

The impact of large animal extinctions on nutrient fluxes in early river valley civilizations

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Abstract. Urbanization began independently in four river valley civilizations ~3,500–5,000 years before the present (ybp) in fertile river valleys that originally had free-ranging large animals, including elephants, that eventually went locally extinct. Such large animals are disproportionately important in the lateral spread of nutrients away from nutrient concentration gradients common near floodplains, and the local extinction of the animals would have reduced this flow of nutrients into surrounding regions. Prior to the use of manure as a fertilizer, this natural spread of nutrients would have increased productivity and food yield, and its absence would have immediately decreased fertility to regions outside the floodplains. Here we calculate this changing nutrient flux using a “random walk” model and estimate that phosphorus (P) concentrations in the vegetation were reduced by >40% outside the floodplain following the loss of these animals and the process could take between 840 and 6,800 years depending on the region and the model parameters used. In the short term, we hypothesize that the decreased fertility may have reduced food yields and driven early agriculturalists from the outer regions away from rivers towards the more fertile floodplains. In the long term, yield and populations in outer regions would have decreased, constraining the potential growth of these civilizations, thus demonstrating how the loss of a key ecosystem service could have important repercussions for humanity that continue over thousands of years.

Key words: early river valley civilizations; elephants; lateral diffusion; megafauna; nutrients; urbanization.

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INTRODUCTION

The first cities (>30,000 individuals) developed in Egypt, Mesopotamia, and the Indus Valley approximately 5,000 years before present, and were soon followed by the independent development of cities in China, Mesoamerica, and Peru (Childe 1950). The first cities of Egypt, Mesopotamia, the Indus valley, and the Yellow River Valley of China all developed in fertile river floodplains with abundant nutrients derived from weathering of primary rock from moun-

tainous regions upstream. These nutrients were replenished annually within the floodplain which allowed for high crop fertility over continuous periods.

Regions surrounding these floodplains may also have been initially fertile with a large lateral nutrient input from animals in the region. Recent studies have highlighted the potential important role played by animals in the lateral transfer of nutrients in regions of nutrient concentration gradients, with the largest animals disproportionately important in this transport (Doughty et

al. 2013, Wolf et al. 2013). If there is an underlying concentration gradient, as is present near many floodplains, random movement of animals eating and defecating will cause a flow of nutrients away from the floodplain. One study estimated that the now extinct Amazonian megafauna may have distributed a significant amount of nutrients to regions outside the floodplains and hypothesized that other fertile floodplains in regions of nutrient concentration gradients may have experienced similar lateral flows due to large animals (Doughty et al. 2013).

It is difficult to estimate pre-industrial nutrient concentrations in the rivers near these early river valley civilizations because their current chemistry has been so drastically modified by modern industrialization. However, recent studies of the Amazon floodplain, which is still largely natural, detail the dynamics of an unmodified floodplain (Lewis et al. 2000, McClain and Naiman 2008). Plants growing in nutrient-rich floodplains generally have higher leaf nutrient concentrations than plants grown outside the floodplain. For instance, vegetation growing in the floodplain has ~50% more leaf phosphorus on average (1.50 mg P g^{-1} leaf which is continuously replenished (Furch and Klinge 1989), compared to the mean leaf phosphorous concentration outside the floodplain of $1.01 \pm 0.26 \text{ mg P g}^{-1}$) (Vitousek and Sanford 1986). Such a difference may have been even greater in the early river valleys, because the rock derived nutrients important for plants (K, Ca, Mg) are at water concentrations ~5–10 times higher for the four rivers supporting early civilizations (Nile, Huang He, Shatt el Arab, Indus) in comparison with the Amazon (Gaillardet et al. 1999).

Early farmers did not likely have an in-depth knowledge of soil fertility. The first direct evidence of fertilizing crops with animal dung comes with urbanization around 5,000 ybp in Mesopotamia (Wilkinson 1982; but see also Bogaard et al. 2013). Soils outside floodplains require a constant supply of nutrients to maintain productivity against the constant removal of nutrients in agricultural products. By contrast, soils within floodplains are resupplied with nutrients by seasonal inundation. Today, several of the regions where the early civilizations existed, such as all of Egypt and most of Mesopotamia, the Indus valley, and China, have

a net loss to the atmosphere of important mineral nutrients such as phosphorus (P) (Mahowald et al. 2008). This flux is mainly from mineral aerosols such as soil particles (82%), as opposed to anthropogenic combustion (5%). This suggests that there may also have been a net loss of P in these regions in the past, although wind patterns in some regions such as Egypt may have changed (Kropelin et al. 2008). The constant loss of nutrients in dust suggests the need for an allochthonous input. In this light, the lateral input from animals may have been the main way to maintain fertility in the more weathered soils outside the floodplains in these regions.

All four nutrient-rich river valleys had endemic populations of diverse large animals, including elephants, until the early historic periods (Olivier 1978, Jepson and Canney 2003). There is written evidence of the severe hunting pressure on elephants from an early stage, and hieroglyphics recorded during the dynasty of Thutmose III (~3,600 ybp) testify to the scale of slaughter. Amen-em-heb, a bureaucrat for the Pharaoh described an expedition in the valley of the Euphrates, in which “we hunted 120 elephants on account of their tusks” (Ebers 1873, Birch 1874) (Fig. 1). It is thought from other hieroglyphic evidence that hunting at this scale was common until the 10th century BCE (Jones 1880). There is fossil evidence for elephants in an oasis near to the Nile valley ~5,000 ybp (Nicoll 2004) and extensive ivory artwork from the pre-dynastic periods. Elephants were endemic in the Yellow River valley (Olivier 1978) and there is indirect evidence suggesting that elephants continued to exist in the Yellow River valleys until slightly before the Shang dynasty (~3500 ybp) (Bishop 1921).

Although elephants may have been able to spread fertility to soils in regions outside the floodplains, coexistence between humans and elephants can be difficult. Elephants regularly destroy crops and kill farmers. Large herbivores such as elephants can cause much damage to farms. For instance, in Uganda, mean damage inflicted by elephants was 874 m^2 (~21% of the farm area) per event compared to 136 m^2 from the next most damaging herbivore (Naughton-Treves 1997). There appears to be a threshold effect between humans and elephants and once human density surpasses $15.6 \text{ people km}^{-2}$ the



Fig. 1. Account by Amen-em-heb, an administrator in the court of Pharaoh Thutmose III (1479–1425 BCE), describing an expedition with the king in Mesopotamia, in which “we hunted 120 elephants on account of their tusks” (Ebers 1873, Birch 1874).

elephant populations tend to either be killed in conflict or leave the area (Hoare and Du Toit 1999). Elephants were extinct in Mesopotamia by ~3,000 ybp, in Northern China by ~2,000 ybp, and in the Indus valley by ~1,000 ybp (Jepson and Canney 2003), but modern human-elephant interactions suggest that their peak numbers probably began to decline well before the actual extinctions.

