,t) + \frac{\alpha}{2}Q[P](x+\Delta x,t) + \frac{\alpha}{2}Q[P](x-\Delta x,t)]$$

We arrive at the equation:

SI-Eq. 6
$$\frac{dP}{dt} = (1-\varepsilon)QD_{excreta}\frac{\partial^2[P]}{\partial x^2}$$

Adding in the fraction of nutrient incorporated into body mass we get the complete budget equation:

SI-Eq. 7
$$\frac{dP}{dt} = (1-\varepsilon)QD_{excreta}\frac{\partial^2[P]}{\partial x^2} + \varepsilon QD_{excreta}\frac{\partial^2[P]}{\partial x^2}$$

The state variable on the left and the right are not the same; P is per area and [P] is per kg DM. Let B be total plant biomass (kg DM km^{-2}) such that [P]B=P. We note that B has the same units as Q. Dividing both sides by B:

SI-Eq. 8
$$\frac{\delta[P]}{\delta t} = (1-\varepsilon)\frac{Q}{B}D_{excreta}\frac{\partial^2[P]}{\partial x^2} + \varepsilon\frac{Q}{B}D_{body}\frac{\partial^2[P]}{\partial x^2}$$

B represents total plant biomass but animal consumption is only from edible parts of that biomass. Therefore B' = αB, where α is the edible fraction of total biomass. We assume for simplicity here that all P made available is taken up, on a fast timescale and used in edible parts. We may revisit this assumption in future work. If these fractions can be assumed equal, then:

SI-Eq. 9
$$\frac{\delta[P]}{\delta t} = (1-\varepsilon)\frac{Q}{\alpha B}D_{excreta}\frac{\partial^2[P]}{\partial x^2} + \varepsilon\frac{Q}{\alpha B}D_{body}\frac{\partial^2[P]}{\partial x^2}$$

If Q/B can be assumed constant, then:

SI-Eq. 10
$$\frac{dP}{dt} = \Phi_{excreta}\frac{\partial^2 P}{\partial x^2} + \Phi_{body}\frac{\partial^2 P}{\partial x^2}$$

where the [P] terms on both sides have been multiplied by αB, and

SI-Eq. 11
$$\Phi_{excreta} = (1-\varepsilon)\frac{Q}{\alpha B}D = (1-\varepsilon)\frac{PD}{\alpha B}*MR*\frac{(DD*PR)^2}{2*PR}$$

SI-Eq. 12
$$\Phi_{body} = \varepsilon\frac{Q}{\alpha B}D = \varepsilon\frac{PD}{\alpha B}*MR*\frac{HR}{8\pi^2 L}$$

We solve the equations above using datasets and methods described in previous work(2). We estimated Φ as a function of M in two ways: first, we calculated the allometries for each term as a function of M (using ordinary least squares) and combined the resulting coefficients to yield an allometric equation for Φ that results from scaling arguments (see Wolf et al. 2013 for the allometries). In our previous work we find Φ_{body} to be several orders of magnitude smaller than $\Phi_{excreta}$ and we therefore remove Φ_{body} from our formulation and in Φ in equation 1 refers to only $\Phi_{excreta}$. In equation 1, we remove the αB and ε term as it is not based on animal mass. Based on our datasets we calculate the below value of Φ which we use as equation 1 in the text and which was originally formulated in Table 1 of Wolf et al. 2013.

SI-Eq. 13
$$\Phi = MR * PD * \frac{(DD * PR)^2}{2 * PR} = 0.78 * 0.05 * M^{1.17}$$

II - Calculation of vertical nutrient movement by marine mammals and sea to land nutrient fluxes by seabirds and anadromous fish

Marine mammal vertical nutrient distribution

To calculate vertical nutrient movement, we created a table of diving marine mammals and regional population estimates (North Atlantic, North Pacific, and Southern Ocean) prior to widespread hunting and post widespread hunting (SI Appendix Table 4). We calculate this vertical distribution of nutrients for nine marine mammals whose common dive depths are greater than 100 meters (**(18)**, SI Appendix Table 4). This proportion would hold for other important limiting nutrients, such as N and Fe. To estimate range, we used the IUCN species range dataset for all diving marine mammals except for great whales (*Balaenoptera physalus* and *Physeter microcephalus*), which we again use the seamap dataset (http://seamap.env.duke.edu/). We divided regional population estimates by species range to estimate population density per pixel for each species and used equation 14 to estimate food consumption (dry matter: DM) based on mean species mass (2).

