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Herbivores increase the global availability of nutrients over millions of years

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Can the presence of herbivores increase global nutrient availability? Animals disperse vital nutrients through ecosystems, increasing the spatial availability of these nutrients. Large herbivores are especially important for the dispersal of vital nutrients due to their long food passage times and day ranges, and large herbivores from past periods (the Pleistocene) may have increased nutrient concentrations on the continental scale. However, such results have been demonstrated theoretically but not yet empirically. Models suggest that the Pennsylvanian subperiod (323–299 million years ago), with no tetrapod terrestrial herbivores, would have had fewer, less-well-distributed nutrients than the Cretaceous period (145–66 million years ago), with the largest terrestrial herbivores ever—the sauropods. Here, I show that these models are supported empirically by remnant plant material (coal deposits) from the Cretaceous ($N = 680$), which had significantly ($P < 0.00001$) increased concentrations (136%) and decreased spatial heterogeneity (22%) of plant-important rock-derived nutrients compared with the Pennsylvanian subperiod ($N = 4{,}996$). Non-biotic physical processes, such as weathering rates, cannot account for such differences, because aluminium—a nutrient not important for plants and animals, but weathered in a similar manner to the above elements—showed no significant difference between the two periods, suggesting that these large changes were driven by plant–herbivore interactions. Populations of large wild herbivores are currently at historical lows; therefore, we are potentially losing a key ecosystem service.

There are now a large number of empirical studies demonstrating that animals move significant quantities of nutrients across landscapes. For example, terrestrial predators transport ocean-derived nutrients to terrestrial ecosystems by feeding on migratory fish[1]. Seabirds transport nutrients from the sea to land, increasing soil phosphorus concentrations on seabird islands compared with non-seabird islands[2]. Moose *Alces americanus* transfer significant amounts of aquatic-derived nitrogen to terrestrial systems[3]. Amazonian woolly monkeys *Lagothrix lagothricha* move large amounts of phosphorus across a floodplain concentration gradient by eating and defecating back and forth across a nutrient concentration gradient[4]. In other words, the monkeys move nutrients through diffusion and without preferentially defecating in the less-fertile area. This study showed that a single species can transport significant quantities of nutrients through diffusion[4]; the logical next question is how do all animals over very long periods affect nutrient abundance and spatial patterns?

To answer this question, two recent studies have compiled mass scaling data for terrestrial mammals and found that bigger animals are disproportionately important for the movement of nutrients away from a concentration gradient (with a 1.17 scaling exponent)[5,6]. These studies used body mass and species range maps for all mammals to globally estimate the nutrient diffusion capacity of mammals across concentration gradients. Mathematically, the nutrient diffusion capacity of mammals is measured in units of square kilometres per year and is similar to thermal diffusivity, which indicates the ability of a substance to move heat away from a hot area. Extinctions and hunting pressures over the past 12,000 years decreased this nutrient diffusivity by large animals to less than 10% of its former value[7] (and such hunting pressures continue today[8]), leading to significant hypothesized decreases in nutrient concentrations at the continental scale[5,6].

Such nutrient distribution capacity of animals likely began with the advent of herbivory itself. Terrestrial tetrapod herbivory began during the Late Pennsylvanian, around 305 million years ago (Ma) and there is fossil evidence of dental occlusion around this time, where teeth from the upper jaw come in contact with those in the lower jaw[9]. Productive large forests with a global estimated net primary production of 33.7 Gt C yr^{-1} (ref. [10]) existed during the Carboniferous (359–299 Ma) and these forests already had arbuscular mycorrhizal symbiotic fungal relationships allowing efficient nutrient extraction by plants[11]. Therefore, nutrient acquisition by Carboniferous forests was similar to today (except without ectomycorrhizae, which evolved later[12]), but without tetrapod herbivory (although herbivorous arthropods up to 1.8 m long were common in coal swamps—*Arthropleura*[13]).

Over the Phanerozoic, there has been a tendency towards the evolution of larger body size as a defence against predation, called Cope's rule[14,15]. Combining Cope's rule with the disproportionate importance of large animals in nutrient distribution suggests that as herbivore size increases over time, nutrients are more evenly distributed across the planet making ecosystems more productive. However, this nutrient diffusion capacity may be curtailed following mass extinction events, such as the extinction of the dinosaurs or the megafauna extinctions of the past 12,000 years. There is evidence that large animals are especially prone to mass extinctions due to their intrinsic low fecundity, which may act as a control on species size[15]. Here I theoretically and empirically test the importance of large animals on nutrient distributions by comparing a period in Earth's history with no tetrapod herbivores to the period with the largest herbivores of all time.

Results

Maximum terrestrial and marine body size increased by more than three orders of magnitude over the Phanerozoic and there were periodic two order of magnitude decreases in maximum body size following mass extinction events (Fig. 1a). The largest change in animal-mediated nutrient diffusion capacity was possibly between

