



Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests

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During the Late Pleistocene and early Holocene 59 species of South American megafauna went extinct. Their extinction potentially triggered population declines of large-seeded tree species dispersed by the large-bodied frugivores with which they co-evolved, a theory first proposed by Janzen and Martin (1982). We tested this hypothesis using species range maps for 257 South American tree species, comparing 63 species thought to be primarily distributed by megafauna with 194 distributed by other animals. We found a highly significant ($p < 0.001$) decreased mean range size of 26% for the megafauna dispersed fruit ($n = 63$ species) versus fruit dispersed by other animals ($n = 194$), results which support the hypothesis. We then developed a mathematical model of seed dispersal to estimate the theoretical impact of megafauna extinction on tree species range and found the estimated dispersal capacity (Φ_{seed}) of a 2 g seed decreases by $> 95\%$ following disperser extinction. A numerical gap dynamic simulations suggests that over a 10 000 yr period following the disperser extinctions, the average convex hull range size of large-seeded tree species decreased by $\sim 31\%$, while the estimated decrease in population size was $\sim 54\%$, indicating a likely greater decrease in species population size than indicated by the empirical range patterns. Finally, we found a positive correlation between seed size and wood density of animal-dispersed tree species implying that the Late Pleistocene and early Holocene megafaunal extinctions reduced carbon content in the Amazon by $\sim 1.5 \pm 0.7\%$. In conclusion, we 1) provide some empirical evidence that megafauna distributed fruit species have a smaller mean range size than wind, water or other animal-dispersed species, 2) demonstrate mathematically that such range reductions are expected from megafauna extinctions ca 12 000 yr ago, and 3) illustrate that these extinctions may have reduced the Amazon's carbon storage capacity.

Strong debate continues on the extent to which large-seeded, Neotropical trees coevolved with now extinct, large-bodied frugivores (Howe 1985, Hubbe et al. 2007, 2013a, b, Garcia et al. 2008), and whether these tree species are ‘anachronisms’ of a bygone megafauna-rich age (Janzen and Martin 1982, Guimaraes et al. 2008). Recent studies demonstrate that extant megafauna play a key role in maintaining tree diversity and ecosystem function in Old World tropical forests (Blake et al. 2009, Campos-Arceiz and Blake 2011, Bueno et al. 2013). For instance, for many large-seeded fruit types, passing through the gut of elephants and other megafauna can improve germination and reduce seed predation (Dinerstein and Wemmer 1988, Cochrane 2003).

Between 132 000 and 1000 yr bp (and mostly < 50 000 yr bp), there was a global loss of large animals, with at least 154 mammal megafauna (≥ 44 kg body mass) species going extinct (Sandom et al. 2014). A critical and unanswered question is how these extinctions affected ecosystem processes and global ecological trajectories (Doughty 2013). Answering this question is central for understanding paleo- and contemporary ecology, and also for generating predictions on the effects of the current extinction crisis.

There is a large literature relating animal behaviour and characteristics such as home range, day range, gut length, metabolic rate, and lifetime to body size (Peters 1986). These

scaling relationships allow predictions to be made for how now extinct megafauna could have affected ecosystems. For instance, mass-scaling relationships would predict that when the average size of South American megafauna species was reduced from 843 to 81 kg during the late Quaternary, the average distance between food consumption locations and excretion locations decreased by 7.0 km from 9.1 to 2.1 km, and lateral nutrient transfer diffusivity in the Amazon basin decreased by > 98%, from 4.4 (2.4–6.5) to 0.03 km² yr⁻¹ (Doughty et al. 2013). More generally, Late Pleistocene and early Holocene megafauna extinctions produced large impacts on nutrient distributions worldwide with the movement of nutrients reduced by 97% in South America, 95% in North America, and by 70% in Eurasia. Here, we modify this model to estimate the effects of megafauna extinction on seed dispersal (Doughty et al. 2013).