Agriculture began in the near East with the development of wheat around 10,500 ybp. Agriculture soon spread to nearby regions and there is evidence for agriculture soon after near the Indus valley and later in the Nile. Agriculture developed independently in the Yellow River valley of China approximately 8,000 ybp (Balter 2007). Therefore, agriculture existed for several thousand years in the fertile valleys prior to early urbanization, possibly without the active use of fertilizer. Yields increase with the use of manure as fertilizer. For instance, one study found that in the dry soils of Niger, grain yields increase from 471 kg ha⁻¹ to 1264 kg ha⁻¹ with an addition of 13 kg P ha⁻¹ (Bationo and Mkwunye 1991).

Early farmers outside the floodplains may have been subsisting on a megafauna nutrient subsidy. Animals at the margins of the floodplains would tend to wander in search of food, fertilizing these regions and reducing the floodplain nutrient concentration gradient. It has been shown that such cross-system subsidies into lower productivity ecosystems exist in a variety of contexts. For example, both spiders (Polis and Hurd 1995), and seabirds (Hutchinson 1950, Young et al. 2010), have been shown to mediate energy and nutrient transfers from the more productive oceans to less productive islands. Species that move nutrients into low nutrient environments are “strong interactors” that are likely to influence the subsequent evolution of the population (Post and Palkovacs 2009). Here

we suggest that this change in nutrient flow following extinctions could equally have changed behavior of early agriculturalists. As human populations within the floodplains grew, people would have taken advantage of the herbivore-maintained fertility of the regions outside the floodplain, and have used them for farming. As these regions eventually experienced a loss of herbivores, nutrients would have stopped flowing to these outer regions and they would have experienced a slow decline in fertility and consequent agricultural productivity. In this paper, we estimate this potential change in nutrient transfer by animals before and after their local extinction or limitation of movement through domestication. We use data on local species ranges, digital elevation model (DEM) data, dust, and climate simulations of the mid-Holocene to estimate the percentage decrease in P following the local extinctions.

METHODS

We estimate the concentrations of phosphorus (P) as a proxy for soil fertility using the following budget equation:

$$\frac{dP}{dt} = \Phi \frac{\partial^2 P}{\partial x^2} - KP + G \quad (1)$$

where K is a first order loss rate from phosphorus (P) leaching and occlusion and G is a gain rate from dust deposition and in situ weathering. We use a simple diffusion based model to predict animal nutrient distribution over long distances and timescales, where the diffusion parameter Φ (km² year⁻¹) is estimated from considerations of animal size, metabolism, and behavior.

Considering multiple animal species over long time periods, animal movement begins to approximate a “random walk”, such that the horizontal flux of nutrients can be modelled as

Table 1. Allometric fits for herbivores >10 kg. For the fecal diffusivity equation we use all herbivores to increase the sample size. See Appendix: Fig. A1 for the graphs corresponding to the equations.

Dependent variable	Units	Equation	<i>n</i>	<i>r</i> ²
Population density	number/km ²	$36.35 \times M^{-0.58}$	105	0.27
Metabolic demand	kg DM number ⁻¹ day ⁻¹	$0.01 \times M^{0.87}$	24	0.89
Day range	km	$0.32 \times M^{0.43}$	42	0.41
Passage rate†	days	$0.29 \times M^{0.28}$
Fecal diffusivity	(kg DM/km ²) × (km ² /day)	$0.05 \times M^{1.17}$	14	0.67

† Equation from Demment et al. (1985) assuming a digestibility of 0.5.

a diffusion-like process analogous to the diffusion of heat (Ovaskainen, 2009; this is extensively justified in the Appendix and in previous papers Doughty et al. 2013, Wolf et al. 2013). To calculate a diffusion term for the animal population itself, we first characterize a diffusivity D (km² year⁻¹) based on the random walk with the form (Berg 1993):

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

where Δx is the daily displacement or day range (DD) of a single animal (DD; km), and Δt is a day. Considering the transport of nutrients in dung, the length scale for diffusivity of ingestion and excretion is the day range multiplied by the average gut passage time (PT; fractions of a day). The time scale is again the food passage time (PT). Therefore, putting this in the framework of the random walk, we estimate that the diffusivity for transport of its dung is:

$$D_{\text{excreta}} \sim = \frac{(\text{DD} \times \text{PT})^2}{(2 \times \text{PT})} \quad (3)$$

where the numerator is again in km² and the denominator is in days.

Next, we estimate the amount of food and nutrients consumed by a population of animals per area. The amount of a nutrient in dry matter consumed and transported by a population of animals is

$$\begin{aligned} \frac{\text{animals}}{\text{km}^2} \times \frac{\text{kg DM}}{\text{animal}} \times \frac{\text{kg P}}{\text{kg DM}}(x, t)\Delta t \\ = \text{PD} \times \text{MR} \times [\text{P}](x, t)\Delta t. \end{aligned} \quad (4)$$

The movement of P (kg DM km⁻²) is the population density of animals (PD; number/km²) consuming dry matter (DM) to fulfill their metabolic requirements (MR; kg DM animal⁻¹ day⁻¹). The product of PD and MR is the

population consumption rate of DM (kg DM km⁻²). The consumption of the nutrient itself is then determined by this rate multiplied by [P] (x, t), which is in units of per kg DM. This is converted to units of area by dividing [P] by αB which is the edible fraction of total biomass, or leaf area index (LAI).

We combine Eqs. 3 and 4 together to calculate a diffusion term (Φ) for dung. To parameterize this equation based on body size and distribution, we make use of a large literature on body size relationships (Peters 1986) describing a wide range of animal physiology and behaviour based on mass (M), such as day range (DD), metabolic rate (MR), population density (PD) and food passage time (PR). We show the scaling relationships between MR, PD, DD, PR and herbivore mass in Table 1. We calculate a diffusion term (Φ) for dung (see Doughty et al. 2013, Wolf et al. 2013 and Appendix for complete derivation and explanation of terms) according to the following equation:

$$\begin{aligned} \Phi &= (1 - \varepsilon) \times \text{MR} \times \frac{\text{PD}}{\alpha B} \times \frac{(\text{DD} \times \text{PR})^2}{2 \times \text{PR}} \\ &= \frac{0.78 \times 0.05 \times M^{1.17}}{\alpha B} \end{aligned} \quad (5)$$

where $(1 - \varepsilon)$ is the fraction of consumed P that is excreted rather than retained in body mass, and αB is edible biomass which we estimate as leaf area index (LAI) per pixel. We calculate that these sum to an overall mass-scaling coefficient for Φ of 1.17 (Table 1), which shows that large animals are disproportionately important in the spread of nutrients based on body mass (a coefficient of 1 represents even scaling with animal mass) (Doughty et al. 2013). The alternative outcome for nutrients is incorporation in the body (ε), but in a previous paper we show that this term is several orders of magnitude smaller

Table 2. Average Φ value ($\text{km}^2 \text{ year}^{-1}$) for each of the river valley civilizations prior to agriculture, modern, % change, and the estimated time to reduce nutrients in outer regions by 80% (from peak to new steady state).