Kg DM/#/day $= 0.021 \times M^{0.716}$ SI-Eq. 14

Based on these consumption patterns, an average ocean redfield ratio of Carbon: Phosphorus = 106:1 (but since most marine mammals are predators and higher tropic levels such as krill have a ratio closer to 50:1(19), we use 50:1), and defecation rate of 80% (20, 21), we estimate movement of P from depth to the surface ocean. We compare this to P concentrations found at depth and at the surface from the Ocean Climate Laboratory/National Oceanographic Data Center/NESDIS/NOAA/U.S. http://rda.ucar.edu/datasets/ds254.0/

Nutrient distribution by seabirds

We use seabird species ranges for either year-round residents or breeding seasons from birdlife.org (22) and their estimated body masses based on Dunning et al. 2007 and Dunning – unpublished data (23) to estimate total global seabird consumption. To estimate metabolic consumption as a function of mass we use equation 14 and to estimate density as a function of mass we use Juanes et al. (1986) which found a strongly significant (P<0.001, r^2=0.27, N=461) relationship for carnivorous birds (24):

$$ind/km^{-2} = 10^\wedge(2.18 + \log 10(M)^*-0.67) \qquad \text{SI-Eq. 15}$$

We use all species of seabirds (223 species) from the following families: Spheniscidae, Diomedeidae, Procellariidae, Pelacanoididae, Hydrobatidae, Pelecanidae, Sulidae, Phalacrocoracidae, Fregatidae, Phaethontidae, Stercorariidae, Laridae, Sternidae, Rhynchopidae, Alcidae (22). We estimate phosphorus in food supply using a redfield ratio of C:P = 106:1 (19).

Seabird guano deposition on land is difficult to calculate because of the uncertainty of the percentage guano arriving on land versus being defecated in the sea. To roughly estimate percentage of nutrients that arrive on land, we use data from a detailed study of nutrient distribution on seven bird islands (Anderson and Polis 1999) as well as a larger seabird dataset from Mulder et al 2011 as a case study to calibrate our larger model (25, 26). A recent review (26) of guano deposition on seabird islands showed that due to its aridity, the P concentrations were unusually high in the island studied by Anderson and Polis (1999). However, below we are able to account for the aridity using a P model (see equations 14-16 below) and we focus on the group of islands described in Anderson and Polis (1999). These seven bird islands had a combined area of about 1 km^2 (0.86 km^2), and on these islands P increased in the soil from 0.35 ± 0.17% P on the non-bird islands to 1.30 ± 0.24% P on the

bird islands. In vegetation, the P increased from 0.16 g m^2 in three plant types (Atriplex, Opuntia, and annuals) to 0.41 g m^2, an increase of 250%. d15N stable isotope data verified that the increased fertility was almost certainly due to the seabird nesting.

We use mass scaling relationships to calculate consumption by the seabirds in this study. Seabird foraging radius scales with mass (27) as does bird gut length and food retention time (28) and scaling theory has generally been applicable to seabirds (29).   We estimate total consumption rates for the species of seabirds living in the identified Gulf of California islands. To estimate a mean percentage of guano transferred from sea to land we calculated (using equations 14 and 15) that the 23 seabird species in the region of the seven Gulf of California islands from (25) consume 12 kg km^{-2}, or ~0.1kg of P km^{-2}. Mass-based scaling of seabird foraging area suggests that the birds nesting on these seven islands have a mean foraging radius of 326km, or about half of the Gulf of California, 80,000 km^2 (27). We justify this by estimating seabird foraging radius of the seabird species based on mass (27) and we estimate that foraging radius is 286km +61*M. Therefore, 8,000kg P yr^{-1} was consumed by these nesting birds and an unknown amount of this was deposited on all the islands with a total area of ~1 km^2. On these islands, total soil P increased by ~1%, which is ~ 1e6 kg of P km^{-2} (25). We can roughly estimate the quantity of P needed to increase P in ~100 kg of soil (in a 1m2 area assuming the top 10cm of soil, a soil density of 1.2 g cm-3) by 1% as ~1kg. To achieve this steady state concentration of P and assuming a loss rate of 0.0014 yr^{-1}(30) (see below for calculation of the loss rate), then a flux of 1400 kg P km^{-2} yr^{-1} must be added yearly to the soil or ~18% of the 8,000kg P per year that was consumed. Therefore, as a rough proxy, we assume 20% of the seabird P will arrive on land. As this is clearly a highly uncertain figure, in a sensitivity analysis, we varied this percentage between 5 to 50%.

