Global nutrient transport in a world of giants

Christopher E. Doughty[a,1], Joe Roman[b,c], Søren Faurby[d], Adam Wolf[e], Alifa Haque[a], Elisabeth S. Bakker[f], Yadvinder Malhi[a], John B. Dunning Jr.[g], and Jens-Christian Svenning[d]

[a]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom; [b]Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138; [c]Gund Institute for Ecological Economics, University of Vermont, Burlington, VT 05445; [d]Section of Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark; [e]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; [f]Department of Aquatic Ecology, Netherlands Institute of Ecology, 6708 PB Wageningen, The Netherlands; and [g]Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907

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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.

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[1]To whom correspondence should be addressed. Email: chris.doughty@ouce.ox.ac.uk.

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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 ($km^2 \cdot y^{-1}$) for terrestrial mammals and whales, and global and regional estimates of vertical nutrient movement of P ($kg \cdot y^{-1}$) by all diving marine mammals and sea-to-land total P movement ($kg \cdot y^{-1}$) 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, $km^2 \cdot y^{-1}$	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, $km^2 \cdot y^{-1}$	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 $P \cdot y^{-1}$	A. fish 1.4e8 $kg \cdot y^{-1}$ Seabirds 6.3e6 ± 5e6	Marine mammals 3.4e8 $kg \cdot y^{-1}$	A. fish 1.9e6 $kg \cdot y^{-1}$ Seabirds 0.89e6 ± 0.66e6	A. fish 0.4e6 $kg \cdot y^{-1}$ Seabirds 0.79e6 ± 0.6e6	A. fish 69e6 $kg \cdot y^{-1}$ Seabirds 2.4e6 ± 1.8e6	A. fish 51e6 $kg \cdot y^{-1}$ Seabirds 0.99e6 ± 0.7e6	A. fish 0.5e6 $kg \cdot y^{-1}$ Seabirds 0.89e6 ± 0.6e6	Marine mammals 1.7e8	Marine mammals 0.9e8	Marine mammals 0.7e8
Current total, kg $P \cdot y^{-1}$	A. fish 5.6e6	Marine mammals 7.9e7 $kg \cdot y^{-1}$	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 ($km^2 \cdot y^{-1}$) 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 ($kg \cdot y^{-1}$) by all diving marine mammals (*SI Appendix*, Table 4) and sea-to-land total P movement ($kg \cdot y^{-1}$) 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 $km^{-2} \cdot y^{-1}$ 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 $km^{-2} \cdot y^{-1}$, and lower values in North America, with 0.16 ± 0.12 kg of P $km^2 \cdot y^{-1}$. We calculate a global flux of 6.3 million (1.5–16 million; *SI Appendix*, Table 2) kg $km^{-2} \cdot y^{-1}$ 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) $km^2 \cdot y^{-1}$; *SI Appendix*, Table 2] than seabirds [6.3 million (1.5–16 million) $km^2 \cdot y^{-1}$; *SI Appendix*, Table 2], but this estimated value has decreased to ~4% (5.6 million $km^2 \cdot y^{-1}$) 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

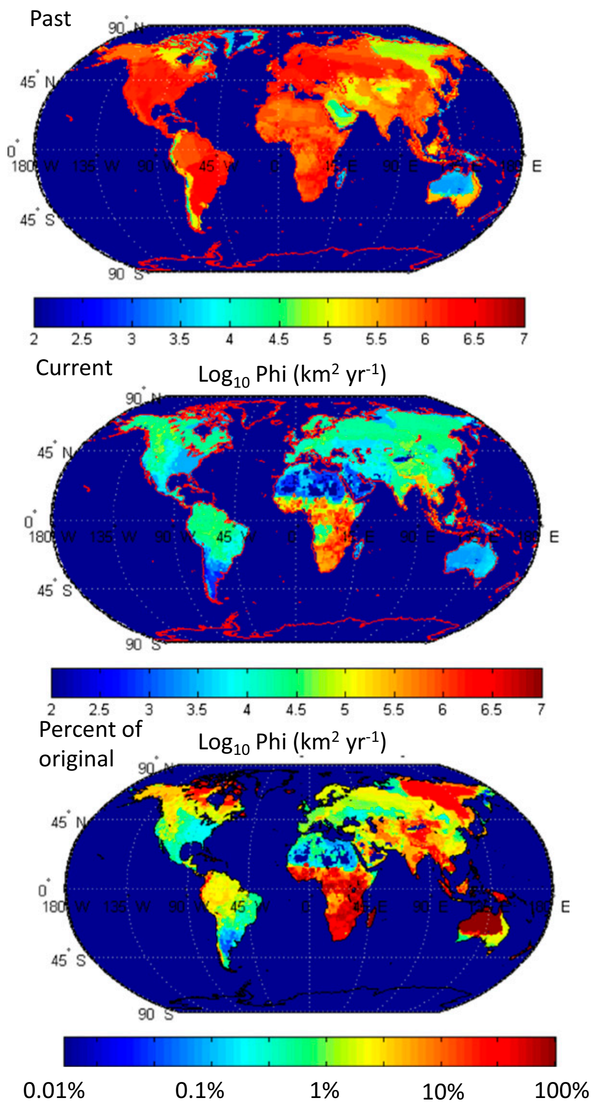

Fig. 1. Lateral nutrient distribution capacity ($km^2 \cdot y^{-1}$) by terrestrial mammals. Lateral diffusion capacity (Φ; Eq. **1**) of nutrients by all mammals as it would have been without the end-Pleistocene and Holocene megafauna extinctions and extirpations (*Top*), as it is currently (*Middle*), and as the percentage of the original value (*Bottom*).