Civilization	Φ 6,000 ybp	Φ current	% of Φ from 6000 ybp	Time to 80% reduction in nutrients
Egypt	1.1 (± 0.5) [†]	0.095	9% (6–16%)	3,000 (970 [‡] –3,200)
Mesopotamia	1.1 (± 0.5) [†]	0.16	15% (10–27%)	4,100 (1,300 [‡] –4,200)
Indus valley	1.1 (± 0.5) [†]	0.22	20% (14–37%)	6,600 (840 [‡] –6,800)
China	1.1 (± 0.5) [†]	0.04	4% (3–7%)	5,200 (1,600 [‡] –5,300)

[†] Estimated as 4 large free ranging animals including $\sim 4,000$ kg (elephant), 1 species $\sim 1,500$ kg (hippo or rhino), 1 species $\sim 1,000$ kg (auroch), and 1 species ~ 200 kg and a mean LAI of $3.5 \text{ m}^2 \text{ m}^{-2}$ (but LAI of 2.5 in the upper bound simulation).

[‡] Uses a constant loss rate of $K = 0.0014 \text{ yr}^{-1}$ (Wolf et al. 2013).

than that coefficient for excreta and we therefore do not include it in this paper (Wolf et al. 2013).

Based on Eq. 5, an average crop LAI of $3.6 \text{ m}^2 \text{ m}^{-2}$ (Asner et al. 2003), and ε of 0.22 (see Appendix), we estimate a mid-Holocene Φ value in the floodplains of $1.1 \text{ km}^2 \text{ yr}^{-1}$ (Table 2) by adding animals that likely used to exist in these floodplains but are now extinct, such as elephants, hippopotamus (Egypt) or rhino (Indus valley, possibly China), aurochs (Van Vuure 2005), and local extinctions or reductions of species in the Cervidae, Bovidae or Suidae families. There is much uncertainty as to which species existed in the different floodplains and when the local extinctions took place, and therefore, in a sensitivity study, we vary Φ in the ancient period between 0.60 and $1.60 \text{ km}^2 \text{ yr}^{-1}$ (0.6 assumes only the addition of elephants in the floodplain and 1.6 assumes a lower LAI of $2.5 \text{ m}^2 \text{ m}^{-2}$). We used the IUCN spatial database on mammal species and their ranges (IUCN 2010) to develop a gridded, global estimate of Φ for modern animals following Wolf et al. (2013). We used this gridded estimate to calculate Φ for modern species for the different floodplain regions.

To take advantage of our knowledge of the unique geometry of each floodplain, we implemented numerical solutions to the 2-D diffusion problem in Eq. 1 using a time step of 10 years (Crank and Nicolson 1947). To create the maps of the floodplain regions, we use 30 arc second SRTM Digital Elevation Model (DEM) data. We use the longitudes and latitudes of $24\text{--}34^\circ \text{ N}$ and $26\text{--}36^\circ \text{ E}$ for Egypt, $26\text{--}36^\circ \text{ N}$ and $40\text{--}50^\circ \text{ E}$ for Mesopotamia, $22\text{--}32^\circ \text{ N}$ and $63\text{--}73^\circ \text{ E}$ for Indus river valley, and $32\text{--}42^\circ \text{ N}$ and $111\text{--}121^\circ \text{ E}$ for the Yellow River valley. DEM data have been shown to provide a reasonably accurate estimate of the ancient floodplains, despite much modern trans-

formations and variations in the river through time (Hritz 2010). In the model, Φ is made to vary spatially, specifically to reflect reductions in movement with elevation, which restricts diffusion in higher altitudes.

We estimate the net deposition of phosphorus (G) using data from Fig. 6e in Mahowald et al. (2008). In a sensitivity study we double and halve these numbers. We estimate P losses from the system (K) based on equations from Buendia et al. (2010). In a lower bound sensitivity study, we also use a constant $K = 0.0014 \text{ yr}^{-1}$ (Wolf et al. 2013). We use climate simulations from NCAR CCSM v4 (from the Coupled Model Intercomparison Project #5) to estimate volumetric soil moisture and leaf area index (LAI) for each site during the mid-Holocene (6,000 ybp). The soil moisture is used to drive the loss rate of phosphorus using the Buendia equations. Herbivores will not graze where it is too arid for vegetation and we use the NCAR CCSM v4 estimates of LAI from 6,000 ybp to limit animal movement in the model in regions where LAI is below a certain threshold ($\text{LAI} < 0.01 \text{ m}^2 \text{ m}^{-2}$), such that Φ is substantially reduced in these regions.

We assume that vegetation growing in the floodplain has an average leaf P concentration of 1.50 mg g^{-1} , which is continuously replenished (Furch and Klinge 1989). Outside the floodplain, the mean leaf phosphorus concentration is assumed to be $1.01 \pm 0.26 \text{ mg P g}^{-1}$ of foliar material (Fyllas et al. 2009). We assume an efficient transfer of the phosphorus from the herbivore dung to the edible biota because nutrients, especially P, generally recycle rapidly and efficiently (Fyllas et al. 2009). We perform sensitivity studies for several of our parameters including Φ (0.6–1.6), loss rate of P, dust input rate, floodplain nutrient concentration difference.

However, to improve visual representation, the figures in this paper only show the sensitivity study where we vary Φ , which we assume to be the largest source of uncertainty.

RESULTS

We estimate that the modern lateral nutrient redistribution capacity (Φ) across the floodplains has been reduced 63–97% from its former capacity due to reduced large animal movement in these regions (Table 2). Our uncertainty is large because we vary Φ between 0.6 and 1.6 km² year⁻¹ and because there are large differences in average modern Φ in these regions. Our best guess Φ of 1.1 in each region includes elephants, which were certainly present at each site and alone account for a Φ of 0.5 (0.5 + current Φ = ~0.6, our lower bound estimate), a hippo- or rhino-sized animal (~1,500 kg) and aurochs (~1,000 kg) which likely were present at some of the sites, and other smaller animals. These fertile regions likely had abundant animal life which was greatly reduced due to human competition, but the exact numbers are highly uncertain, which our large Φ uncertainty incorporates.

We use the Crank-Nicolson method to numerically solve the lateral nutrient flux in the floodplain regions (Fig. 2). Each site has variable dust deposition ranging from nutrient loss (Egypt) to regions of gain (eastern Mesopotamia; Mahowald et al. 2008). The flux of nutrients into outer regions that were not annually replenished decreased substantially with time in each of the four floodplain regions. The biggest nutrient losses were found to be in the regions immediately outside the floodplains to regions ~100 km from these border regions (Fig. 2). However, these losses vary geographically due to differing soil moisture, current animal numbers, and net P atmospheric deposition.