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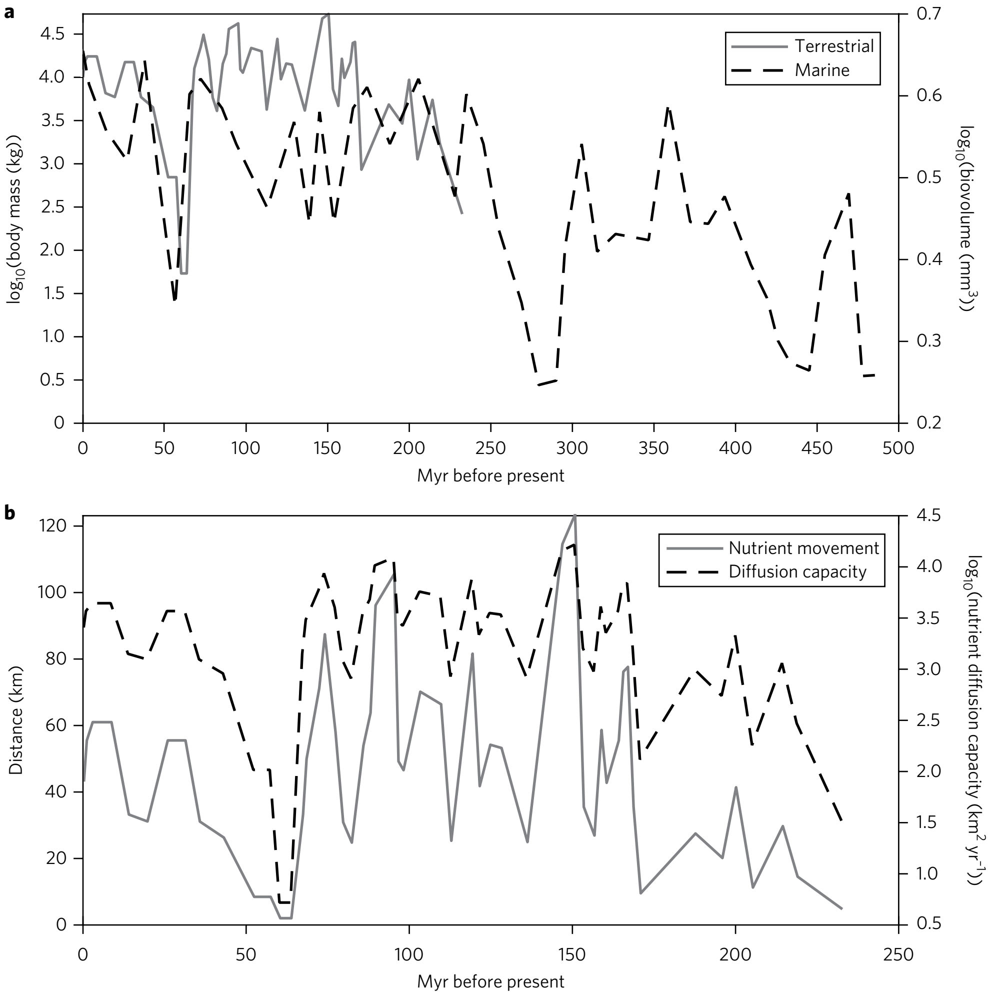

Fig. 1 | Maximum body size and nutrient movement. a, Maximum body size for terrestrial and marine systems over the Phanerozoic[14,15,17]. **b**, Movement of nutrients between consumption and defecation (equations (1) and (2)) and lateral nutrient diffusion capacity (equation (3)) of the largest terrestrial animal from each 5–10 Myr period.

the Carboniferous, before tetrapod herbivory but with large forests, and the Cretaceous, home to the largest terrestrial herbivores in Earth's history, the sauropods (Fig. 1a)). Dinosaur ontogeny is different from that of mammals as they lay eggs and have smaller, independent young, versus the larger, cared-for young of mammals[16]. Therefore, although the largest animal size was much larger in the Cretaceous than now, the median animal size (due to the abundance of small young) was more similar. I estimate median Mesozoic body size following ref. [16] for Sauropodomorpha (13,300 kg), Ornithischia (891 kg), Theropoda (158 kg) and all dinosaur taxa (1,448 kg).

If we assume movement, feeding and biomechanical attributes of these extinct animals were similar to extant mammals (an assumption I explore in a sensitivity study and discuss later), I would predict based on median body size alone that the mean sauropod day range (Methods, equation (1)) was 14.8 km (7–16 km) (all taxa, 6.5 km), the mean food passage time (Methods, equation (2)) was 3.4 days (2.7–5.1 days) (all taxa, 1.9 days), and the average distance between food consumption location and excretion location was 51 km (25–76 km) (all taxa, 12.6 km) (Fig. 1b). Based on similar assumptions (see Methods for an explanation), the largest herbivore or detritivore of the Carboniferous (genus *Arthropleura*) would have moved only 0.2–0.4 km on average between food consumption and defecation.

However, animals rarely move in a straight line and without knowing anything else about extinct animal motion, the most parsimonious assumption is that their motion resembles a 'random walk'. Based on the assumptions from the previous paragraph and a 'random walk' mathematical model, the lateral nutrient transfer diffusivity Φ (Methods, equation (3)) for the median sauropod weight of 13,300 kg was ~3,300 km^2 yr^{-1} (all taxa, 250 km^2 yr^{-1}). The nutrient diffusion capacity of the largest herbivore of the Cretaceous was approximately three orders of magnitude greater than the Pennsylvanian subperiod (3,300 km^2 yr^{-1} versus 1 km^2 yr^{-1}). Sauropods would not be expected to produce more dung per area than *Arthropleura* (see Methods for details), and the size dependence of the nutrient diffusion capacity is instead a function of the movement of nutrients between consumption and defecation (day range multiplied by food passage time). Such large changes in nutrient diffusion capacity also occurred during previous mass extinction events. For instance, following the K/T extinction event, nutrient diffusion capacity of the largest herbivores dropped from 3,300 km^2 yr^{-1} to 5 km^2 yr^{-1} (Fig. 1b) and the capacity of the Cenozoic never fully returned to that of the Mesozoic (it took 10–20 Myr for a herbivore > 1,000 kg to evolve in the Cenozoic)[15]. Today, due to extinctions and population declines of large animals, global terrestrial nutrient diffusion capacity has dropped to ~8% of the hypothesized Pleistocene values, or approximately an order of magnitude lower than the hypothetical Pleistocene value[7]. However, nutrient diffusion capacity in other regions, such as southern South America, have dropped by more than three orders of magnitude,