Seed dispersal distance is a key phase in plant life cycle because seedlings of many species have higher mortality under the parent plant than when dispersed away from parents due to species-specific predators and pathogens (the Janzen–Connell effect (Janzen 1970, Connell 1971)). This effect has been verified by numerous studies (Schupp 1992, Burkey 1994, Hansen et al. 2008, Terborgh 2013), and large-bodied frugivores may be especially important for reducing this effect because of their large dispersal distances (Blake et al. 2009). For instance, studies from Sri Lanka and Myanmar on seed dispersal distances by elephants have shown a mean dispersal distance of 1–2 km and maximum distances of 6 km (Campos-Arceiz et al. 2008), while a study from Congo showed that 88% of seeds moved more than 1 km and 14% moved more than 10 km, with a maximum dispersal of 57 km (Blake et al. 2009). Elephants currently play a disproportionately important role in seed dispersal compared to small animals by moving more seeds from more species over greater distances than any other taxon of frugivore (Blake et al. 2009), often also increasing seed germination rates (Campos-Arceiz and Blake 2011). Furthermore, Blake et al. (2009) show that species with seeds dispersed only by elephants require this mode of dispersal to overcome the Janzen–Connell effect and that in the presence of elephants, these species are randomly distributed compared to more aggregated distributions when only dispersed by other mechanisms (Blake et al. 2009).

Moreover, it has been suggested that there is a positive relationship between seed size and wood density (Brodie and Gibbs 2009) meaning that preferential dispersal of large-seeded species by elephants and other megafauna may increase forest carbon content. Recent studies have shown African tropical forests (with megafauna) have a mean aboveground biomass of 396 Mg biomass ha⁻¹ compared to 289 Mg biomass ha⁻¹ in the Amazon (without megafauna), with more large trees in Africa (Lewis et al. 2013). Some of this difference could potentially be due to the presence of megafauna in Africa (Poulsen et al. 2013).

Given the apparent fitness advantages for dispersal in the tropics, and the abilities of megaherbivores to disperse certain fruits widely, scientists have begun to argue for the existence of a substantial role for long-extinct megaherbivores in shaping the present South American flora (Janzen and Martin 1982, Guimaraes et al. 2008). Recently, Guimaraes et al. (2008) found at least 103 South American tree species with fruit characteristics that suggest dispersal by megafauna (Guimaraes

et al. 2008). This paper categorized the megafauna fruits as either type I, which are fleshy fruits 4–10 cm in diameter with up to 5 large seeds (each ~ 2.0 cm diameter), or type II, which are fleshy fruits > 10 cm diameter with numerous (> 100) small seeds. These fruits are drupes (40%), berries (30%), or leguminous (19%), with restricted colouring (predominately brown, green or yellow), heavy (50–1000 g total per fruit mass), and with high seed load per fruit relative to species not dispersed by megafauna. The largest extant terrestrial mammals in South America, tapirs, may not compensate for the loss of megafaunal seed dispersal. Indeed, studies have shown that Asian tapirs *Tapirus indicus* disperse fewer large seeds than Asian elephants, and that most seeds do not survive gut passage (Campos-Arceiz et al. 2012, O’Farrill et al. 2013), although, in contrast, New World tapirs may be good seed dispersers (Fragoso 1997, Fragoso and Huffman 2000). Jansen et al. (2012) suggested that on Barro Colorado Island in Panama, relatively small-bodied agoutis (*Dasyprocta*) can spread 35% of dispersed seeds > 100 m, and may therefore substitute for extinct megafauna, though this result may have been due to the unusually high population density of agoutis on the island (Wright et al. 1994).

A review of the seed size literature showed that larger-seeded species have a survival advantage over small-seeded species during seedling establishment, as well as longer lifespans, which together compensate for the lower quantity of seeds produced per mature adult (Moles and Westoby 2004). Other authors have focused on survivorship of large-seeded plants to stresses such as shade or drought while plants are in their juvenile stages (Poorter and Rose 2005, Muller-Landau 2010). These arguments, in addition to the classic seed number/seed size tradeoff, highlight the apparent advantage that large-seeded plants must possess during some life-history stages in order to persist evolutionarily, because they are otherwise at such a clear disadvantage in dispersal without large frugivores (Galetti et al. 2013).