We show changes in concentrations of P in pixels for each of the four floodplains where P concentrations show large changes through time (Fig. 3). Each curve changes with time in a slightly different way, due to differing soil moisture, current animal numbers, and net P deposition. Egypt, which has no net P deposition (it gains P through dust, but loses even more than it gains), has the steepest decline following

the reduction of megafauna. The curve reaches 80% to steady state after about 3,000 years (970–3,200), which is faster than the remaining sites (Table 2). The other sites all have some depositional P input in regions of the study. Mesopotamia has the next steepest drop at 4,100 years (1,300–4,200) followed by China at 5,200 years (1,600–5,300), and then the Indus valley at ~6,600 years (840–6,800). The loss rate (K) is highly uncertain, and our lower bound estimates above and in Table 2 shows the timescale assuming a constant loss rate of 0.0014 yr⁻¹.

Distance from the river has an important impact on P concentrations through time. For instance, in the Indus Valley, with a Φ of 1.1 km² year⁻¹ there is a gradual decline from the river to ~300 km away from the river (Fig. 4). However, as Φ is decreased to 0.22, this curve becomes gradually steeper and a steady state value is reached at ~100 km from the river versus ~300 km with the previous Φ value. The large animals increase P by an average of 110 kg km⁻² over 308 km from the floodplain, but by a maximum of 226 kg P km⁻² ~66 km away from the river. This varies between our different scenarios from a maximum (Φ = 1.6 scenario) average difference of 140 kg km⁻² over 310 km (peaks at 254 kg P km⁻² ~77 km away from the river) and a minimum (Φ = 0.6 scenario) average difference of 90 kg km⁻² over 235 km (peaks at 175 kg P km⁻² ~66 km away from the river).

DISCUSSION

Conflict is inherent between agriculturalists and megafauna, since both are in pursuit of the same net primary production energy for sustenance. For instance, a study in modern Africa found that when the human population density exceeds 15.6 people per km² elephants tended to become locally extinct (Hoare and Du Toit 1999). This conflict tended to lead to either the local extinction of large animals or their eventual domestication. It has been estimated that elephants were extinct in Mesopotamia by ~3,000 ybp, in Northern China by ~2,000 ybp, in the Indus valley by ~1,000 ybp (Jepson and Canney 2003), and it is not clear at what point they went extinct in Egypt, but they were likely there into the mid-Holocene. Modern human-elephant interactions suggest that their peak numbers

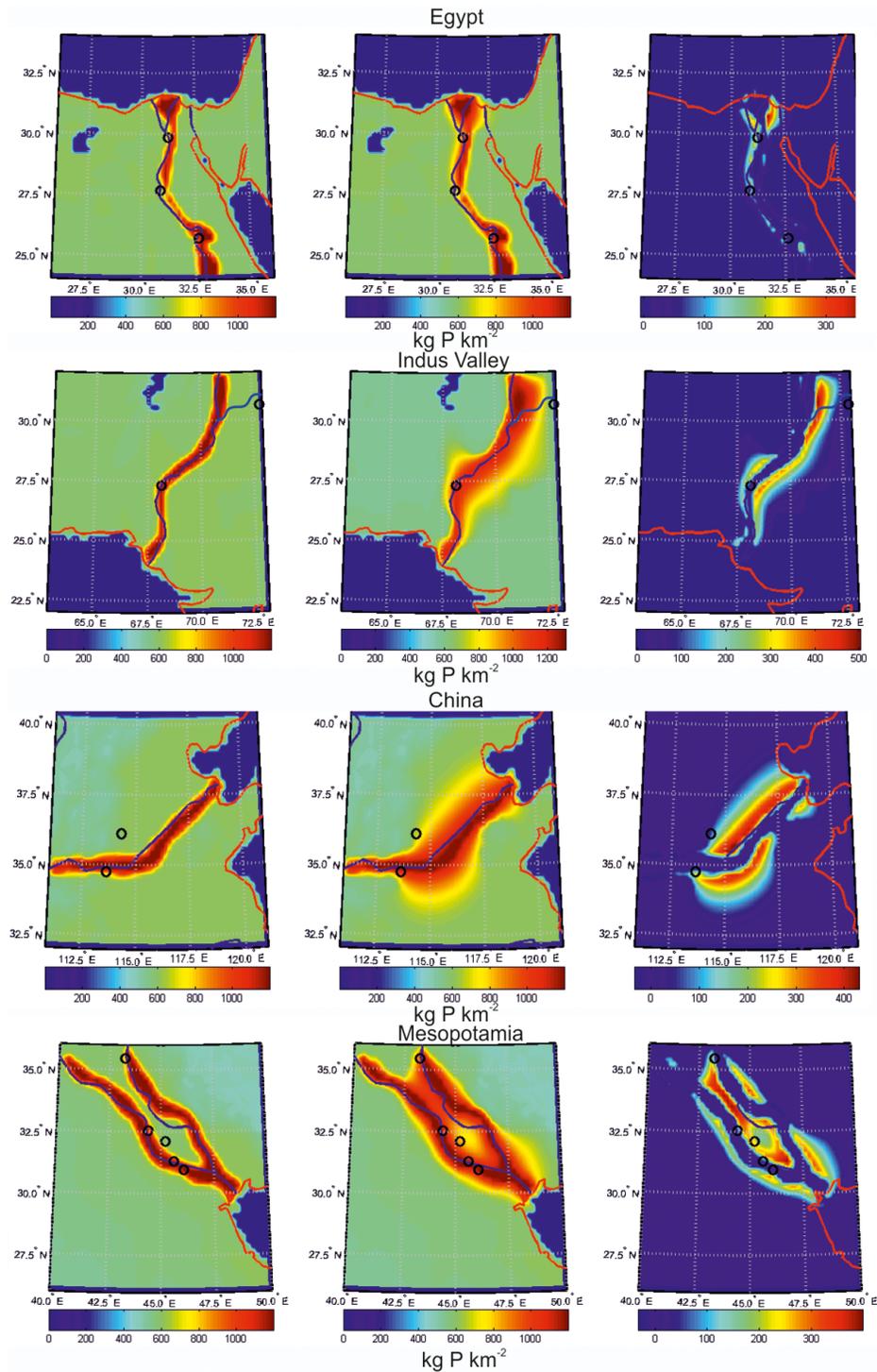


Fig. 2. Estimated P concentrations (kg P km^{-2}) for four river valley civilizations, Egypt, Indus Valley, China, and Mesopotamia. For each civilization, the left figure is without large animal nutrient distribution ($\Phi \text{ km}^2 \text{ year}^{-1}$ according to Table 2), the middle figure is with ($\Phi = 1.1$), and the right figure is the difference. Black circles are the coordinates of some of the first cities in each region.