Table 1 | Median values (ppm ± s.e.) of Cretaceous ($N=680$) and Pennsylvanian subperiod ($N=4,996$) coal deposits for plant-important nutrients (calcium, magnesium, phosphorus, potassium, sulfur) and for an element not preferentially taken up by plants (aluminium), and the percent change

Element	Median Cretaceous (ppm)	Median Pennsylvanian subperiod (ppm)	% change	c.v. Cretaceous	c.v. Pennsylvanian subperiod	% change
Calcium	3,500 ± 274	1,070 ± 125	227****	0.57 ± 0.09	0.77 ± 0.11	−27***
Magnesium	828 ± 62	457 ± 15	81****	0.48 ± 0.06	0.76 ± 0.08	−37****
Potassium	524 ± 78	1,545 ± 44	−66****	1.08 ± 0.25	0.85 ± 0.09	28****
Phosphorus	392 ± 43	81.6 ± 8	350****	0.64 ± 0.18	1.42 ± 0.11	−55****
Sulfur	1.55 ± 0.17	0.82 ± 0.03	89****	0.57 ± 0.06	0.71 ± 0.04	−20*
Aluminium	13,900 ± 1,260	12,600 ± 271	10 (NS)	0.53 ± 0.08	0.56 ± 0.03	−5 (NS)
Mean (excluding aluminium)			136****			−22****

Coefficient of variation (c.v.) (s.d./median) (±s.e.) and the percent change for equal-sized regions of 1,000 km^2 for the Cretaceous ($N=54$) and Pennsylvanian subperiod ($N=231$). Significance is determined using Wilcoxon rank-sum test and indicates *$P<0.10$. **$P<0.05$, ***$P<0.001$, **** $P<0.00001$. NS, not significant.

which is the scale of the global change between the Cretaceous and the Pennsylvanian subperiod.

Plant material from the Cretaceous and the Pennsylvanian subperiod was often buried faster than it decayed, forming peat and then later coal. Most coal deposits recovered in the continental United States over the past century are from the Pennsylvanian subperiod and the Cretaceous, and elemental analyses of this coal are available from online databases (Coalqual)[18]. The elemental concentrations within coal are hypothesized to be determined by the elemental concentrations of the parent vegetation, especially for elements important for plants such as phosphorus[19,20]. Permian coals from India and Australia, and Cretaceous coals from Western Canada have higher phosphorus concentrations than Carboniferous coals from Europe and the United States[19,20]. It has been previously suggested that dinosaurs may have increased phosphorus deposits in Cretaceous coals[21]. Based on the hypothesized three order of magnitude change in nutrient diffusion capacity of the largest animals (but probably more if all animals are considered), I would expect a more even distribution of nutrients in the Cretaceous period than the Pennsylvanian subperiod with mainly abiotic (wind and water) mechanisms to redistribute nutrients. The Coalqual data support this supposition and when all available plant-important nutrient data (Ca, Mg, K, P and S) were averaged into equal-sized regions of 1,000 km^2 for the Pennsylvanian subperiod ($N=231$) and the Cretaceous ($N=54$), nutrient distribution was significantly more variable ($P<0.000001$, Wilcoxon rank-sum test) in the Pennsylvanian subperiod than in the Cretaceous, with an average increased coefficient of variation (c.v.) of 22% (Table 1 and Fig. 2). There was no significant difference ($P>0.05$) in c.v. between the two periods for aluminium, an element toxic to and therefore not concentrated by plants. Such trends were constant under a wide range of region sizes and threshold minimum number of points (Supplementary Figs. 1 and 2).

Cretaceous herbivores consuming floodplain plants over millions of years would theoretically move large quantities of weathered floodplain nutrients towards the *terra firme*[5,6], thus increasing total nutrient concentration in the Cretaceous compared with the Pennsylvanian subperiod (all else being equal). Simulations of such floodplains in the Amazon suggest that the more recent megafauna extinctions decreased nutrient concentrations in much of the basin by more than half[6]. Once incorporated into the biota of the *terra firme* vegetation, if there were abundant herbivory, the nutrients would be continually spread, thus further minimizing nutrient concentration gradients. With no significant herbivory in the Pennsylvanian subperiod, the nutrients seasonally absorbed by floodplain plants would be washed out to the ocean since there were no herbivores to consume the plants and defecate them into the *terra firme*. The Coalqual data show that nutrient concentrations important for plants and animals were significantly higher in Cretaceous coals than Pennsylvanian subperiod coals ($P<0.00001$, rank-sum test) by an average of 136% (Table 1 and Fig. 3). To reduce spatial autocorrelation, I aggregated the data into 90 km^2 regions because this minimized the Akaike's information criterion (AIC) following a simultaneous auto-regressive (SAR) analysis (see Methods for details). In contrast to the large significant differences for plant-important nutrients, aluminium, an element toxic to plants, was the only element with no significant change between the two periods (although the direction of potassium was not as expected, which I explore in the Supplementary Information). The mean Clarke value[22] for global phosphorus coal deposits (250 ± 10 ppm, $N=14,812$) is much higher than the 175 ± 3 ppm mean for Pennsylvanian subperiod coals ($N=4,803$) calculated here, suggesting that Pennsylvanian subperiod coal deposits have anomalously low phosphorus concentrations compared with global concentrations of coal phosphorus (as noted previously[19,20]), which may be due to the lack of tetrapod herbivores.