There is still great debate about the anachronisms theory proposed by Janzen and Martin (1982). One of the issues is that the candidate megafauna fruits (Guimaraes et al. 2008) are composed of species/genera that may have evolved prior to the arrival of proboscideans (gomphotheres) in South America following the Great American Interchange 3 million yr ago (or as early as 9 mya). Therefore, if the species evolved prior to the arrival of the gomphotheres, then the gomphotheres could not have coevolved with the fruit unless 1) such tree species have had time to evolve characteristics for attracting megafauna post-gomphothere arrival or 2) other potential megafaunal dispersers in South America, such as *Macrauchenia* or giant sloths, coevolved with the fruit species before the gomphotheres arrived. Both of these are difficult to answer with certainty. However, isotopic evidence indicates that in the Amazon region the gomphothere *Stegomastodon* and the rhino-sized ungulate *Toxodon* both consumed C3 plants such as fruit, with the *Toxodon* representing a large-herbivore group that evolved in South America prior to the Great American Interchange (Franca et al. 2015).

Here, we use an unprecedented data set of New World plant distributions and plant traits to test if the Late Pleistocene and early Holocene megafaunal extinctions caused a reduction in the ranges of large-seeded tree species in the tropical Americas. The Botanical Information and

Ecology Network (BIEN), a working group of botanists, ecologists, and computer scientists, has assembled a standardized database of georeferenced occurrences, abundances and traits (such as seed size and wood density) of New World vascular plant species. Using the BIEN database, we document the relationship between seed size and range size in Amazonian trees, and examine the impact of range size reductions on basin-wide patterns of wood density and forest carbon content. We then support these results by theoretically showing how we would expect the megafauna extinctions to affect species distributions using scaling theory to estimate seed dispersal distances. In particular, we ask the following specific questions: 1) are large-seeded trees less widely distributed than small-seeded trees in the Amazon basin? 2) How much would we expect animal-dispersed, large-seeded species range to decrease based on scaling theory predictions of seed dispersal? 3) Is there a positive relationship between seed size and wood density in the Amazon basin, and could the extinctions have theoretically affected forest carbon content by reducing average wood density?

Methods

Tree species data

To understand the relationship between seed size and species range we used the BIEN database (ver. 2) for Amazonian forests, which combines botanical species trait data and geographic range maps for New World plant species (Botanical Information and Ecology Network; <<http://bien.nceas.ucsb.edu>>) (Enquist et al. 2009, Lamanna et al. 2014). This database combines observations from herbarium specimens and vegetation plots, and includes ~ 596 678 unique, georeferenced, New World plant occurrence records spanning 95 259 distinct species. We estimated range size for species with at least five data points (varied in a sensitivity study, Supplementary material Appendix 1, Table A1 and A2) by calculating the area of the smallest convex polygon ('convex hull') that incorporates all occurrences for a species (in a sensitivity study we also used the species distribution model Maxent (Phillips and Dudík 2008) to estimate range size). Species lists were chosen by first finding species that are known to be dispersed by large animals as documented in the Kew database (<<http://data.kew.org/sid/dispersal.html>>). In this way, we identified a list of 194 woody tree species with other animal-dispersed neotropical seeds, which was carefully verified for accuracy (species listed in Supplementary material Appendix 1). We compared this to species with attributes of megafauna-distributed fruits identified by Guimaraes et al. 2008 (n = 63 that fit our above criteria) listed in the supplementary material (Guimaraes et al. 2008). Because the identification of such fruit is still relatively controversial, we also produced a second smaller, much more conservative species list (n = 6, Supplementary material Appendix 1, Table A4). Finally, we identified 89 species that were either wind or water dispersed. We then examined the relationship between range size and seed mass, and the relationship between seed mass (g) and wood density (g cm⁻³) (n = 120 species with data for both), utilizing species trait data from BIEN.

Model framework

We can make inferences about average movement of seeds by the now extinct South American megafauna based on mass-scaling relationships. For this purpose we need to formulate an equation where the main input is animal mass because we know little about the now extinct megafauna beyond what we can determine from their skeletal remains. To calculate the movement of seeds based on animal size and seed size, we calculate the lateral movement of seeds (Φ_{seed}), which is proportional to the local concentration of seeds with units of (distance²/time). Φ_{seed} is composed of two parts, the first explaining the movement of the animal (diffusivity, D), and the second part (Q) explaining the quantity of seeds moved by animals. This framework is based on Doughty et al. (2013) and Wolf et al. (2013).