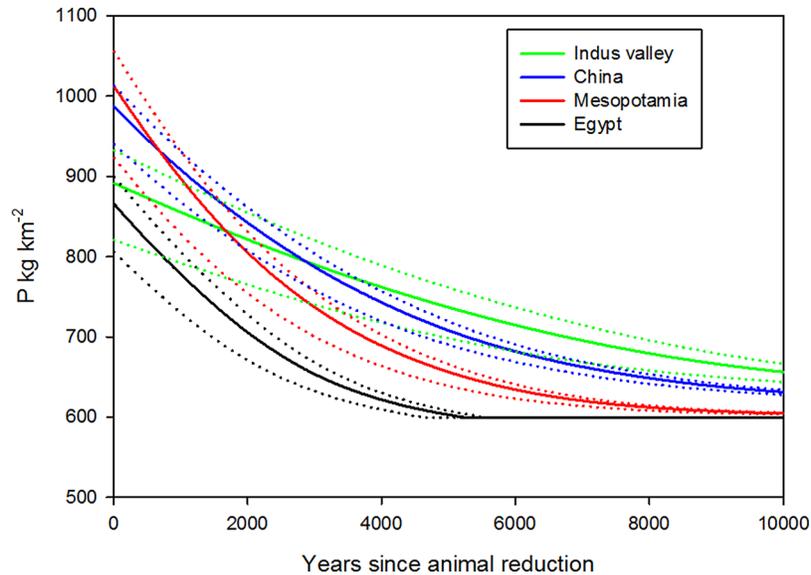


Fig. 3. Change in P concentrations (kg km^{-2}) using a Φ of $1.1 \text{ km}^2 \text{ year}^{-1}$ for a pixel outside the floodplain in each of the four river valley civilizations (Indus valley in green, China in blue, Mesopotamia in red, and Egypt in black) over a period of 10,000 years. The dotted lines indicate a subset of our sensitivity studies for each region where we have tested a Φ of 0.6 and $1.6 \text{ km}^2 \text{ year}^{-1}$.

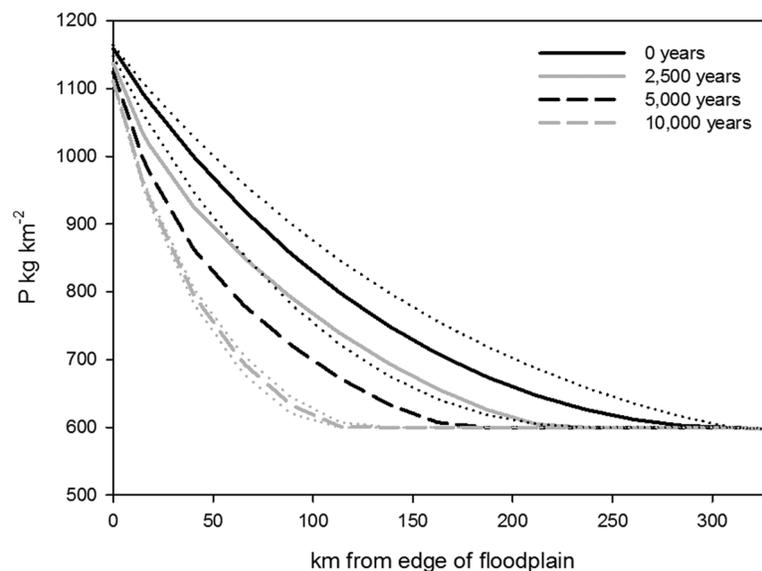


Fig. 4. An estimate of the decrease in P concentrations (kg km^{-2}) away from the river in the Indus Valley over four time periods following a reduction of a Φ from $1.1 \text{ km}^2 \text{ year}^{-1}$ to $0.22 \text{ km}^2 \text{ year}^{-1}$ at time 0 and from 0 km from the river to 330 km away from the river. The dotted lines indicate a subset of our sensitivity studies for each region where we have tested a Φ of 0.6 and $1.6 \text{ km}^2 \text{ year}^{-1}$.

probably began to decline well before the actual extinctions. African and Asian elephants initially survived only in remnant populations in Africa and Eurasia, such as hills or forests that humans did not extensively farm or settle (Surovell et al. 2005). This competition for the prime locations of fertile floodplains was lost by elephants and other megafauna as these regions became intensively farmed and eventually urbanized.

The loss rate of nutrients from the regions surrounding the floodplains would be driven both by decreased input following the local extinction of megafauna and by natural leakage to groundwater and runoff and eventual expulsion to the ocean. This term is highly dependent on local hydraulic conditions, but we estimate that it would begin immediately and reduce P from its peak to a new steady state by 80% after 840–6,800 years (Table 1). This decrease in nutrient flux would create a problem inherent to these early civilizations of decreasing yields in areas outside the floodplains. The earliest known direct evidence of a system of fertilizing soils is ~5,000 years ago in Mesopotamia (Wilkinson 1982; but see also Bogaard et al. 2013). Prior to this, the soil would lose fertility with continued farming. Adding animal dung can significantly increase yields, even in very arid systems (Bationo and Mkwunye 1991).

This loss of soil fertility would have both short term and long term effects. In the long term, reduced fertility would limit yields, limit population growth and, potentially, the long term strength of these civilizations. An interesting economic question is: what was the value of the ecosystem service of this early nutrient flux? If this partially led to the long term diminution of power of these civilizations by reducing soil fertility in non-floodplain regions, then the value would have been immense.

However, there is an interesting possible short-term impact of the loss of nutrient replenishment in outlying lands. There is a large and complex literature on the rise of early cities (Childe 1950, Carter 1977, Ur 2010), including theories that involve environmental, religious, economic or military themes, but all require an initial increase in human population density. For instance, in his seminal paper on the urban revolution, Childe (1950) hypothesizes that agriculture began to produce a food surplus large enough to release

resident specialists from food production. Could the population surplus have been because farmers from outer regions experienced yield declines forcing them to move to the floodplains? These people might then have been supported by increased yields within the floodplains due to decreased animal herbivory and increased soil nutrients (since these nutrients would not flow towards the outer regions). Several civilizations independently began to urbanize a few thousand years following the onset of agriculture. Why not sooner or later? Possibly, as agriculturalists and megafauna interact, megafauna inherently decline through competitive pressure, which would decrease fertility in regions outside the floodplains. Depending on dust input and soil moisture driven nutrient loss, we estimate that this process may take between ~800–7,000 years. Therefore, we might expect that a few thousand years after the onset of agriculture in fertile river valley regions, megafauna will be competitively excluded from the floodplains leading to decreased nutrient fluxes, declining yields and potential forced movement of farming peoples towards the floodplains.

In Egypt, between 8,500 and 5,300 ybp, increased precipitation led to abundant communities throughout Egypt, which eventually migrated towards the Nile as decreased solar forcing reduced the African monsoon (Kuper and Kropelin 2006, Kropelin et al. 2008). The return to full desert conditions ~3,500 ybp has been linked to the emergence of pharaonic civilization along the Nile (Kuper and Kropelin 2006), a time when human-elephant conflict is evident (Fig. 1). Increased aridity clearly acted as an environmental pressure on outer populations, concentrating them into the floodplain. In the case of Egypt, aridity, more than the reduction of soil nutrients, would have driven people towards the floodplain; nevertheless the mechanism of encouraging migration towards the floodplains is similar. Hydraulic changes, either through increased aridity as in Egypt, or the development of irrigation, clearly play a dominant role in affecting human movement, but in this paper, we suggest a secondary, more subtle, role of changing nutrient status and its effect on yields which might also play a role in human migration in these regions.