Plants concentrate useful elements in their leaves and when these leaves are consumed by herbivores the nutrients can be spread elsewhere through diffusion (movement of high concentrations towards lower concentrations). For instance, a recent paper compiled data from tropical forests and found that leaf potassium concentrations were ~100 times greater than soil potassium concentrations[23]. However, this same paper found that leaf aluminium concentrations were approximately equal to soil aluminium concentrations because plants do not preferentially uptake aluminium. Therefore, herbivores would not spread aluminium through diffusion because it is not concentrated within the leaves and there is no concentration gradient. There were no significant differences ($P>0.05$) in aluminium concentrations nor spatial distribution between the two periods while there were highly significantly differences ($P<0.00001$) for all the plant-important nutrients. Aluminium is weathered at the same rate as plant-important nutrients indicating that the difference in their spread and abundance is due to the herbivory present in the Cretaceous.

Discussion

Rock weathering, the ultimate source of all rock-derived nutrients, is a function of biology (plant roots and mycorrhizae) and physical chemistry (temperature and precipitation)[11]. The colder, drier global conditions of the Pennsylvanian subperiod could have reduced weathering rates compared with the Cretaceous. However, due to continental movement, Pennsylvanian subperiod coal deposits from the continental United States were produced in the 'tropics' (at the Equator) while Cretaceous coal deposits of the continental

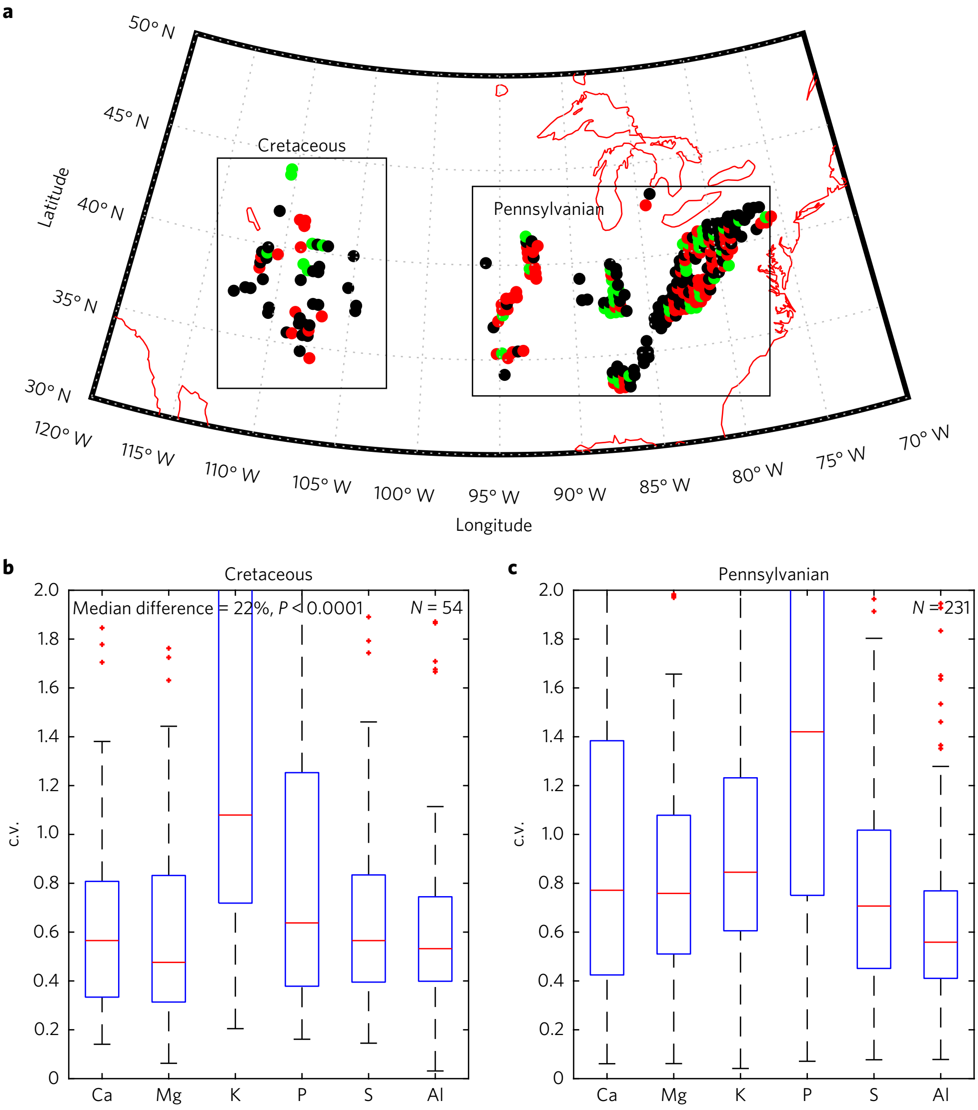

Fig. 2 | Elemental distribution in the Cretaceous and Pennsylvanian subperiod. a, Coal elemental data separated into equal regions of 1,000 km^2 ($N = 54$ for Cretaceous and $N = 231$ for Pennsylvanian subperiod) and c.v (s.d./median) for the mean of all plant-important nutrients within each region (black <0.6, red >0.6 and <1.0, green >1). Cretaceous coal is centred in the box in the west while Pennsylvanian subperiod coal is centred in the box near the Appalachians. **b**,**c**, Box-and-whisker diagram for each element (Ca, calcium; Mg, magnesium; K, potassium; P, phosphorus; S, sulfur; Al, aluminium; $N = 54$ for Cretaceous (**b**) and $N = 231$ for Pennsylvanian (**c**) subperiod). The central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers. *P*-value is a Wilcoxon rank-sum test for the confidence interval of all plant-important elements combined (not including Al).

