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The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia

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In the late Pleistocene, 97 genera of large animals went extinct, concentrated in the Americas and Australia[1]. These extinctions had significant effects on ecosystem structure[2], seed dispersal[3] and land surface albedo[4]. However, the impact of this dramatic extinction on ecosystem nutrient biogeochemistry, through the lateral transport of dung and bodies, has never been explored. Here we analyse this process using a novel mathematical framework that analyses this lateral transport as a diffusion-like process, and we demonstrate that large animals play a disproportionately large role in the horizontal transfer of nutrients across landscapes. For example, we estimate that the extinction of the Amazonian megafauna decreased the lateral flux of the limiting nutrient phosphorus by more than 98%, with similar, though less extreme, decreases in all continents outside of Africa. This resulted in strong decreases in phosphorus availability in eastern Amazonia away from fertile floodplains, a decline which may still be ongoing. The current P limitation in the Amazon basin may be partially a relic of an ecosystem without the functional connectivity it once had. We argue that the Pleistocene megafauna extinctions resulted in large and ongoing disruptions to terrestrial biogeochemical cycling at continental scales and increased nutrient heterogeneity globally.

The consequence of megafauna extinctions on nutrient budgets is of particular interest because large animals play a disproportionately important role in this translocation of nutrients because they travel farther and have longer food passage times than smaller animals[5,6] (Methods). Animals are vectors of nutrients through their dung and flesh. This movement takes two main forms: the concentration of nutrients into 'hotspots'[7,8], and diffusion, the dispersion of nutrients from regions of high nutrient concentrations to regions of low nutrient concentrations[9]. Although the bulk of research has examined the former process, there is a growing body of literature documenting animal-mediated translocation of nutrients across gradients, thus providing fertility to nutrient limited ecosystems[10,11].

There are significant challenges in extrapolating these site studies to large spatial scales (continental or global scale) and over long timescales (hundreds to thousands of years). It is an even greater challenge to apply these insights to extinct fauna, about which little is known aside from body size and distribution. However, if we consider all animal species over long time periods, we propose that animal movement begins to approximate a 'random walk', such that the horizontal flux of nutrients can be modelled as a diffusion-like process analogous to the diffusion of heat (see Supplementary Information for further justification and discussion of this approximation). To estimate the diffusivity of nutrients based on body size and distribution, we make use of a large literature on body size relationships[12] describing a wide range of animal physiology and behaviour based on size (M), such as day range (DD), metabolic rate (MR), population density (PD) and food passage time (PR). We calculate a diffusion term (Φ) for dung (see Methods and Supplementary Information for derivation and explanation of all terms) according to the following equation:

$$\Phi = (1-\epsilon) * \mathrm{MR} * \frac{\mathrm{PD}}{\alpha B} * \frac{(\mathrm{DD} * \mathrm{PR})^2}{2 * \mathrm{PR}} = \frac{0.78 * 0.05 * M^{1.17}}{\alpha B} \quad (1)$$

We calculate the overall mass-scaling coefficient for Φ to be 1.17 (Figs 1 and 2a). The scaling coefficient specifically for larger herbivores (>10 kg) is even greater at 1.41 (Supplementary Information). Because the scaling coefficients are greater than one, this means that large animals are disproportionally important in the