The exact quantity in which lateral nutrient

fluxes would have changed following local animal extinctions are hampered by limited data about the animals in the ecosystems, the nutrient concentrations within the floodplains and the hydrology driving the loss rate. In addition, areas of high productivity may lead to smaller home range sizes, which may mean animals don't travel as far, which we partially address by limiting animal movement to regions of lower productivity in the model. We address many of these uncertainties using a large range of sensitivity studies. However, we acknowledge large uncertainties in the model as well as a lack of experimental data to verify our conclusions. However, in the future we hope to test the predictions using data archived in lake core records (McLauchlan et al. 2013). Despite the very large uncertainties, even the lower bound estimates indicate a large effect of the loss of nutrient fluxes which would have translated into reduced food yields prior to the development of fertilizers, and therefore suggest that this impact is important and should be quantified more completely in future studies.

Prior to the era considered here, there was a much greater wave of megafauna extinctions at the Pleistocene/ Holocene boundary, which we have previously proposed had a much greater impact on nutrient fluxes globally (Doughty et al. 2013). It has also been hypothesized that these extinctions decreased herbivory globally, which may have accelerated the development of agriculture in the early Holocene when it developed independently in several regions of the world near the time of the extinctions (Doughty 2010, Doughty and Field 2010). Overall these studies highlight the vast ecological changes following the gradual defaunation of the world of the early to mid-Holocene (Doughty 2013) and how early humans may have initially benefited from these changes (more NPP available) but later suffered (more heterogeneous nutrient distribution globally).

Today, we are experiencing massive new losses and restrictions in movement of elephants and other large animals (Maisels et al. 2013). This loss may have a long term impact on global fertility as large nutrient gradients build up without animals to redistribute them over long periods of time. The loss of megafauna in these early civilizations may have led to the loss of a

valuable ecosystem service and over long time frames, the diminution of power in these areas. These animals may have had an unrecognized ecosystem service to these civilizations that we can now, with hindsight, recognize and calculate. Likewise, we should recognize the valuable ecosystem service played by present-day large animal populations and properly consider their value into the future.

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SUPPLEMENTAL MATERIAL

APPENDIX

Justification for the random walk

Note that much of this material is similar to the Supplementary Online Material from Doughty et al. (2013) and repeated with permission.

Individual animals do not move randomly, but the net movement of many animals over long time periods (>1000 years) begins to approximate random motion. There is a large literature describing how different animal species overlap in space by consuming different foods and moving and sleeping in different patterns to avoid a variety of predators (Mcnaughton 1988, Ilse and Hellgren 1995, Augustine and McNaughton 1998). Internal demographics of animal groups will also change which will lead to shifting ranges and boundaries of the group over time (White et al. 1996).

Next, large herbivores patterns will change in response to changing climate. For instance, herbivores often track landscape patterns in grass productivity (Frank et al. 1998) which will change in response to variable rainfall patterns (Ellis and Swift 1988), which have experienced large global shifts over the past 15,000 years. Such interannual variation in climate alters the productivity of the landscape, which drives changes in animal foraging intensity (Bailey et al. 1996, Boone et al. 2002). These shifting patterns will serve to further move herbivore patterns from their current routes. For instance, in Kenya, during wet years there is a net nutrient input into certain patches because the impala dominate, but in dry years there may be a net loss, because the cattle dominate (Augustine et al. 2003). Due to these reasons, the net movement of all animals over long periods will approach an approximation of randomness.

As long as there is an underlying substrate concentration gradient, over long periods of time if the net movement is approximately random, animals will move the nutrients across the gradient. This seems to contradict literature showing that megafauna concentrate nutrients in small scale patches (Augustine et al. 2003). However, there is no contradiction, only a difference in the time, distance, and lack of a substrate concentration gradient. The study on megafaunal nutrient concentration focused on

small nutrient patches in central Kenya (~1 ha nutrient-rich vegetation per 1 km² nutrient-poor vegetation) within homogenous nutrient-poor metamorphic soil substrate. To the north of that study sites are rich basaltic soils of N. Kenya and Ethiopia. As these small patches of nutrient concentration shift across the landscape on decadal and larger timescales, nutrients will flow from the nutrient-rich basalt to the nutrient-poor metamorphic substrate from patch to patch, through the large herbivores, over hundreds of kilometers and thousands of years. We have used our model to show a similar process for Kruger Park between nutrient rich basalts and granites in a previous paper (Wolf et al. 2013).

There is evidence that the small scale nutrient hotspots shown in the Augustine et al. (2003) paper will shift with time. That paper depicts the creation of nutrient hotspots by the corralling of cattle where significant quantities of dung accumulate over time (Augustine et al. 2003). They then measure a significant decline in the nutrients of these areas as they are abandoned over time. It is unlikely that these nutrients are lost but instead redistributed, thus showing how nutrient hotspots can build up but then move over short time periods (~40 years).

This process has also been experimentally demonstrated in a recent study where the authors measured the total seed biomass transported between the white water floodplains and the terra firme forests by a population of woolly monkeys. They show that a single, relatively small species can transport phosphorus in quantities similar to that arriving from atmospheric deposition (Stevenson and Guzman-Caro 2010). There was no net movement of seed biomass between the two regions, but P was transported between the sites only due to the nutrient concentration gradient. There are several other similar studies showing the net movement of nutrients by animals (Frank et al. 1994, Abbas 2012). Our mathematical framework enables us to estimate this process over all animals and long periods of time.

In this paper, we estimate diffusive lateral nutrient fluxes by herbivores away from flood plains. In diffusion, the flux is inversely propor-

tional to the local concentration difference in material, with a constant of proportionality termed the “diffusivity” D (length²/time). The equation that best incorporates the diffusive properties of animals is the following reaction diffusion equation:

$$\frac{dP}{dt} = D \times \frac{\partial^2 P}{\partial x^2} - KP + G \quad (\text{A1})$$

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

Random walk

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

$$D = \frac{(\Delta x)^2}{2\Delta t} \quad (\text{A2})$$

where Δx is a change in distance and Δt is a timestep of duration t . In general, a diffusivity can be derived from a random walk (Skellam 1951, Okubo and Levin 2001, Ovaskainen and Crone 2009). A possible derivation of the random walk (Murray 2002) is as follows:

$p(x, t)$ is the probability that a particle leaving from $x = 0$ at $t = 0$ arrives at position x by time t . After a timestep of duration Δt , the particle has moved with probability α to the left or the right a distance of Δx , or remained in place with probability $(1 - \alpha)$:

$$p(x, t + \Delta t) = p(x, t)(1 - \alpha) + \frac{\alpha}{2}p(x + \Delta x, t) + \frac{\alpha}{2}p(x - \Delta x, t). \quad (\text{A3})$$

Rearranging terms gives:

$$p(x, t + \Delta t) - p(x, t) = \frac{\alpha}{2}[p(x + \Delta x, t) + p(x - \Delta x, t) - 2p(x, t)]. \quad (\text{A4})$$

By Taylor expansion, the first two terms in the brackets equal:

$$p(x, t + \Delta t) = p(x, t) + \Delta x \frac{\delta p}{\delta x} + \frac{(\Delta x)^2}{2} \frac{\partial^2 p}{\partial x^2} + \text{hot} \quad (\text{A5})$$

$$p(x, t - \Delta t) = p(x, t) + \Delta x \frac{\delta p}{\delta x} + \frac{(\Delta x)^2}{2} \frac{\partial^2 p}{\partial x^2} + \text{hot}. \quad (\text{A6})$$

Discarding the higher order terms (hot), incorporating Eqs. A5 and A6 into the right-hand side of Eq. A4, and dividing both sides of the equation by Δt gives:

$$\frac{p(x, t + \Delta t) - p(x, t)}{\Delta t} = \alpha \frac{(\Delta x)^2}{2\Delta t} \frac{\partial^2 p}{\partial x^2}. \quad (\text{A7})$$

Taking the limit, as Δt and Δx are allowed to become arbitrarily small they equate to the diffusivity D , and result in the classic heat equation:

$$\frac{\delta p}{\delta t} = D \frac{\partial^2 p}{\partial x^2}, \quad \text{where } \lim_{\Delta x, \Delta t \rightarrow 0} \alpha \frac{(\Delta x)^2}{2\Delta t} = D. \quad (\text{A8})$$

Eq. A8 gives the dynamic equation for a probability density function for the position of particle. For our paper, this particle will represent the P within food in the gut of an animal.

Estimate of D_{excreta}

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

Δx is the daily displacement or day range (DD) of a single animal (km), and Δt is a day. The length scale for diffusivity of ingestion and excretion is the day range multiplied by the average gut passage time (PT; fractions of a day). The time scale is again the food passage time. Therefore, putting this in the framework of the random walk, we estimate that the diffusivity for transport of its dung is $D_{\text{excreta}} \sim (\text{DD} \times \text{PT})^2 / (2 \times \text{PT})$, where the numerator is in km² and the denominator is in days.

Estimate of D_{body}

Next, we calculate a D term for nutrients incorporated into the animal’s body. The diffusivity for nutrients in an animal’s body mass, D_{bones} is related to the lifetime of the animal L (days) and the residence time of these nutrients is L . The length scale is the home range (HR; km²). The mean displacement over the lifetime of an animal is related to the range length (RL) and approximately $\text{HR}^{0.5}/2\pi$. Therefore, if HR is the range used throughout an animal’s lifetime, then $D_{\text{body}} \sim \text{RL}^2/2L$ or $\text{HR}/(8\pi^2 L)$, where the numerator is in km² and the denominator is in days.

Consumption of nutrients

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

$$P(x, t + \Delta t) = P(x, t) - \text{losses} + \text{gains}. \quad (\text{A9})$$

The losses term is represented in Eq. A9 by $\alpha p(x, t)$, the fraction of animals leaving x at time t . The loss of a nutrient in dry matter consumed and transported by a population of animals is

$$\begin{aligned} & \alpha \frac{\text{animals}}{\text{km}^2} \times \frac{\text{kg DM}}{\Delta t} \times \frac{\text{kg P}}{\text{kg DM}}(x, t) \Delta t \\ & = \alpha \text{PD} \times \text{MR} \times [P](x, t) \Delta t = \alpha Q[P](x, t) \Delta t. \end{aligned} \quad (\text{A10})$$

The loss rate of P (kg DM km⁻²) is the population density of animals (PD; number/km²) consuming dry matter (DM) to fulfill their metabolic requirements (MR; kg DM animal⁻¹ day⁻¹). The product of PD and MR is the population consumption rate of DM (denoted Q here), such that $Q\Delta t$ is the mass of DM consumed in Δt (kg DM km⁻²). The consumption of the nutrient itself is then determined by $Q[P](x, t)$, which has units kg P km⁻², equivalent to P , the numerator on the left. Gains from adjacent regions will be represented as $Q[P](x + \Delta x, t)$ and $Q[P](x - \Delta x, t)$. A fraction ε of the consumed nutrient is incorporated into body mass, while the rest $(1 - \varepsilon)$ is excreted.

We estimate ε as 22.4% for megafauna based on the gross food assimilation efficiency of elephants (Rees 1982). Incorporation of phosphorus into the body is, of course, more complicated with relative P fraction of biomass increasing with size due to the greater investment in bone growth in larger vertebrates (Elser 1996). It also changes with animal age as full grown adult vertebrates need less P than immature growing animals. However, since we account for both the fraction in the biomass and the fraction excreted and there are no fates of the nutrient other than body mass or excrement, we use the simple value of 22.4%. To account for the large uncertainty in this term, in a sensitivity study we increase and decrease it by 0.1 (12.4% and 32.4%).

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

$$\begin{aligned} P(x, t + \Delta t) &= P(x, t) \\ &\quad - (1 - \varepsilon)[\alpha Q[P](x, t) \\ &\quad + \frac{\alpha}{2} Q[P](x + \Delta x, t) \\ &\quad + \frac{\alpha}{2} Q[P](x - \Delta x, t)]. \end{aligned} \quad (\text{A11})$$

By analogy to the derivation for Eq. A3, we arrive at the equation:

$$\frac{dP}{dt} = (1 - \varepsilon) Q D_{\text{body}} \frac{\partial^2 [P]}{\partial x^2}. \quad (\text{A12})$$

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

$$\frac{dP}{dt} = (1 - \varepsilon) Q D_{\text{excreta}} \frac{\partial^2 [P]}{\partial x^2} + \varepsilon Q D_{\text{body}} \frac{\partial^2 [P]}{\partial x^2}. \quad (\text{A13})$$

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

$$\frac{\delta P}{\delta t} = (1 - \varepsilon) \frac{Q}{B} D_{\text{excreta}} \frac{\partial^2 P}{\partial x^2} + \varepsilon \frac{Q}{B} D_{\text{body}} \frac{\partial^2 P}{\partial x^2}. \quad (\text{A14})$$

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. We assume for simplicity here that all P made available is taken up, on a fast timescale and used in edible parts. We may revisit this assumption in future work. If these fractions can be assumed equal, then:

$$\frac{\delta P}{\delta t} = (1 - \varepsilon) \frac{Q}{\alpha B} D_{\text{excreta}} \frac{\partial^2 P}{\partial x^2} + \varepsilon \frac{Q}{\alpha B} D_{\text{body}} \frac{\partial^2 P}{\partial x^2}. \quad (\text{A15})$$