We calculate the loss rate based on a P model of 0.0014 yr^{-1}(30). We estimate P losses from the system based on the following equations from (30):

SI-Eq. 14 $\qquad\qquad LQ(s) = k_l s^c$

SI-Eq. 15 $\qquad\qquad L_o = (k_r * LQ(s) + k_f) * P_o$

SI-Eq. 16 $\qquad\qquad L_d = LQ(s) * \dfrac{Pd}{n*Zr*s}$

where s is the yearly averaged soil moisture (dimensionless); c is 3; k_l is runoff or leakage at saturation, which is 0.1 (yr^{-1}); k_r is the losses regulation rate 0.002 (yr^{-1}); P_o is organic P; P_d is the dissolved P; Zr is soil depth (1m); n is soil porosity (0.4); L_o is the loss rate of P_o; and L_d is the loss rate of P_d. k_f, or a loss rate from ice, wind, humans, or fire, is 0.00005. We estimate the steady state ratios of P_o to P_d following figure 2 in Buendia et al. 2010(30).

Nutrient movement by anadromous fish

To estimate anadromous fish nutrient movement from the sea to land on a global basis, we first compile a list of likely anadromous fish species (110 species and an additional 10 possibilities listed as maybe) from (31) shown in column 1 of SI Appendix table 5(32). We then searched the IUCN database (http://www.iucnredlist.org/technical-documents/spatial-data) for species maps. We found maps for 42 species. We substituted a similar species within the same genus for 47 species (column 2 of SI Appendix table 5). Thirty-three species, for which there were no data for any species within the genus, were left blank.

To estimate historical population densities of such fish, we used a range of studies. Populations of anadromous fish have declined to less than 10% of their historical numbers in the Pacific Northwest (33), the Netherlands (34), and the North Atlantic (35). In the North Atlantic, the relative abundances of 13 of 24 species had dropped to less than 2% of historic levels; abundances had dropped to less than 10% in the others. There were also large declines in the anadromous sea lampreys (36) and sturgeons (37). In regions where anadromous fish populations were measured, population reductions from historic highs in global populations were similar to those found in the Pacific Northwest of the USA, where data was particularly strong. Gresh et al. (2000) estimated movement of P for both historical and modern populations for the entire Columbia river basin, Oregon coast, Washington coast, Puget sound, and California (33).

For each region, we calculated the P moved for each species on a per area basis. Because the Gresh et al. study provided the strongest regional level data of P movement, we then applied this for each species globally to get an estimate of nutrient movement by anadromous fish. We do not have good data for mean body mass for most species. These

species are clearly a wide range of sizes. However, size and population density often vary

inversely. On average, it is a reasonable assumption that animal biomass per species per area

is relatively constant. The theoretical explanation for this phenomena is termed the ''law of

energy equivalence'', which argues that the population-level biomass should be equal across

a range of animal sizes (38). Therefore, for species in which mass is unknown, we estimate

that fish biomass per unit area, which should, to first order, be a function of the total number

of species present. In recognition of the high uncertainty in this estimate, we vary several

terms in our analysis by up to 200% in a sensitivity study (SI Appendix Table 1 and 2).

Sensitivity analysis

There are large uncertainties in many of the spatial maps, scaling coefficients, and assumptions used in our analysis. We have attempted to quantify this uncertainty in a sensitivity study where we calculate an estimated global flux of P based on the low and high uncertainty value. In table one, we describe the variable and the largest source of its uncertainty. In table two, we quantify this uncertainty, explain how we quantified the uncertainty, and show the results of how our final values could change based on both the low and high estimated values.