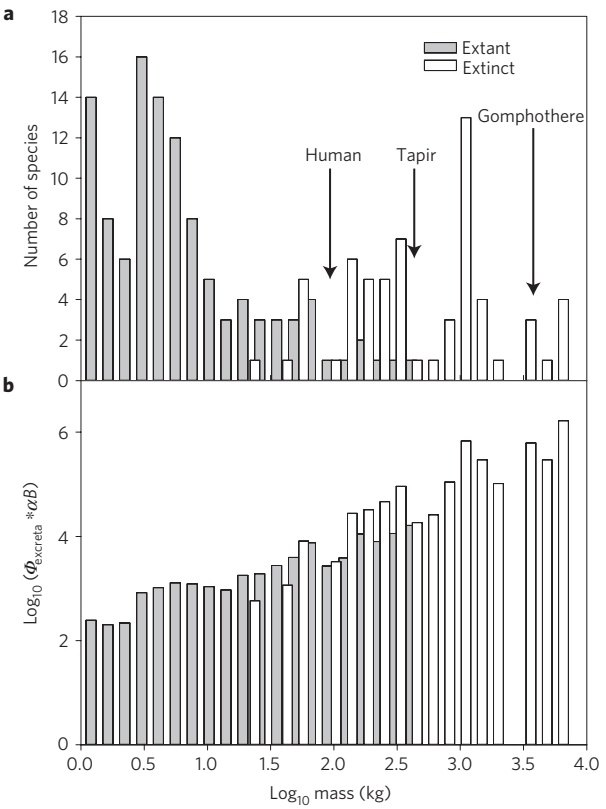

Figure 1 | Megafauna extinctions in South America and their impact on Φ. **a**, A histogram of extinct (white) and living (grey) South American fauna (>1 kg). **b**, The diffusivity term $\log_{10}$ ($\Phi_{excreta} * \alpha B$) calculated for each size class for extinct and living South American fauna (>1 kg) in units of km^2 yr^{-1}.

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spread of phosphorus because of their high food consumption rates, their large daily ranges, and their long gut residence times, despite their lower population density.

We next explore how the extinction of the Amazonian megafauna affected the distribution of *P* across the Amazon basin, although a very similar framework could be applied to many other potentially limiting micronutrients such as sodium, which has recently been suggested to be limiting for animals in tropical forests away from coastal regions[13]. The extinctions of the Pleistocene megafauna in South America took place over several thousand years, but were particularly concentrated following human arrival during periods of intensified climate change in South America (13,500–11,500 years ago; refs 1,14). Most known fossils of extinct megafauna have been found in regions that were known to be savannas during the Pleistocene. However, it is likely that forest-dwelling megafauna are underrepresented in the fossil record owing to the poor preservation of fossils in humid tropical forests. There is isotopic evidence that several of the extinct megafauna were browsers that would have lived in a forest environment[15]. Large body size does not preclude a forest habitat, as demonstrated by the extant forest-dwelling species of elephants, rhinos, hippos and bovids in Asia and Africa.

The extinctions in South America led to drastic changes in animal size distributions, with 70% of animal species >10 kg going extinct (62 species), including such large iconic species as gomphotheres, giant sloths and glyptodonts (Fig. 1). The mean size of animals >10 kg throughout South America dropped from 843 to 81 kg. Using our mass-scaling relationships we estimate that mean home range dropped from 61.8 to 4.8 km^2, mean day range decreased by 58%, mean food passage time decreased by 46%, mean lifetime decreased by 33% and the average distance between food consumption location and excretion location decreased by 7.0 km from 9.1 to 2.1 km. From equation (1) we estimate that the lateral nutrient transfer diffusivity Φ in the Amazon basin decreased by >98%, from ~4.4(2.4–6.5) to 0.027 $km^2\,yr^{-1}$. The extinction of the megafauna effectively 'turned off' the potential for lateral nutrient flow in terrestrial Amazonia.

We explore the consequences of this reduction of lateral nutrient transfer by modelling the phosphorus concentration *P* at a location as a function of lateral animal diffusion, input from dust deposition and *in situ* weathering, and loss to leaching. There is much evidence that phosphorus is the key limiting nutrient in many Amazonian forests. The appropriate *P* budget equation is

$$\frac{dP}{dt} = \Phi\frac{d^2P}{dx^2} - KP + G \qquad (2)$$

where *K* is a first order loss rate from phosphorus leaching and occlusion and *G* is a gain rate from dust deposition and *in situ* weathering. Dust from the Sahara is estimated to provide an average of 0.48 kg P $km^{-2}\,yr^{-1}$ to the Amazon basin[16], and we estimate *in situ* weathering rates on poor eastern Amazonian soils (Supplementary Information; ref. 17). However, a much larger source of phosphorus is contributed by the uplift of fresh bedrock from the Andes Mountains, or uplift and exposure of fertile Miocene sediments in Western Amazonia, which create a sharp boundary in fertility in Western Amazonia[18]. Andean tributaries 'whitewater rivers' deliver 806 Mg of P per year to the lowlands compared to only 43 Mg P per year for clear or black rivers[17]. This P arrives in the lowlands through flooded forests and other river estuaries which flood ~17% of the Amazon basin at the peak[19]. Consequently, vegetation growing in these whitewater floodplains has an average leaf P concentration of 1.50 mg g^{-1} ($N = 88$ tree species) versus 0.55 mg g^{-1} ($N = 220$ tree species) in *terra firme* and black water sites[20] (Supplementary Table S1).