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 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 $kg \cdot y^{-1}$ 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

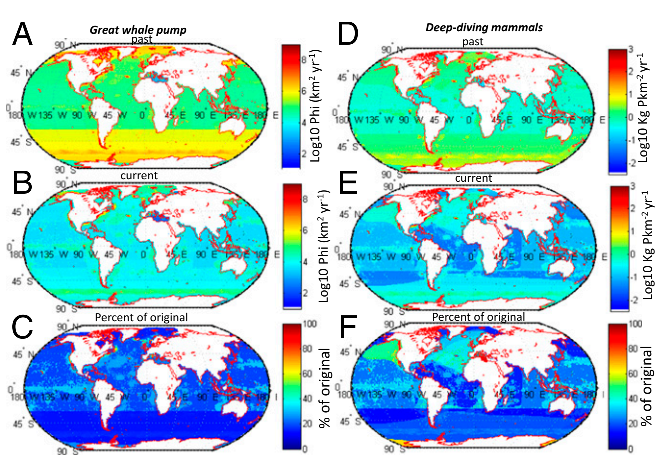

Fig. 2. Horizontal and vertical nutrient distribution capacity by great whales. Lateral movement capacity (Φ, $km^2 \cdot y^{-1}$; Eq. **1**) by great whales (listed in *SI Appendix*, Table 3) for past whale densities before widespread human hunting (*A*), current whale densities (*B*), and the percentage 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), log_{10} kilograms of P per square kilometer per year ($kg \cdot Pkm^{-2} \cdot y^{-1}$), for past marine mammal densities before widespread human hunting (*D*), current marine mammal densities (*E*), and the percentage of the original value (*F*).

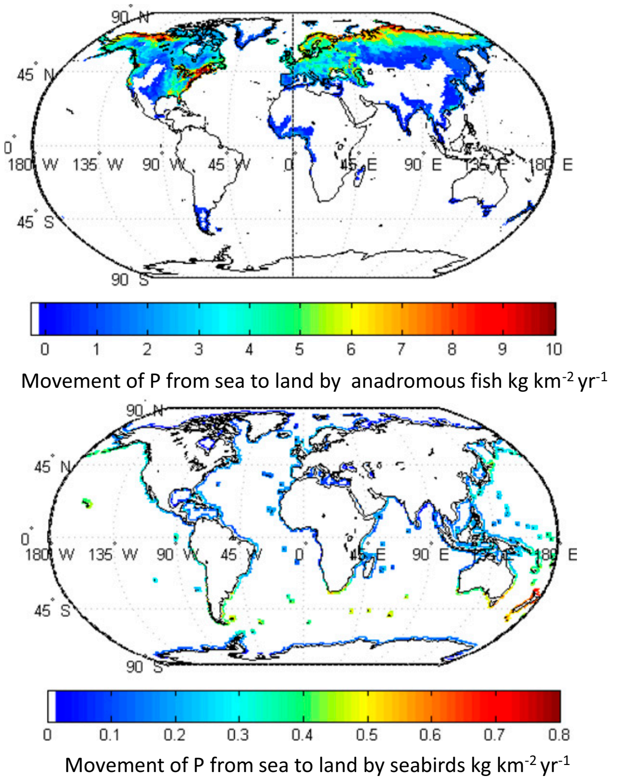

Fig. 3. Nutrient movement of P from ocean to land by anadromous fish and seabirds. (*Top*) Global estimates of historical P ($kg{\cdot}km^{-2}{\cdot}y^{-1}$) moved by the bodies of anadromous fish in the past. Nutrient movement by anadromous fish may be underestimated in tropical regions due to a lack of data. (*Bottom*) Global estimates of guano movement to coastal land by all seabirds, assuming 20% of the guano arrives on land (measured in $kg{\cdot}km^{-2}{\cdot}y^{-1}$) 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 P_2O_5) 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 become 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 CO_2 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

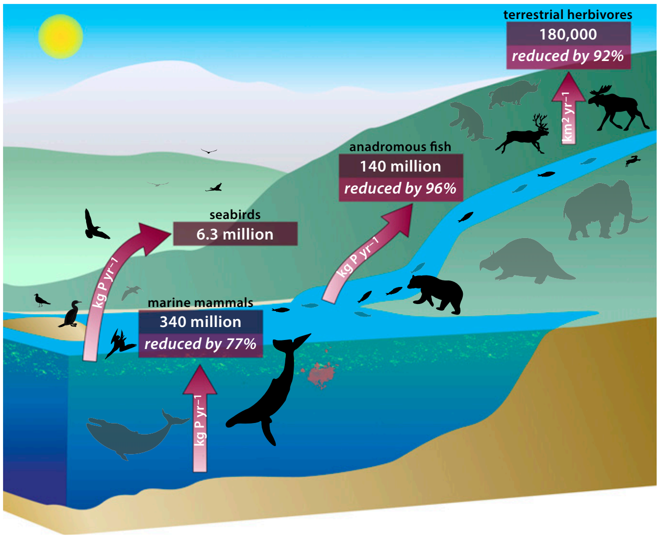

Fig. 4. Potential interlinked system of recycling nutrients. The diagram shows a potential route of nutrient transport of the planet in the past. Red arrows show the estimated fluxes or diffusion capacity of nutrients listed in Table 1. Grey animals represent extinct or reduced population densities of 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):

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

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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