If Q/B can be assumed constant, then:

$$\frac{dP}{dt} = \Phi_{\text{excreta}} \frac{\partial^2 P}{\partial x^2} + \Phi_{\text{body}} \frac{\partial^2 P}{\partial x^2} \quad (\text{A16})$$

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

$$\begin{aligned} \Phi_{\text{excreta}} &= (1 - \varepsilon) \frac{Q}{\alpha B} D \\ &= (1 - \varepsilon) \frac{\text{PD}}{\alpha B} \times \text{MR} \times \frac{(\text{DD} \times \text{PR})^2}{2 \times \text{PR}}. \end{aligned} \quad (\text{A17})$$

$$\Phi_{\text{body}} = \varepsilon \frac{Q}{\alpha B} D = \varepsilon \frac{\text{PD}}{\alpha B} \times \text{MR} \times \frac{\text{HR}}{8\pi^2 L}. \quad (\text{A18})$$

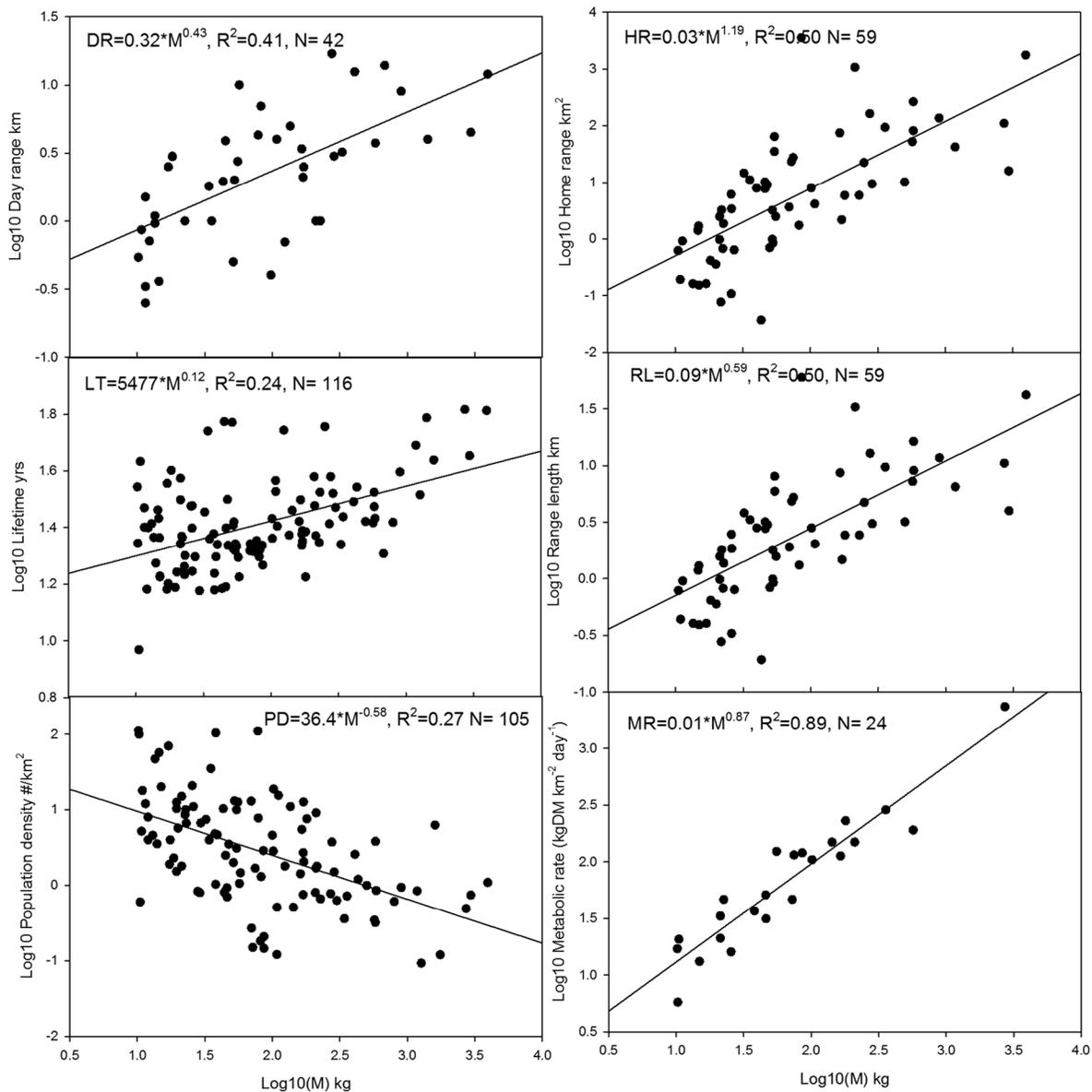


Fig. A1. \log_{10} mass versus \log_{10} -transformed values of day range (km) (top left), home range (km^2) (top right), lifetime (yr) (middle right), range length (the square root of home range) (km) (middle left), population density (number of individuals per km^2) (bottom left), and metabolic rate ($\text{kg DM km}^{-2} \text{day}^{-1}$) (bottom right) for herbivores >10 kg.

We solve the equations above using datasets and methods described in the next section.

Coefficients for Φ from data

We compiled data for as many herbivore species as we could find for weight, day range, home range, lifetime, population density, and metabolic rate. We used a common taxonomic

authority (Wilson and Reeder 2005), available online at <http://www.bucknell.edu/msw3/export.asp>. We compiled data for terrestrial mammals at the species level ($n = 5278$ unique taxa) but only used herbivores in our calculations. We collected data for longevity and metabolic rate from the AnAge database (de Magalhaes and Costa 2009);

population density (Damuth 1987); day range (Carbone et al. 2005); and home range (Kelt and Van Vuren 2001), which all include M as a predictor variable, as well as M (Smith et al. 2003). We use the equation from (Demment and Van Soest 1985) for food passage time.

We estimated Φ as a function of M in two ways: first, we calculated the allometries for each term as a function of M (using ordinary least squares) and combined the resulting coefficients to yield an allometric equation for Φ that results from scaling arguments (Fig. A1 and Table 1). For example, to calculate the grey and black lines for

QD_{scaled} , we calculated the allometries for each attribute and combine them (Fig. A1 for herbivores >10 kg). Second, we multiplied the terms together to estimate Φ directly and fit the allometric equation using the data themselves. We were able to calculate QD_{fit} for the following 14 species: *Eulemur fulvus*, *Propithecus verreauxi*, *Alouatta palliata*, *Cercopithecus mitis*, *Colobus guereza*, *Dipodomys merriami*, *Perognathus longimembris*, *Apodemus flavicollis*, *Apodemus sylvaticus*, *Rattus rattus*, *Capreolus capreolus*, *Odocoileus virginianus*, *Cervus elaphus*, *Kobus ellipsiprymnus*.