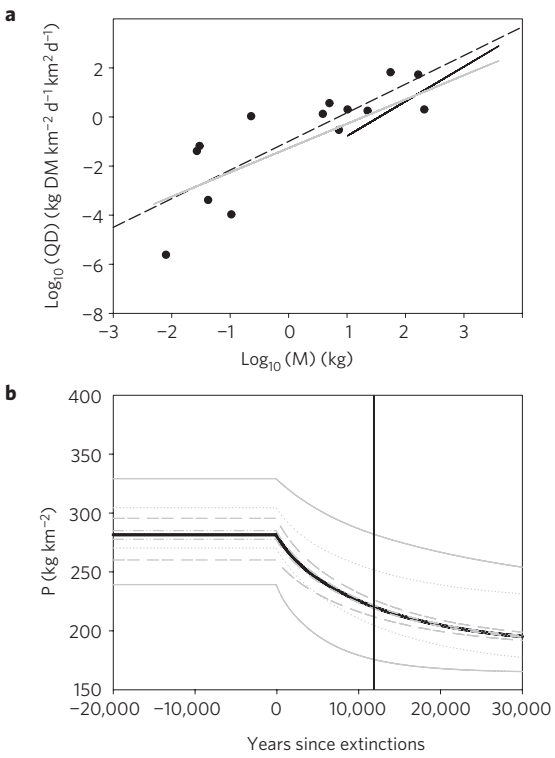

Figure 2 | Calculation of the diffusion coefficient and the impact on continental averaged South American ecosystem *P* distribution. a, Dashed line is the linear regression of $\log_{10}$ mass versus $\log_{10}$ transformed values for diffusivity (QD; kg dry matter $km^{-2}\,d^{-1} * km^2\,d^{-1}$) for all herbivores for which we have all animal values necessary (black dots) for QD ($N = 14$). Solid grey line uses the allometric equations calculated for each parameter separately and combines them to estimate QD for all herbivores and herbivores >10 kg (black line; Supplementary Information). **b**, A time series showing the step change in *P* concentrations averaged over the 2D Amazon basin simulations following extinctions 12,000 years ago. The black line is our best estimate and the grey lines are a series of sensitivity studies where we double and halve our best estimates for dust input (*G*; dotted), loss rate (*K*; solid), ε (dash dot), and $\Phi_{excreta}$ (dashed). The black vertical line indicates present day (~12,000 years following the extinctions).

This strong contrast between fertile and infertile substrates creates strong discontinuities in the supply of P (refs 20,21). The site-to-site variability in available soil P concentration is a strong determinant of vegetation P content, leading to the observation that edaphic factors control plant carbon:phosphorus ratios much more than phylogenetic factors[22]. Edaphic constraints on plant nutrient uptake in turn have strong impacts on vegetation photosynthesis, productivity, demographic rates, and biomass accumulation throughout the Amazon basin[21] in addition to species composition[18].

We solve equation (2) for *P*, with a step-change reduction in Φ at the time of the megafaunal extinction. Before the extinctions, we simulate that P was relatively well-dispersed across Amazonia, with lateral animal diffusion transporting P from the rich floodplains and western Amazonia to the much of the rest of the basin (Fig. 3a). After the extinctions, the megafauna nutrient 'pump' switched off, and this lateral transfer became much more local, and the high-phosphorus regions retreated to areas bordering the whitewater floodplains and other fertile areas (Fig. 3b,c). Even 12,000 years after the megafaunal extinction, our best estimate indicates that the Amazon basin has not yet adjusted to a post-megafaunal low nutrient steady-state—we estimate it is 67% (46–85%) of the way along the transition (Fig. 2b) (This estimate is highly dependent