Impact of predation on our results

Many ecosystems have lost predators at higher rates than herbivores. How might the absence of predators affect nutrient transfer by herbivores? Human-induced loss of predators may enable mid-sized herbivores to reach unnaturally high densities, for example, in deer populations (39). However, in many parts of the world human hunting has replaced natural predator hunting, thus keeping modern herbivore populations down. If certain mid-sized herbivores were more abundant, how might this affect nutrient movement? Megaherbivores (> 1000kgs) are unique because their large size makes them less susceptible to predation, like predator-free populations of deer today, and they would have existed in high population densities. However, the large size of megaherbivores (> 1000kgs) would have made them more important than mid-sized herbivores for the transport of nutrients (1, 2). Therefore, in the past, there would have been abundant megafauna and predation limited mid-sized herbivores. Today this situation has been replaced by a community without megafauna but with potentially more abundant but less diverse mid-sized herbivores, but with more restricted movement.

Table 1 – Description of the variables modified in the sensitivity analysis and a description of what the uncertainty is.

Variable	Description	Uncertainty	reference
Megafauna range maps	Predicting the spatial regions where the now extinct megafauna had lived	Predicting ranges of extinct animals is difficult due to taphonomic bias. Using the range maps from Faurby and Svenning (40), there is a correlation between predicted and historic ranges of 0.856 for 39 species in North America. Since the historic ranges are not known with certainty and since the precision in these 39 species are not guaranteed to be representative of the entire megafauna set, we used an uncertainty of double this (+/-30%)	(40)
Animal body mass	The estimated mean body mass of a species	The uncertainty of individual species are generally captured with +/-25. However, we use an error of +/-10% which is for entire communities because as long as the estimates are unbiased the combined error for all co-occurring species will be smaller since some are under and some are over estimated.	
Phi coefficient	This is the nutrient diffusion coefficient from equation 1 previously calculated in Doughty et al. and Wolf et al. (2013).	This coefficient is based on 17 species. However, larger datasets with some values missing show similar values. An estimate for just large animals (>44kg) estimated a larger coefficient (1.45).	(1, 2)
Assumption of random motion	For mathematical expediency, we use a random walk model when averaging for all animals in an ecosystem over long periods of time.	This is a well-tested model used in hundreds of papers. Simulations over shorter time periods can be done numerically on regional scales to test the assumption.	(9-11)
Whale historical population density	Estimates of historic populations of great whales	There is great uncertainty in past global population densities of great whales prior to human hunting.	See table 3 and 4
Whale range maps	We used a combination of the IUCN databases plus whale sighting records	IUCN map are very broad and do not account for regions with greater or fewer populations. We correct for this by using whale sighting data. This is probably biased towards regions more populated by people	(32, 41)
Whale lateral	The estimated distance moved between whale	Due to data limitations, the coefficient is based on all	(2, 6, 7)

diffusion coefficient	food consumption and defecation based on mean body size.	mammal data and is not specific to whales. This is likely a large underestimate, since (7) showed space use for whales had a much higher exponent than for terrestrial mammals.	
Vertical movement of nutrients by marine mammals	Estimate of nutrients moved by deep diving animals to the surface waters	This term is dependent on estimating population densities, metabolic rates, and the ratio of food consumed at depth and defecated in surface waters.	(2)
Seabird range maps	Estimate of number and spatial area of each seabird species	IUCN species range maps for seabirds are likely accurate over land regions, but much less accurate over ocean regions.	(22)
Seabird food consumption	Estimate of metabolic consumption and population density based on mass scaling laws.	These are based on scaling coefficients and are likely within the 95% confidence interval of the calculated slope.	(2, 24)
Guano deposition on land	Estimating the percentage of seabird guano that arrives on land.	Much guano is defecated at sea versus deposited at nesting sites. The percentage likely varies widely for each species. However, we estimate this based on data from (25, 26).	(25, 26)
Anadromous fish abundance	Which fish species are anadromous? Where do they live? What were there historical population numbers?	The best reference on this (31) details 110 anadromous fish species, along with 10 other possible ones. This likely underestimates the total number of anadromous fish species because it is difficult to estimate. We do not have species range maps for all of these species and this is another likely source of underestimation. There is little data on historical abundances outside of N. America and Europe. We assume historical abundances everywhere were similar to N. America and Europe.	(31, 32)
Anadromous fish nutrient movement	We use estimates of regional P movement by all anadromous fish in the Pacific Northwest of the US from Gresh et al. 2000. This paper quantifies historical population densities and P contained within these bodies.	We have no data on mean species size and there is no data on historical population estimates outside of N. America and Europe.	(33)