Estimate of D

We estimate D based on the random walk with the form:

$$D = \frac{(\Delta x)^2}{2\Delta t} \quad (1)$$

where Δx is a change in distance and Δt is a time step of duration t . In general, diffusivity can be derived from a random walk (Skellam 1951, Okubo and Levin 2001, Ovaskainen and Crone 2009). The 'random walk' has been derived previously (Berg 1993). A Levy walk, which is a probability distribution with a heavy tail, is another possible way to model this process (Nathan and Muller-Landau 2000, Levin et al. 2003) for other potential animal seed distribution functions. However, because of our uncertainty on the behaviour of the megafauna, we use the simplest distribution, the random walk.

In our study, 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 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 seeds is Eq. 2. The M term shows that the variable is a function of mass (M).

$$D(M) = \frac{(DD(M) \times PT(M))^2}{2 \times PT(M)} \quad (2)$$

Estimate of Q

We estimate live viable seeds spread by a population of animals per area, which we estimate as a function of seed size (S) and animal size (M). This is a function of the amount of fruit consumed by a population density of animals (PD; ind. km⁻²) consuming fruit (DM) to fulfil part (FC) of their metabolic requirements (MR; kg DM/animal/d). This fruit must be able to be swallowed (edible – E) by the animal, which is related to the size of the seed and the esophagus size of the animal (although un-swallowed fruit can also be dispersed, but we do not account for this). This is multiplied by percent fruit consumption (PFC) by the animal, the amount of fruit provided per seed (a function of the size of the seed; FS, g seed⁻¹), and then multiplied by the seed

mortality (SM), or the fraction of seeds that survive and can become seedlings, which is also a function of seed size (Eq. 3).

$$Q = \text{edible} \times \frac{\text{ind}}{\text{km}^2} \times \frac{\text{food}}{\text{ind}} \times \frac{\text{fruit}}{\text{food}} \times \frac{\text{seed}}{\text{fruit}} \times \text{seed mortality} \quad (3)$$

The product (Q) of the above terms, which has units of seeds km^{-2} , is the population consumption rate of intact viable seeds and can be shown as abbreviations and whether the variable is a function of seed size (S), animal size (M), or both (S,M).

$$Q(S, M) = E(S, M) \times \text{PD}(M) \times \text{MR}(M) \times \text{PFC} \times \text{FS}(S) \times \text{SM}(S) \quad (4)$$

Therefore, Φ_{seed} is a function of Q multiplied by D in units of seeds km^{-2} .

$$\Phi_{\text{seed}} = Q \times D \quad (5)$$

We combine all the terms together in Eq. 6, which makes Φ_{seed} a function of animal size and seed size:

$$\Phi_{\text{seed}} = \left(\frac{(\text{DD}(M) \times \text{PT}(M))^2}{2 \times \text{PT}(M)} \times E(S, M) \times \text{PD}(M) \times \text{MR}(M) \times \text{PFC} \times \text{FS}(S) \times \text{SM}(S) \right) \quad (6)$$

We use mass scaling relationships derived in a previous paper for PD, MR, DD, PT, which are explained in Wolf et al. 2013 (varied in a sensitivity study – Supplementary material Appendix 1, Table A1 and A2) and equal to the following equations as a function of animal mass (M):

$$\text{Population density} - \text{PD} = 36.4 \times M^{-0.58} \quad (7)$$

$$\text{Metabolic rate} - \text{MR} = 0.01 \times M^{0.67} \quad (8)$$

$$\text{Day range} - \text{DD} = 0.32 \times M^{0.43} \quad (9)$$

$$\text{Food passage time} - \text{PT} = 0.29 \times M^{0.28} \quad (10)$$

These equations are only valid for mammalian herbivore distributors and the important role of bird dispersal is not included. The edibility (E) of the seeds is based on esophagus size (E(S, M), in cm), which we assume is linearly related to animal size with the equation $0.0027 \times M + 1.734$ (slope varied between 0.001 and 0.005). Large animals can also eat smaller fruit but because there are more consumers of small fruits we assume that the smallest seeded fruits are preferentially spread by small animals. To account for this, we assume that smaller seeds (> 20 times smaller than estimated esophagus size) are more likely to be eaten and dispersed by smaller versus larger animals (Guimaraes et al. 2008). We estimate fruit consumption (FC) as any given fruit tree species providing $\sim 1\%$ of the diet (ranged between 0.1 and 10%) because in Africa, studies with elephants have found that 30% of the diet (Short 1981) is fruit of ~ 70 – 90 different species (Poulsen et al. 2001, Blake et al. 2009). To estimate the amount of fruit per seed (FS), we calculate that the average wet weight of fruit is seven times the seed and,