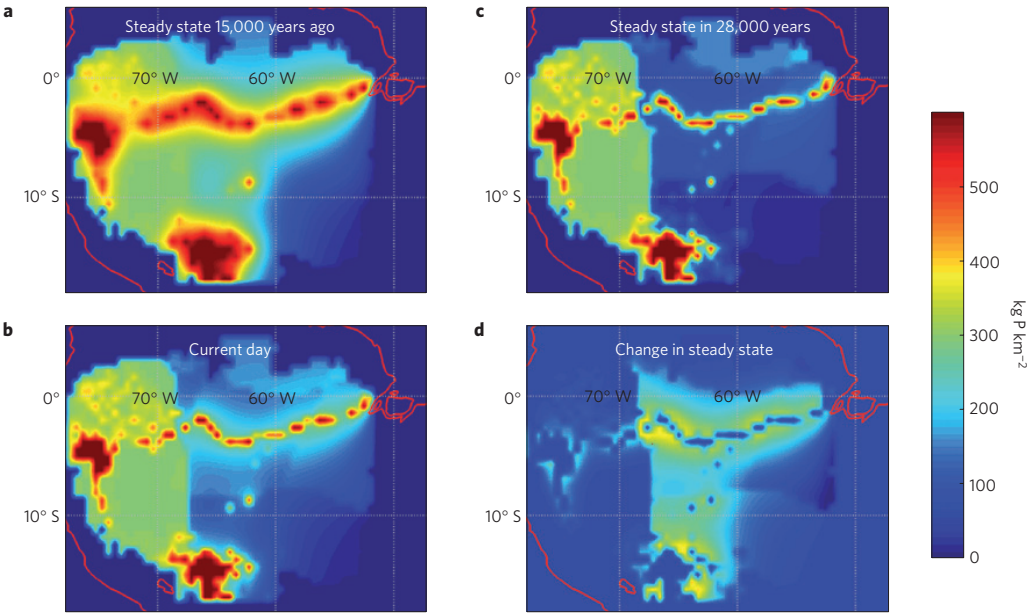

Figure 3 | Map showing changing ecosystem P concentrations in South America due to megafauna extinctions. a, The steady-state estimate of P concentrations in the Amazon basin before the megafaunal extinctions with a lateral diffusivity $\Phi_{excreta}$ value of 4.4 km^2 yr^{-1}. **b**, The current-day estimate of P concentrations 12,000 years after the extinctions with current animals and a $\Phi_{excreta}$ value of 0.027 km^2 yr^{-1}. **c**, Estimated P concentrations in the Amazon basin 28,000 years in the future. **d**, The difference between the pre- and post-extinction equilibrium (**a** and **c**).

Table 1 | Average $\Phi_{excreta} * \alpha B$ (km^2 yr^{-1}) for each continent calculated for modern species and modern plus extinct species.

	North America	South America	Australia	Eurasia	Africa
Number of species extinct	65	64	45	9	13
Mean weight of extinct animals (kg)	846	1,156	188	2,430	970
Modern $\Phi_{excreta} * \alpha B$	13,876	12,934	21,804	21,779	265,621
Modern + extinct fauna $\Phi_{excreta} * \alpha B$	140,716 (±38,000)	283,854 (±81,000)	48,250 (±8,000)	118,349 (±29,000)	324,848 (±18,000)
Percentage of original	10% (±2%)	5% (±1%)	45% (±6%)	18% (±4%)	82% (±4%)

Bottom row is the percentage of the original $\Phi_{excreta} * \alpha B$ remaining. The error represents an uncertainty in extinct species distribution of 30%.

on the loss rate (K) which is a large source of uncertainty.). Our simulated modern-day distribution of P does not include the large diversity of parent material and soil evolutionary stages which greatly impact observations of soil P across Amazonia (Supplementary Fig. S3), and instead represents the change in accessible P in the biomass-necromass-soil continuum ('ecosystem P') and not total P. Ecosystem P concentrations in intact Amazonian forests could, therefore, potentially continue to decrease (to >90% of steady state) for 17 (between 3 and 43) thousand years into the future as a legacy of the Pleistocene megafauna extinctions.

Although we have concentrated our analysis on Amazonia, it is likely that there were similar changes in nutrient transfer on all continents that experienced megafaunal extinction, albeit with variations in the local nutrient gradients and the key limiting macro- or micronutrients. Using data on Pleistocene megafaunal body masses, we estimate that Φ decreased drastically on all continents. Africa, the continent on which modern humans co-evolved with megafauna, is the only continent with most (82%) of the lateral nutrient distribution capacity still intact (Table 1). The largest declines (90–95%) were in the Americas. It seems that Eurasia also showed a large decline despite only nine extinctions, because the extinct megafauna were large (for example mammoths) whereas Australia showed a moderate decline despite a large number of extinctions, because the extinct megafauna were relatively small. However, these are estimates of non-pressured population densities, and ranges and current values for Africa and Eurasia are probably reduced owing to current pressures on megafauna, because of decreases in megafaunal population size and restrictions on their free movement across landscapes.