Table 2 – Values used in our sensitivity analysis: the estimated range in uncertainty, how this uncertainty was assessed, and a global calculation of the P flux for the low and high estimates. Expert opinion was estimated by a group of experts (the authors of the paper) of the variable value in which the group was 95% certain the true value would fall within. If the number is calculated as a slope, then the 95% confidence interval (1.96*standard error on the slope) is the potential error.

variable	Value used	Potential error estimate	How the error was assessed	Past Global P flux	Current Global P flux	reference
Megafauna range maps	See figure 1	±30% for megafauna ±10% for current animals	Expert opinion	13-23e4 km^2 yr^{-1}	1.1-2.1e4 km^2 yr^{-1}	(40)
Animal body mass	See (40, 42)	±10%	Expert opinion	16-20e4 km^2 yr^{-1}	1.4-1.9e4 km^2 yr^{-1}	(40, 42)
Phi coefficient	1.17	±0.24	Slope error	3-130e4 km^2 yr^{-1}	0.4-10e4 km^2 yr^{-1}	(2)
Assumption of random motion	Random walk model	Run model numerically	Computer simulation	Simulations available upon request.	Simulations available upon request.	(9-11)
Whale population density	See table 4	±50% historical ±20% current	Expert opinion	170-510 million kg yr^{-1}	64-96 million kg yr^{-1}	See table 3 and 4
Whale range maps	See figure 2	±30% historical ±10% current	Expert opinion	240-310 million kg yr^{-1}	70-90 million kg yr^{-1}	(32, 41)
Whale lateral diffusion coefficient	Eq. 1	+30% -10%	Slope error and expert opinion	5.7 - 8.3e5 km^2 yr^{-1}	2.9-4.2 e4 km^2 yr^{-1}	(2, 6, 7)
Vertical movement of nutrients by marine mammals	Eq. 2 and 80% of food consumed at depth moved vertically	Eq. 2 - ±0.04 65-95%	Slope error and expert opinion	260-430 million kg yr^{-1}	54-110 million kg yr^{-1}	(2)
Seabird range maps	See Figure 3	±20%	Expert opinion	5-7.6 million kg yr^{-1}	NA	(22)
Seabird food consumption	Eq. 2 and 3	Eq. 2 - ±0.04	Slope error	3-9 million kg yr^{-1}	NA	(2, 24)

		Eq. 3 - ±0.10				
Guano deposition on land	20%	5-50%	Slope error and expert opinion	1.5-16 million kg yr^{-1}	NA	(25, 26)
Anadromous fish abundance	See figure 3	+200% -50%	Slope error and expert opinion	71-430 million kg yr^{-1}	3-16 million kg yr^{-1}	(31, 32)
Anadromous fish nutrient movement	Scaling results from Gresh et al. 2000	+100% -50%	Expert opinion	71-280 million kg yr^{-1}	3-12 million kg yr^{-1}	(33)

Table 3 – Data table used to calculate lateral nutrient distribution capacity of great whales in oceans. Numbers are in thousands. NA is the North Atlantic, NP is the North Pacific, SH is the Southern Ocean. Unless otherwise stated all data references are from Christensen 2006 (43). Estimating past populations of animals has inherent large uncertainties due to poor historical data. Numbers with especially high uncertainty are listed as a range with a footnote below explaining the possible discrepancy from Christensen 2006 (43). Due to the large uncertainty in these numbers, in a sensitivity study, we estimate the uncertainty of our estimates at 30% (SI appendix Table 2).