United States were produced in 'temperate regions' (at 30° latitude)[24]. Therefore, although the world was warmer in the Cretaceous (mean 18 °C), the coal from our study was produced in the cooler temperate regions (mean annual temperature, 8–16 °C; mean annual precipitation 0.75–1.5 m yr^{-1} (ref. [25])), while the world was cooler in the Pennsylvanian subperiod (mean 14 °C), but the coal was produced in the warmer tropics (mean annual temperature, 15–20 °C; mean annual precipitation, 2–3 m yr^{-1} (ref. [10])). Ectomycorrhizal fungi probably evolved in the Mesozoic[12] but only became apparent in the fossil record in the middle Eocene (ca. 50 Ma (ref. [26])) and globally dominant in the Cenozoic. Taylor et al. predicted that the increased dominance of ectomycorrhizal fungi towards the end of the Cretaceous more than doubled total biological weathering rates by the end of the Cretaceous increasing in a sigmoidal pattern[11]. Therefore, if we assume roughly similar temperature and precipitation patterns for the coal-producing regions (although the Pennsylvanian subperiod conditions were likely warmer and wetter; Supplementary Table 5) a sigmodal increase of ectomycorrhizal fungi weathering over the Cretaceous could have increased total weathering by up to 30% (Supplementary Table 5), a large amount, but not enough to fully account for the increased nutrient fluxes observed in the Cretaceous.

Other non-herbivory related explanations for these results include a lack of lignin decomposers in the Carboniferous leading to areas of accelerated growth and sequestration of nutrients in certain areas. However, in Supplementary Fig. 3, I show that due to nutrient limitation, over time, nutrients sequestered in both fast- and slow-growing regions would be similar. The abundance of organic material and anoxic conditions of coal-producing regions will lower redox potential, impacting microbial activity and chemistry. However, such reductions of redox potential are unlikely to impact how elements were transported into these regions. Aluminium has a redox potential between Ca, Mg and K and P and S (Supplementary Table 4) suggesting that redox potential could not account for

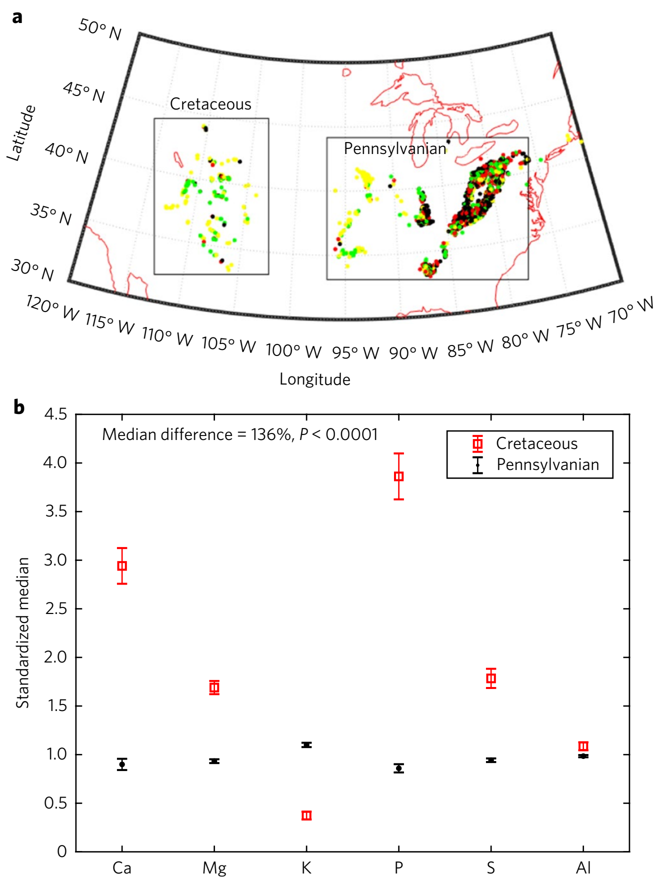

Fig. 3 | Normalized median values in the Cretaceous and Pennsylvanian subperiod. **a**, Normalized median (median value divided by median of all data) aggregated into 90 km^2 regions for all plant-important elements (black <1.0, red >1.0 and <1.5, yellow >2.5). **b**, Normalized median for each element ($N=680$ for Cretaceous and $N=4{,}996$ for Pennsylvanian subperiod). *P*-value is a Wilcoxon rank sum-test for all elements combined, as is the reported total median difference.

aluminium alone showing no change between the Pennsylvanian subperiod and the Cretaceous. Aluminium is highly pH regulated but we would not expect large changes in soil pHs between these two periods (Supplementary Table 4).

Although both periods were forested, there were large evolutionary changes between the Pennsylvanian (dominated by sporophytes such as sphenopsids, ferns and lycopsids) and the Cretaceous (dominated by Gymnosperms). Could different cation uptake rates between these different groups account for our results? This needs to be explored further, but one study found higher percentages of cations (Ca, Mg, K, P) in ferns (common in the Pennsylvanian) than conifers (common in the Cretaceous), which is contrary to our findings, suggesting that herbivores had an even larger impact[27]. The Pennsylvanian subperiod lasted around 24 Myr while the Cretaceous lasted 79 Myr. In general, longer periods will have greater abiotic and biotic variation, but in our results, the longer period (the Cretaceous) had less variation, suggesting this also cannot explain the results.