assuming 50% water, dry fruit is 3.5 (ranged between 1 and 7) times the seed weight, based on data from (Guimaraes et al. 2008). For simplicity, we estimate seed mortality (SM) is equal among seed types (1), and does not influence our model here. Our simple model has many assumptions and to understand the impact of each of our assumptions we have varied each estimated parameter in a sensitivity study by the amounts listed above to show the impact on the outcome (Supplementary material Appendix 1, Fig. A1 and Table A1 and A2).

We then calculated Φ_{seed} based on Eq. 6 for a specific case study of 12 mammalian distributors of fruit, including four now extinct megafauna. The four now extinct megafauna used in our test case were chosen based on stable isotope evidence of C3 plant consumption and the location of fossil evidence, and could have inhabited forest areas of the Amazon and eaten fruit: the giant ground sloth *Eremotherium* (3500 kg), the gomphothere *Stegomastodon* (6000 kg), the rhino-like *Toxodon* (1100 kg), and *Trigonodops lopesi* (1600 kg) (Sanchez et al. 2004, MacFadden 2005); other possible herbivores from that period include *Catagonus stenocephalus*, *Glyptotherium cylindricum*, *Holmesina paulacoutoi*, *Macrauchenia patachonica* and *Palaeolama major* (Sandom et al. 2014). However there is great uncertainty on which megafauna lived in the Amazon forest (Cristoffer and Peres 2003). In our test case, we combine the four extinct animals with eight theoretical extant animal sizes as: 2, 10, 15, 25, 50, 150, 300, 1100, 1600, 3500, 6000 kg. To simulate the Late Pleistocene and early Holocene megafauna extinction, we remove the four largest species.

Based on the above assumptions, we then estimate how various seed sizes (between 0.1 and 5 g) would have been distributed with and without the megafauna. For each seed size, we calculate Φ_{seed} with and without megafauna. We solve for a one day distribution of seeds using equation 12 (derived in Wolf et al. 2013) as a 1D solution to Eq. 11, where G is a gain rate (which is 0), K is first order loss rate, X is distance and T is time.

$$\frac{ds}{dt} = \Phi_{\text{seed}} \frac{d^2s}{dx^2} - K \times S \quad (11)$$

$$S(x, t) = \left(S_0 - \frac{G}{K} \right) \times \text{erfc} \left(\frac{X}{\text{sqr}t(4 \times \Phi_{\text{seed}} \times T)} \right) + \frac{G}{K} \quad (12)$$

We use Eq. 12 to solve for the distribution of 2 g seeds for the two Φ_{seed} values. Based on these distribution capacities, we create a simple gap dynamic model. In this model, we calculate a randomly distributed population of trees of species X on 5% of a 100 by 100 pixel grid within a 500 by 500 pixel grid (to minimize edge effects). We then assume each time step is 10 yr and at every time step each pixel has a 10% chance of mortality (this assumes an average 100-yr lifetime of a tree). If a tree dies, a canopy gap will open up and species X can grow in this gap based on the approximate dispersal distance from another tree of species X. To do this, at every time step, for every tree of species X, we calculate a 9 by 9 matrix surrounding the tree with a dispersal likelihood for each pixel based on the above calculated diffusivities. We run this simple simulation for 10 000 yr (1000 time steps) with a Φ_{seed} including megafauna and then for 10 000 yr without megafauna. At the end of the simulations we

randomly sample 5% of the pixels for species X and create a convex hull around the samples. This step is to replicate the stochastic nature of real species observations to obtain data for the BIEN dataset. After each simulation, we repeat this process 20 times (simulating 20 separate random collections of species) to estimate how the convex hull methodology captures the range size of randomly sampled areas compared to the actual modelled (not estimated by convex hull) change in species X. We ran this model 30 times and average our results to estimate the difference between average species distributions and species distributions estimated by the convex hull methodology. To estimate the average time to species extinction, we run the model 5 times for 50 000 yr (5000 time steps) and average the results.