Species	Pre NA	Pre NP	Pre SH	Pre Other	2001 NA	2001 NP	2001 SH	2001 Other	Reference
Balaenoptera borealis	10.6	68.4	167	0	7	14.7	27.4	0	
Physeter macrocephalus	0	0	0	1110	0	0	0	360	Global populations from (44)
Balaenoptera physalus	73	65	625	0	56	31	23	0	
Eschrichtius robustus	0	25	0	0	0	16	0	0	
Balaenoptera musculus	7.5	6	256-327[*1]	0	0.4	3	1-3[*2]	0	
Balaenoptera brydei	0	52	94	0	0	41	91	0	Christensen and IUCN Red List
Megaptera novaengliae	112	20	140-199[*3]	0	20	20	22.5-40[*4]	0	Estimates for pre-NA from (45); estimates for contemporary humpbacks in NP from (46), pre NP #s have been rounded up to reflect this increase
Balaenoptera acutorostrata	211	47	379	0	157	32	318	0	
Balaenoptera	211	47	379	0	157	32	318	0	

bonaerensis								
Eubalaena glacialis	14	0	0	0	0.4	0	0	0
Eubalaena australis	0	0	70-86[*5]	0	0	0	10-12[*6]	0
Eubalaena japonica	0	31.75	0	0	0	0.4	0	0	(47)
Balaena mysticetus	0	0	0	89	0	0	0	9

[*3]Estimated population for Antarctic blue whales could be 256,000.

[*4]For Antarctic blue whales in 1997 the population was 2,300 individuals. If one projects that to 2001 given the estimated growth rate for this population (6.4%/year as agreed by the IWC), one gets an abundance of 3,000.

[*3]In the Southern Hemisphere, Humpback whales estimated pre-exploitation abundance (K) is 140,000 given the IWC most recent assessments.

[*4]The most recent abundance estimate for all whales combined is 80,000 in 2010. It is hard to extrapolate back to 2001 (which is the year shown in the table), but a crude calculation indicates the 2001 abundance would have been at least 40,000 whales.

[*5]The IWC estimated populations at about 70,000 whales under the assumption of an intrinsic growth rate of 7%/year (which is consistent with the three major right whale breeding populations).

[*6]The abundance of Southern Right Whales in 2001 projected from the IWC assessments is 10,000.

Table 4 – Data table used to calculate vertical nutrient distribution by marine mammals. Dive depths are from Ponganis 2011 (18). Population sizes are from Christensen 2006 (43) unless otherwise stated.

Species	Pre NA	Pre NP	Pre SH	Pre Other	2001 NA	2001 NP	2001 SH	2001 Other	weight	Diving depth	reference
Cystophora cristata	700	0	0	0	70	0	0	0	200	100-600	IUCN Red List
Globicephala macrorhynchus	33	624	0	0	33	624	0	0	2000	100-800	IUCN Red List
Hyperoodon ampullatus	58	0	0	0	49	0	0	0	6500	800	
Globicephala melas	871	0	0	0	795	0	0	0	2500	100-800	
Phocarctos hookeri	0	0	120	0	0	0	12	0	400	NaN	Pre hunting estimates are based on range reduction
Mirounga angustirostris	0	200	0	0	0	200	0	0	2000	437	
Mirounga leonine	0	0	1000	0	0	0	650	0	2000	269-552	Iucn Red List
Physeter microcephalus	0	0	0	1110	0	0	0	360	14000	400-900	Global populations from (44)
Balaenoptera physalus	7.5	6	327	0	0.4	3	1	0	150000	180-200	
Ziphius cavirostros	0	97	0	100	0	97	0	100	2500	1070-1334	
Leptonychotes	0	0	500	0	0	0	500	0	500	150-	

Table 5 – Species list of anadromous fish from(31), species used in our estimates (if no species range map was available, we used a similar species from the same genus), the status is the certainty of if the fish were anadromous (maybe is not certain, and blank is more certain), and the estimated pixel area (in km^2) occupied by the species which includes both the land and river area within the pixel.