The metabolism of dinosaurs (ectotherm versus endotherm) is a large still-unresolved debate that has been ongoing for over a century. However, the most recent literature suggests they were either endotherms (like mammals)[28] or mesotherms[29]. If they were mammal-like endotherms, the scaling of metabolic consumption is likely accurate, but if they were mesotherms or ectotherms, I likely overestimate their movement and food needs (this is addressed in the Methods). Sauropods may have used stomach stones to better grind plant material, or they may have compensated for limited oral processing by greatly increasing food retention time in the digestive system[30]. A recent paper estimated that dinosaurs had a food intake level similar to mammals, but a retention time similar to reptiles (an order of magnitude greater than mammals), suggesting we most likely underestimate the nutrient diffusion capacity of the Cretaceous[31]. Therefore, overall, I may overestimate food consumption by sauropods, but underestimate digestion time, and in a sensitivity study in Supplementary Table 2, I estimate the distance travelled between consumption and defecation was between 41 and 76 km. In the Cretaceous, although sauropods were abundant in the Southern Hemisphere, they were less common in the Northern Hemisphere, where advanced ornithischians such as hadrosaurs and ceratopsians, which were significantly smaller than sauropods, were the dominant large herbivores, especially in North America. Therefore, we might expect a larger change in nutrient diffusion in other parts of the world than North America.

This study uses an empirical dataset to show that large herbivore–plant interactions are important in reducing spatial heterogeneity of nutrient supply and, possibly, increasing the supply of important nutrients. Combining Cope's rule with large animals' inherent role in nutrient distribution means that the planet may have an intrinsic mechanism for improving nutrient dispersal over time. Since the Pleistocene, there has been a mainly human-caused[8] mass extinction event of large animals that has reduced the nutrient diffusion capacity of the planet by an order of magnitude[7]. These data show that the removal of large animals could potentially reduce nutrient concentrations by >130%, increase heterogeneity by >20%, and that the re-evolution of such large-bodied species can naturally take more than 10 Myr (ref. [15]). Therefore, we should make a special focus to conserve our remaining large animals, as the largest, most charismatic are facing the greatest extinction pressures[8].

Methods

I aggregated maximum terrestrial body size datasets from Smith et al.[15] for the Cenozoic, from Benson et al.[17] for the Mesozoic and from Heim et al.[14] for marine systems for the Phanerozoic. Based on the maximum body size from each terrestrial dataset over 10 Myr, I multiplied equation (1) for day range with equation (2) for food passage time to estimate mean distance travelled between food consumption and defecation, where M is mean animal body mass[5,6]. I used equation (3) to estimate nutrient diffusivity in units of square kilometres 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)[5,6].

$$\text{Day range} = 0.45 \times M^{0.368} \tag{1}$$

$$\text{Food passage time} = 0.29 \times M^{0.26} \tag{2}$$

$$\text{Nutrient diffusivity}\,(\Phi) = 0.05 \times M^{1.17} \tag{3}$$

Derivation of equation 3. Lateral nutrient distribution capacity was mathematically formulated and found to be strongly size dependent in two previous studies[5,6]. I now use this framework to calculate how the largest herbivores through time have diffused nutrients away from hotspots. This methodology ignores barriers such as deserts, mountains and major rivers and therefore may overestimate transport kinetics in continental interiors. Nutrient diffusion capacity as formulated in equation (3) is 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 the previous formulation by excluding parameters not dependent on animal mass). It is based on a 'random walk' model, which is a widely used methodology for simulating animal movement[32,33].

Individual animals do not move randomly, but the net movement of all animals over long time periods (>1,000 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[34–36]. Internal demographics of animal groups will also change, which will lead to shifting ranges and boundaries of the group over time[37]. Below, I show how long-term movement of nutrients by all animals in an ecosystem over long periods of time can be calculated 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:

$$\frac{\mathrm{dP}}{\mathrm{d}t} = D \times \frac{\partial^2 \mathrm{P}}{\partial x^2} - K\mathrm{P} + G \tag{4}$$

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 section. P is for phosphorus.

Random walk. To calculate a diffusion term, I estimate D based on the random walk with the form:

$$D = \frac{(\Delta x)^2}{2\Delta t} \tag{5}$$

where Δx is a change in distance and Δt is a time step of duration t. In general, a diffusivity can be derived from a random walk[32,33]. This mathematical framework is necessary because animals rarely move in a straight line.

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 timescales than those moved in the flesh. I therefore calculate D for each separately. Below I start with dung.

Δx is the daily displacement or day range 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 timescale is again the food passage time (PT). Therefore, putting this in the framework of the random walk, I estimate that the diffusivity for transport of its dung is $D_{\text{excreta}} \cong (\mathrm{DD} \times \mathrm{PT})^2/(2 \times \mathrm{PT})$, where the numerator is in km^2 and the denominator is in days.

Estimate of D_{body}. Next, I 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). 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 (Ra) and approximately $\mathrm{HR}^{0.5}/2\pi$. Therefore, if HR is the range used throughout an animal's lifetime, then $D_{\text{body}} \cong \mathrm{Ra}^2/2L$ or $\mathrm{HR}/(8\pi^2 L)$, where the numerator is in km^2 and the denominator is in days.

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

$$P(x, t+\Delta t) = P(x,t) - \text{losses} + \text{gains} \tag{6}$$

The losses term is represented in equation (6) by $\alpha\mathrm{P}(x,t)$, the fraction (α) of animals leaving x at time t. The loss of a nutrient in dry matter consumed and transported by a population of animals is:

$$\begin{aligned} &\alpha \frac{\text{animals}}{\mathrm{k}m^2} \times \frac{\mathrm{kg}\frac{\mathrm{DM}}{\Delta t}}{\text{animal}} \times \frac{\mathrm{kgP}}{\mathrm{kgDM}}(x,t)\Delta t \\ &= \alpha \mathrm{PD} \times \mathrm{MR} \times [\mathrm{P}](x,t)\Delta t \\ &= \alpha \mathrm{Q}[\mathrm{P}](x,t)\Delta t \end{aligned} \tag{7}$$

The loss rate of P (kg DM km^{-2}) is the population density of animals (PD; number per km^2) consuming dry matter (DM) to fulfil their metabolic requirements (MR; kg DM per animal per 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 - ε) is excreted.