We realize that there are a large number of assumptions that go into our estimates and model simulations. To get a better sense of this uncertainty, we have done a sensitivity study for each uncertain parameter (Supplementary material Appendix 1, Table A1 and A2).

Results

Species range estimates

We compared mean species range size for 194 species with seeds distributed by animals to 63 species with species thought to be distributed by megafauna (Guimaraes et al. 2008) and found that mean species range was ~ 26% smaller for megafauna species versus species distributed by animals (Table 1 and Fig. 1). Mean species range of wind or water dispersed species were ~ 36% greater than those distributed by animals, and all three categories were significantly different from one another ($p < 0.001$, Kruskal–Wallis one way analysis of variance on ranks). There was also a significant ($r^2 = 0.05$, $p < 0.005$, Fig. 1) negative relationship between seed size and range size for other animal-dispersed seeds with larger seeds having a smaller average range. There was also a negative relationship between seed size and range size for megafauna dispersed seeds (but not significant, possibly due to small sample size – $n = 40$). Note, this is smaller than $n = 63$ listed in Table 1 because we do not have seed size data for all species). Wind or water dispersed seeds had no significant relationship between seed size and range size. For the animal-dispersed species, we found a positive correlation ($r^2 = 0.11$, $p < 0.0005$) between wood density and seed size (Fig. 2).

Table 1. Mean species range (Log_{10} species range (km^2)) based on convex hull model from the BIEN dataset, mean seed size (g), mean tree wood density (g cm^{-3}) and tree species sample size. ** Indicates significant differences ($p < 0.001$) and ° indicates marginal significant ($p < 0.1$) differences between mean values using a Kruskal–Wallis one way analysis of variance on ranks.

	Mean species range Log_{10} species range (km^2)	Mean seed size (g)	Mean wood density (g cm^{-3})	Sample size
Animal dispersed	$12.59 \pm 0.03^{**}$	1.54 ± 0.29	$0.61 \pm 0.02^{\circ}$	194
Megafauna dispersed	$12.38 \pm 0.07^{**}$	2.13 ± 0.99	$0.67 \pm 0.02^{\circ}$	63
Wind or water dispersed	$12.72 \pm 0.05^{**}$	1.26 ± 0.31	$0.60 \pm 0.02^{\circ}$	89

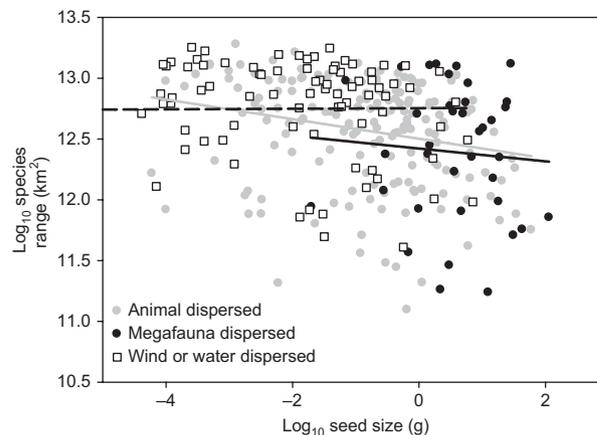


Figure 1. (Grey circles) Log_{10} transformed seed mass (g) for animal-dispersed tree species ($n = 194$), (black circles) likely megafauna dispersed species from the Guimaraes et al. (2008) dataset ($n = 63$), and (open squares) wind or water-dispersed seeds ($n = 89$) versus their average log_{10} transformed range size (km^2) using the convex hull methodology to determine range size. Full species lists are in the Supplementary material Appendix 1, Table A3. Grey line is significant linear regression of animal-dispersed seeds, black line is non-significant linear regression of megafauna-dispersed seeds, and dashed lines is a non-significant linear regression for wind and water-dispersed species.