Following the extinction of the megafauna, humans eventually appropriated much of the net primary production that had been consumed by the extinct animals[23,24]. Did we also take over their role of nutrient dispersal? People currently provide nutrients as fertilizer to agricultural systems, but much of this gets concentrated near agriculture, suggesting that humans act as concentrating agents rather than diffusive agents like the herbivorous megafauna. Therefore, compared to earlier eras, the post-megafaunal world is characterized by greater heterogeneity in nutrient availability[25].

Our framework for estimating nutrient diffusion by animals can be applied to modern ecosystems globally, and even incorporated into global land biosphere models demonstrating the ecosystem service of nutrient dispersal. This service is analogous to that played by arteries in the human body, with large animals acting as arteries of ecosystems transporting nutrients further and smaller animals acting as capillaries distributing nutrients to smaller subsections of the ecosystem. Therefore, after the demise of its large animals, the Amazon basin has lost its nutrient 'arteries' and the widespread assumption of P limitation in the Amazon basin may be a relic of an ecosystem without the functional connectedness it once had[3]. This new mathematical framework provides a potential tool of quantifying the important but rarely recognized biogeochemical services provided by existing large animals. Therefore, those

remaining large animals under current threat in African and Asian forests can be properly valued.

More generally, we live on a planet where the nutrient supply in any one location largely reflects underlying geomorphology or abiotic input from rivers or airborne deposition (Fig. 3b,c). Our analysis suggests that this abiotic paradigm may be peculiar to a post-megafaunal extinction world. In Amazonia (and probably in many other parts of the world), we propose (and discuss methods of validation in the Supplementary Information) that large animals played a major role in diffusing nutrients across the landscape, thereby moderating the importance of local geomorphology in determining nutrient supply. To the extent humans contributed to the megafaunal extinctions, this suggests that major human impacts on global biogeochemical cycles stretch back to well before the dawn of agriculture. Aspects of the Anthropocene may have begun with the Pleistocene megafaunal extinctions.

Methods

Our mathematical derivation is presented more fully in the Supplementary Information, and the results summarized here. The equation that best incorporates the diffusive properties of animals is equation (3):

$$\frac{\partial P}{\partial t} = \Phi_{\text{excreta}} \frac{\partial^2 P}{\partial x^2} + \Phi_{\text{body}} \frac{\partial^2 P}{\partial x^2} \quad (3)$$

P is the phosphorus concentration per unit surface area, and Φ is an effective diffusivity that captures the process of nutrient consumption and defecation (Φ_{excreta}) and the process of P accumulation in bones and loss at death (Φ_{body}). In the Supplementary Information, we calculate Φ_{body} and show that it is >1,000 times smaller than Φ_{excreta}, and therefore we neglect this term in subsequent analyses. Φ_{excreta} is the product of two main terms, the lateral diffusion rate (D), which describes animal movement, and the rate of fractional consumption of edible biomass (Q). D is calculated as the limit of a random walk process[9] and is equal to $(\Delta x)^2$ (a step size in the walk) divided by $2\Delta t$ (the duration of the step). For ingestion and excretion, the step size is the mean daily displacement DD (km d^{-1}) multiplied by the average gut passage time PR (days). The timescale is the average gut passage time PR (days). To estimate the plant matter and P consumed by groups of animals, we estimate the population density of animals (PD; #/km^2) that consume dry matter (DM) to fulfill their metabolic requirements (MR; kg DM/animal/day). B represents total plant biomass (kg DM/km^2), of which α is the edible fraction. We assume αB is equivalent to foliar net primary productivity[26]. Some fraction ε of P is incorporated into the bodymass, whereas the remainder $(1-\varepsilon)$ is excreted. For megafauna, we estimate ε to be 0.22 (ref. 27; varied by $\pm$0.1 in a sensitivity study). A number of the key terms determining Φ_{excreta} are associated with body mass, including day range, DD (ref. 28), gut passage time PR (ref. 6), metabolic rate[29], and population density PD (ref. 30). The appropriate mass-scaling power-law coefficients for herbivores >10 kg are: day range 0.43; gut passage time 0.28; metabolic rate 0.87; population density −0.58. These are detailed and justified in the Supplementary Information.

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Author contributions

C.E.D. developed the original idea of the paper. C.E.D., Y.M. and A.W. developed the mathematical framework and C.E.D. and A.W. ran the models. C.E.D. led the writing of the paper with contributions from Y.M. and A.W.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to C.E.D.

Competing financial interests

The authors declare no competing financial interests.