Anadromous fish	species used	status	estimated area (km^2)
Acipenser baerii	*Acipenser baerii*		1.01E+05
Acipenser brevirostrum	*Acipenser brevirostrum*		9.06E+05
Acipenser fulvescens	*Acipenser fulvescens*	maybe	5.61E+06
Acipenser gueldenstaedtii	*Acipenser gueldenstaedtii*	maybe	3.41E+06
Acipenser medirostris	*Acipenser medirostris*		6.01E+05
Acipenser nudiventris	*Acipenser nudiventris*	maybe	2.04E+06
Acipenser oxyrinchus	*Acipenser oxyrinchus*		2.45E+06
Acipenser ruthenus	*Acipenser ruthenus*		4.17E+06
Acipenser stellatus	*Acipenser stellatus*		3.48E+06
Acipenser sturio	*Acipenser sturio*		4.26E+06
Acipenser transmontanus	*Acipenser transmontanus*	maybe	1.21E+06
Acipenser usohuso	NaN		0.00E+00

Alosa aestivalis	*Alosa aestivalis*	1.02E+06
Alosa alabamae	*Alosa alabamae*	8.97E+05
Alosa caspia	*Alosa caspia*	1.07E+06
Alosa chrysochloris	*Alosa tanaica*	2.94E+05
Alosa fallax	*Alosa fallax*	2.99E+06
Alosa kessleri	*Alosa kessleri*	1.15E+06
Alosa mediocris	*Alosa mediocris*	6.88E+05
Alosa pontica	*Alosa volgensis*	8.39E+05
Alosa pseudoharengus	*Alosa pseudoharengus*	2.25E+06
Alosa sapidissima	*Alosa sapidissima*	1.97E+06
Anchoviella lepidentostole	NaN	0.00E+00
Anodontostoma chacunda	NaN	0.00E+00
Arius felis	*Arius arius*	1.94E+06
Arius heudeloti	*Arius uncinatus*	4.62E+04
Arius militaris	*Arius acutirostris*	2.59E+05
Arius graeffei	*Arius gagora*	1.54E+05
Arius latiscutatus	*Arius gigas*	1.80E+06
Arius madagascariensis	*Arius madagascariensis*	1.18E+05
Batanga lebretonis	NaN	0.00E+00
Clupanodon thrischacunda	*Clupeonella caspia*	5.59E+05
Clupeonella cultiventris	*Clupeonella caspia*	5.59E+05
Coregonus albula	Coregonus albula	2.70E+06
Coregonus artedii	*Coregonus alpinus* maybe	6.63E+03

Coregonus artedii	*Coregonus autumnalis*	6.76E+06
Coregonus autumnalis	*Coregonus baerii*	1.63E+05
Coregonus canadensis	*Coregonus lavaretus* maybe	2.01E+04
Coregonus clupeaformis	*Coregonus nasus*	8.14E+06
Coregonus laurettae	*Coregonus oxyrinchus*	1.19E+05
Coregonus lavaretus	*Coregonus megalops*	2.02E+05
Coregonus muskun	*Coregonus peled*	4.50E+06
Coregonus nasus	*Coregonus reighardi*	3.09E+05
Coregonus oxyrinchus	*Coregonus vandesius* maybe	4.42E+04
Coregonus ussuriensis	*Coregonus zenithicus* maybe	1.56E+06
Dormitator latifrons	*Dormitator lebretonis*	2.53E+06
Dormitator maculatus	NaN	0.00E+00
Dorosoma cepedianum	*Dorosoma cepedianum*	5.52E+06
Dorosoma petenense	*Dorosoma petenense*	1.62E+06
Eleotris pisonis	*Eleotris oxycephala*	2.22E+06
Gasterosteus aculeatus	*Gasterosteus aculeatus*	9.70E+06
Geotria Australis	*Geotria australis*	1.82E+06