The results of our sensitivity studies (Supplementary material Appendix 1, Table A1 and A2) indicate that model choice when estimating range size, number of occurrences as a minimum threshold, and tree species with fruit distributed by megafauna can all impact our results (Supplementary material Appendix 1, Table A3 and A4). Specifically, predicted range size increases as we increase the number of occurrences as a threshold (Supplementary material Appendix 1, Fig. A2). Convex hull predicts larger mean ranges than does Maxent modelling (Supplementary material Appendix 1, Table A2). A smaller potential species list (Supplementary material Appendix 1, Table A4) produces a larger mean range size than does the full species list (Supplementary material Appendix 1, Table A2 and A3). However, when comparing different groups under similar scenarios, our results generally still stand.

Model estimates

We attempted to estimate the seed dispersal capabilities of the now extinct megafauna using mass based scaling attributes (Eq. 6) to estimate Φ_{seed} . However, prior to this analysis it was important to see if our model could accurately predict the seed dispersal abilities of existing megafauna, such as the elephant. Fortunately, there are good estimates of seed distribution capabilities by elephants in the Congo basin (Blake et al. 2009). The Blake et al. (2009) dataset found a mean seed dispersal of $345.6 \text{ seeds km}^{-2} \text{ d}^{-1}$ for elephants spreading 73 different species (Blake et al. 2009). The mean elephant density was 0.66 km^{-2} , which, due to poaching, is likely to be below carrying capacity in that ecosystem (although our predicted density for a 3000 kg animal is even lower at $0.35 \text{ individuals km}^{-2}$). Using our scaling estimates, we predict that within a 1 km^2 area a 3000 kg species will

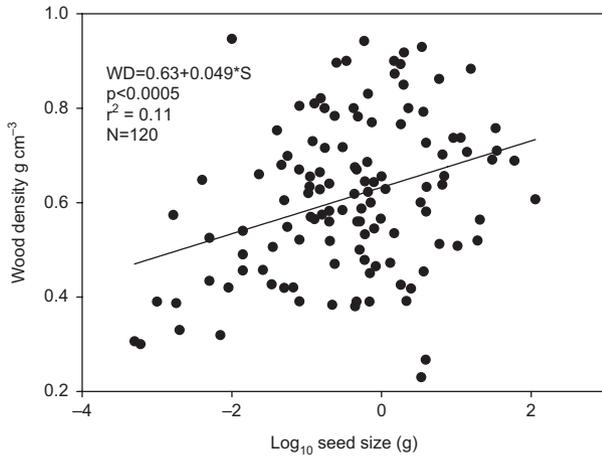


Figure 2. Log_{10} seed size (g) versus mean tree wood density (g cm^{-3}) for the same animal-dispersed seeds from Fig. 1.

have a population density of 0.35 km^{-2} with each individual consuming 11 kg of dry matter d^{-1} , which we assume is $\sim 30\%$ fruit from $\sim 70\text{--}90$ different species (Blake et al. 2009), so any given fruit tree species will be $\sim 1\%$ of the diet (varied between 0.1 and 10% , Supplementary material Appendix 1, Fig. A1). We estimate that for each gram of seed there is 3.5 g of fruit, equalling $247 \text{ seeds km}^{-2} \text{ d}^{-1}$ for an individual fruit tree species. This is slightly lower, but within range, of the $346 \text{ seeds km}^{-2} \text{ d}^{-1}$ found by Blake et al. 2009, likely due to the lower population density estimates.

We also have good data on mean dispersal distance to compare to our diffusivity (D) value. The Blake et al. 2009 study found 14% of large seeds were transported $> 10 \text{ km}$ and 31% went $> 5 \text{ km}$ from the parent tree. We estimate that a 3000 kg animal would have had a day range of 10 km and a passage time of 2.7 d , leading to an average movement of 27 km between feeding and seed defecation. However, they would be unlikely to walk in a straight line away from the tree. Because we know little about the behaviours of the extinct megafauna, we use a random walk model. We estimate a Φ_{seed} for a 3000 kg animal of $337 \text{ km}^2 \text{ d}^{-1}$ (using Eq. 7) and solve for a one-day distribution of seeds using the 1D solution to equation 1 described in Wolf et al. 2013 (using Eq. 12) and calculate that a 3000 kg animal would move 51% of fruit with a 2 g seed $> 5 \text{ km}$ and 23% of seeds $> 10 \text{ km}$ (black line Fig. 3a). This is slightly greater than estimated in the Blake et al. 2009 study, possibly due to overestimating elephant passage time. In our sensitivity study, by varying our parameters (which are highly uncertain), our range of estimates greatly widens and clearly encompasses the results from the Blake et al. 2009 study (Supplementary material Appendix 1, Fig. A1).