I estimate ε as 22.4% for megafauna based on the gross food assimilation efficiency of elephants[38]. Such an efficiency is not known for extinct animals such as dinosaurs. Incorporation of phosphorus into the body is, of course, more complicated with relative phosphorus fraction of biomass increasing with size due to the greater investment in bone growth in larger vertebrates[39]. It also changes with animal age as full grown adult vertebrates need less phosphorus than immature growing animals. However, since I 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, I use the simple value of 22.4%.

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

$$\mathrm{P}(x,t+\Delta t) = \mathrm{P}(x,t) - (1-\varepsilon)\left[\alpha \mathrm{Q}[\mathrm{P}](x,t) + \frac{\alpha}{2}\mathrm{Q}[\mathrm{P}](x+\Delta x,t) + \frac{\alpha}{2}\mathrm{Q}[\mathrm{P}](x-\Delta x,t)\right] \tag{8}$$

I arrive at the equation:

$$\frac{\mathrm{dP}}{\mathrm{d}t} = (1-\varepsilon)QD_{\text{excreta}}\frac{\partial^2[\mathrm{P}]}{\partial x^2} \tag{9}$$

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

$$\frac{\mathrm{dP}}{\mathrm{d}t} = (1-\varepsilon)QD_{\text{excreta}}\frac{\partial^2[\mathrm{P}]}{\partial x^2} + \varepsilon QD_{\text{excreta}}\frac{\partial^2[\mathrm{P}]}{\partial x^2} \tag{10}$$

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. I note that B has the same units as Q. Dividing both sides by B:

$$\frac{\delta[\mathrm{P}]}{\delta t} = (1-\varepsilon)\frac{Q}{B}D_{\text{excreta}}\frac{\partial^2[\mathrm{P}]}{\partial x^2} + \varepsilon\frac{Q}{B}D_{\text{body}}\frac{\partial^2[\mathrm{P}]}{\partial x^2} \tag{11}$$

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

$$\frac{\delta[\mathrm{P}]}{\delta t} = (1-\varepsilon)\frac{Q}{\alpha B}D_{excreta}\frac{\partial^2[P]}{\partial x^2} + \varepsilon\frac{Q}{\alpha B}D_{body}\frac{\partial^2[P]}{\partial x^2} \tag{12}$$

If Q/B can be assumed constant, then:

$$\frac{\mathrm{dP}}{\mathrm{d}t} = \Phi_{\text{excreta}}\frac{\partial^2 \mathrm{P}}{\partial x^2} + \Phi_{\text{body}}\frac{\partial^2 \mathrm{P}}{\partial x^2} \tag{13}$$

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

$$\Phi_{\text{excreta}} = (1-\varepsilon)\frac{Q}{\alpha B}D = (1-\varepsilon)\frac{\mathrm{PD}}{\alpha B} \times \mathrm{MR} \times \frac{(\mathrm{DD} \times \mathrm{PR})^2}{2 \times \mathrm{PR}} \tag{14}$$

$$\Phi_{\text{body}} = \varepsilon\frac{Q}{\alpha B}D = \varepsilon\frac{\mathrm{PD}}{\alpha B} \times \mathrm{MR} \times \frac{\mathrm{HR}}{8\pi^2 L} \tag{15}$$

I solve the equations above using datasets and methods described in previous work[5]. I estimated Φ as a function of M in two ways: first, I 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 ref. [5] for the allometries). In the previous work, I found Φ_{body} to be several orders of magnitude smaller than Φ_{excreta} and I therefore remove Φ_{body} from the formulation and the Φ in equation (3) refers to only Φ_{excreta}. In equation (3), I remove the αB and ε term as it is not based on animal mass. Based on our datasets, I calculate the below value of Φ, which I use as equation (3) in the text and which was originally formulated in Table 1 of ref. [5].

$$\Phi = \mathrm{MR} \times \mathrm{PD} \times \frac{(\mathrm{DD} \times \mathrm{PR})^2}{2 \times \mathrm{PR}} = 0.05 \times M^{1.17} \tag{16}$$

Estimate body mass and scaling parameters of *Arthropleura*. Without tetrapod herbivores in the Pennsylvanian subperiod, the largest herbivore or detritivore was *Arthropleura*. Without parts that fossilize, it is difficult to accurately estimate body mass and I could find no estimates of body mass. To roughly estimate a maximum body size, I use size estimates based on fossilized tracks from ref. [13] that estimated a *Arthropleura* with a length of 102 cm long and a width of 29.5 cm, although they may have got as big as 1.8 m. Currently, the largest millipede is the giant African millipede, which can be 40 cm length, 7 cm width and 200–400 g. The *Arthropleura* from ref. [13] was approximately three times larger in all dimensions and therefore, the weight would be 27 times greater—5–10 kg. However, all of the assumptions have a great deal of uncertainty and I therefore estimate that the weight was between 2.5 and 20 kg. I estimate median size would be approximately half maximum size. With these dimensions and weight, based on equations (1) and (2), I roughly estimate that they would travel between 0.2 and 0.4 km between consumption and defecation.

To compare estimated dung production per area for Arthropleura and an average Sauropod, I use data from ref. [40] to estimate dung production for a range of different millipedes. The largest in the study weighed 7 g with a pellet production of 4 g m^{-2} yr^{-1} for the species. This is approximately equal to our estimate of mean dung produced per area for an average sauropod of 3 g m^{-2} yr^{-1} based on mean body size and mass-based estimates of population density and metabolic rate.