Hemisalanx prognathus	NaN	maybe	0.00E+00
Herkotslichthys gotoi	NaN		0.00E+00
Herkotslichthys koningsbergeri	NaN		0.00E+00
Hucho perryi	Hucho hucho		3.55E+05
Hypomesus transpacificus	Hypomesus olidus		1.66E+07
Hypomesus olidus	Hypomesus transpacificus		1.06E+05
Ilisha novalcula	Ilisha novacula		8.56E+05
Ilisha africana	NaN		0.00E+00
Ilisha megaloptera	NaN		0.00E+00
Lampetra japonica	Lampetra aepyptera		1.30E+06
Lampetra wagneri	Lampetra hubbsi		2.31E+05
Lampetra tridentata	Lampetra richardsoni		8.01E+05
Lampetra ayresii	Lampetra ayresii		6.69E+05
Lampetra fluviatilis	Lampetra planeri		3.72E+06
Lampetra tridentata	Lampetra ninae		4.22E+04
Lepisosteus osseus	Lepisosteus osseus		4.99E+06

Leucopsarion petersi	NaN		0.00E+00
Lovettia seali	NaN		0.00E+00
Lycengraulis olidus	NaN		0.00E+00
Lycengraulis simulator	NaN		0.00E+00
Microgadus tomcod	*Microgadus tomcod*		1.68E+05
Microphis brachyurus	*Microphis brachyurus*		2.35E+05
Mordacia mordax	NaN		0.00E+00
Morone saxatilis	*Morone saxatilis*		1.63E+06
Morone americanus	*Morone americana*		1.19E+06
Nematalosa vlaminghi	NaN		0.00E+00
Nematalosa galatheae	NaN		0.00E+00
Neosalanx jordani	*Neosalanx brevirostris*	maybe	2.53E+06
Oncorhynchus gilae	*Oncorhynchus gilae*	maybe	2.01E+05
Oncorhynchus nerka	*Oncorhynchus nerka*	maybe	2.62E+06
Oncorhynchus tshawytscha	NaN		0.00E+00
Oncorhynchus keta	NaN		0.00E+00
Oncorhynchus kisutch	NaN		0.00E+00
Oncorhynchus masou	NaN		0.00E+00
Osmerus mordax	*Osmerus mordax*		4.26E+06
Osmerus eperlanus	*Osmerus eperlanus*		2.63E+06

Pellona ditcheli	*Pellonula vorax*	1.83E+06
Pellonula leonensis	NaN	0.00E+00
Pellonula vorax	NaN	0.00E+00
Petromyzon marinus	*Petromyzon marinus*	4.34E+06
Prosopium cylindraceum	*Protosalanx chinensis*	1.25E+06
Protosalanx chinensis	*NaN*	2.17E+07
Protosalanx hyalocranium	NaN maybe	0.00E+00
Pungitius pungitius	*Pungitius pungitius*	0.00E+00
Retropinna retropinna	*Retropinna retropinna*	4.81E+05
Retropinna tasmanica	NaN	0.00E+00
Retropinna semoni	NaN	0.00E+00
Salangichthys microdon	NaN	0.00E+00
Salangichthys ishikawae	NaN	0.00E+00
Salanx ariakensis	*Salanx chinensis*	4.62E+05
Salanx cuvieri	*Salanx cuvieri* *maybe*	2.65E+05
Salanx acuticeps	NaN maybe	0.00E+00
Salmo salar	*Salmo salar*	2.12E+06
Salmo trutta	*Salmo trutta*	1.01E+07
Salmo gairdneri	*Salmo macrostigma*	3.68E+05
Salmo clarki	*Salmo labrax*	2.34E+06
Salmo penshinensis	*Salmo platycephalus*	5.25E+04

Salvelinus alpinus	*Salvelinus alpinus*	1.22E+07
Salvelinus fontinalis	*Salvelinus umbla*	1.71E+05
Salvelinus malma	*Salvelinus murta*	4.15E+03
Salvelinus leucomaenis	*Salvelinus inframundus*	6.14E+04
Salvelinus confluentis	*Salvelinus confluentus*	2.63E+06
Spirinchus lanceolatus	*Spirinchus thaleichthys*	5.37E+05
Spirinchus thaleichthys	NaN	0.00E+00
Sokellia anisodon	*Stokellia anisodon*	6.82E+04
Strongylura kreffti	*Strongylura marina*	1.25E+06
Tenualosa ilisha	*Tenualosa ilisha*	2.40E+06
Tenualosa macrura	*Tenualosa thibaudeaui*	2.61E+05
Tenualosa reevesi	NaN	0.00E+00
Tenualosa toli	NaN	0.00E+00

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