Ectothermy versus endothermy in dinosaurs. There has been an ongoing debate for over a century as to whether dinosaurs are warm or cold blooded. A recent study used a large dataset of growth patterns to suggest that dinosaurs were neither but in fact mesotherms[28]. However, this result was disputed[27]. Therefore, the dispute is clearly not resolved, but most current evidence tends to indicate that dinosaurs were endotherms[41–43]. If dinosaurs were ectotherms or mesotherms then our scaling coefficients likely overestimate their food consumption. However, sauropods had very small teeth that were probably insufficient for grinding the quantity of food necessary to maintain their body mass. There is an additional debate about whether this means dinosaurs had gizzards with stomach stones (which have been found in fossilized remains) or if they just had very long food processing times[30,31]. In either case, for these reasons, I may underestimate food passage time. However, even if this is true, there may be no overall bias in the estimate of distance travelled between food consumption and defecation because lower metabolic rates would indicate a smaller day range but the food would stay in the animal for more days leading to an overall similar estimate multiplying equations (1) and (2). I explore these possibilities in a sensitivity study (Supplementary Tables 1 and 2).

COALQUAL data. I compared coal nutrient concentrations and distributions for available nutrients important for plants and animals (calcium, magnesium, phosphorus, potassium and sulfur) and one element that is toxic to plants and animals (aluminium) from the COALQUAL database[18] for the Pennsylvanian subperiod and the Cretaceous. Specifically, I downloaded all trace element and sample description data and then screened the data by system (Pennsylvanian and compared this with the Cretaceous). I did not include nitrogen because its main source is dispersed nitrogen fixation of atmospheric N_2 by nitrogen-fixing bacteria and not rock weathering like the other nutrients. I used quality parameters from the COALQUAL database to remove low-quality data (such as labelled with 'N or B', where N indicates not detected, or B indicates blank). Each of the datapoints used in this study has abundant metadata about the specific methodology used (including collector, analytic technique and sample description) and can be found online in the COALQUAL database[18].

I divided all the data into regions of 1,000 km^2 (using the equal area weighting Matlab command 'hista') for regions that had three or more data points ($N=231$ regions for Pennsylvanian subperiod and $N=54$ for the Cretaceous), I compared the coefficient of variation within each 1,000 km^2 plot (standard deviation divided by the median). I acknowledge that there are many possible ways to calculate this and in Supplementary Fig. 1, I show the results under a broad range of scenarios using size thresholds ranging from 100 to 1,000 km^2 in 100 km^2 increases with a threshold sample size of three or more data points per plot. This figure shows that under all scenarios of region size, the results do not change, except for aluminium, which is not significant in the results. I also acknowledge that by using different thresholds of minimum number of points I am potentially biasing the results towards regions with less data. For this reason, in Supplementary Fig. 2, I make the calculations using a range of minimum number of points from 3 to 12 and show that under all scenarios of sample size thresholds the results do not change except for aluminium which is not significant in our results.

Coal is not a perfect representation of the elemental values of former plant material and coal generally has lower nutrient concentrations that are important for plants such as P, than plants[19,20]. In the dataset used, coal plant nutrient values (Ca, Mg, K and P) were lower than current mean values by an average of 3.9-fold (3.9-, 3.3-, 3.6- and 5.1-fold, respectively)[44]. Nutrient concentrations in vegetation are generally higher than those observed in coal and this could be due to either changes to the plant material following plant death in the swamp environment or later when this material is buried and the increased temperatures or pressures preferentially add or remove certain elements. Water is squeezed out of peat due to increased subterranean pressures and increased heat will expel other elements and gaseous alteration products such as methane leading to a more carbon rich deposit. However, there is no evidence that these processes might differ between the Pennsylvanian subperiod and the Cretaceous and thus bias the results.

It was surprising to note that K showed a highly significant opposite trend to other plant-important nutrients. Potassium is a key element for both plants and animals but it is replaced by sodium for many important uses in animals[23]. It is possible that animals exuded potassium though a faster mechanism than the other plant-important nutrients because the animals used sodium and not potassium. This may have caused the observed changes in potassium between the Cretaceous and the Pennsylvanian subperiod.

Statistics. The data are not normally distributed, so I used the non-parametric statistic Wilcoxon rank-sum test (Matlab, Mathworks; https://www.mathworks.com/products/matlab.html) to determine the level of statistical significance. To control for spatial autocorrelation of the data[45], I used SAR error models. SAR models were fit using the R (https://www.r-project.org/) library 'spdep' following ref. [46]. The dataset has many close sample points but fewer isolated ones, and I therefore define neighbourhoods by distance to reference point. In this case, I tried distances from 20 to 120 km and found that AIC was minimized at 90 km. AIC compares the model explanatory power while compensating for additional model parameters.

Sensitivity analysis. There are large uncertainties in many of the spatial maps, scaling coefficients and assumptions used in the analysis. I have attempted to quantify this uncertainty in a sensitivity study where I calculate distance between food consumption and defecation based on the estimated uncertainty. In Supplementary Table 1, I describe the variable and the largest source of its uncertainty. In Supplementary Table 2, I quantify this uncertainty, explain how I quantified the uncertainty, and show the results of how our final values could change based on the estimated values. I have a separate sensitivity study for the possible changes in weathering rates between the Cretaceous and the Pennsylvanian subperiod (Supplementary Table 3) where I estimate changes in weathering rates based on climate simulations of mean annual temperature and mean annual precipitation, estimates of uplift rates, mycorrhizae evolution and atmospheric CO_2 concentrations for the coal-producing regions in the study[45,46].

Data availabilty. All coal data are available online at http://ncrdspublic.er.usgs.gov/coalqual/.

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C.E.D. conceived the idea, analysed the data and wrote the paper.

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