Our modelling framework indicates that with the Pleistocene megafauna, larger seeds have a much greater dispersal capacity than smaller seeds (Fig. 3a). However, if the largest animals are removed, the dispersal capacity of the largest seeds drops to near zero and the relationship with megafauna becomes a liability (Fig. 3b). Notably, our model estimates that for a 2 g seed, Φ_{seed} drops from $654 \text{ seeds km}^{-2} \text{ d}^{-1}$ to $40 \text{ seeds km}^{-2} \text{ d}^{-1}$ following the megafauna extinctions, a drop of $\sim 95\%$. There is no change to seeds $< 1 \text{ g}$, but a large change in dispersal to seeds larger than this (Fig. 3c).

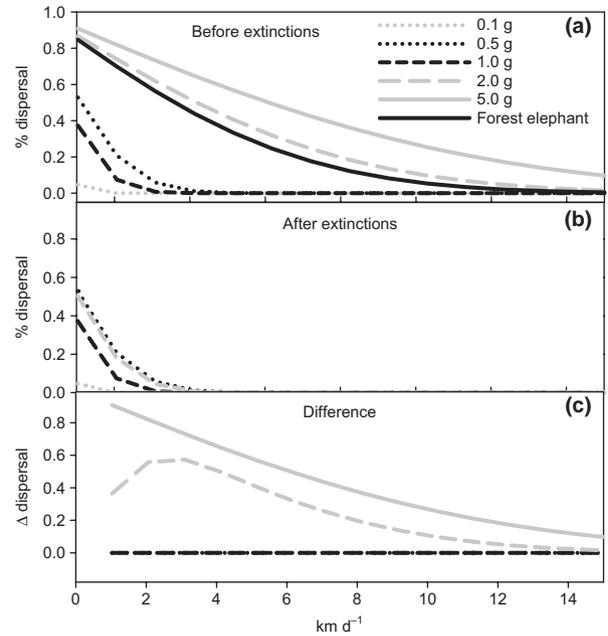


Figure 3. (a) Estimated dispersal of seeds over a day of various seed sizes ($0.1\text{--}5 \text{ g}$) assuming the presence of 11 species listed in the methods including four species of now extinct megafauna. (b) Dispersal of the same seed sizes following the extinction of the four megafauna species. (c) The difference between (a) and (b). Black solid line is the estimate of dispersal by a 3000 kg herbivore moving a 2 g seed (same size as an African forest elephant *Loxodonta cyclotis*) to compare with Blake et al. (2009) datasets.

To test how the reduction in dispersal ability might have affected species distributions, we used our numerical model to assess the impact of the extinctions of the larger dispersers on the dispersal of a 2 g seed. In our simple model, a 2 g seed has not lost all dispersers but we estimate that mean dispersal distance has dropped from 5 to 1 km for this seed without the megafauna (Fig. 3a vs 3b). Gaps periodically open up in the model and can be filled by nearby seeds depending on dispersal distance (5 vs 1 km). Following the loss of the megafauna, the 2 g seed tree becomes much more clumped and overall less abundant (Fig. 4 top). The decrease in abundance is because the seed with a smaller dispersal distance has a smaller chance of finding a gap than a seed with a greater dispersal distance.

To compare our simulations to the actual species ranges calculated using the BIEN dataset, we calculated a convex hull around our simulated data (Fig. 4 bottom). Then, we randomly sampled 5% of the pixels for the species distribution and created a convex hull around those points and repeated this process 20 times. We did this to demonstrate how subsampling of tree distributions are inherently stochastic with a certain inherent error based on which trees are sampled. Because of the stochasticity inherent in the model, we ran this entire process 20 times, averaging the results, and found that the extinction of large animals reduced the average convex hull size of large-seeded fruit species by $\sim 31\%$. This estimate was smaller than the actual modelled decrease in the numbers of the trees, which dropped by $\sim 54\%$. Because convex hull captures only the extremities of the range distribution, it does not capture the area of range occupancy and abundance of the reduction. We, therefore, hypothesize that the real decrease

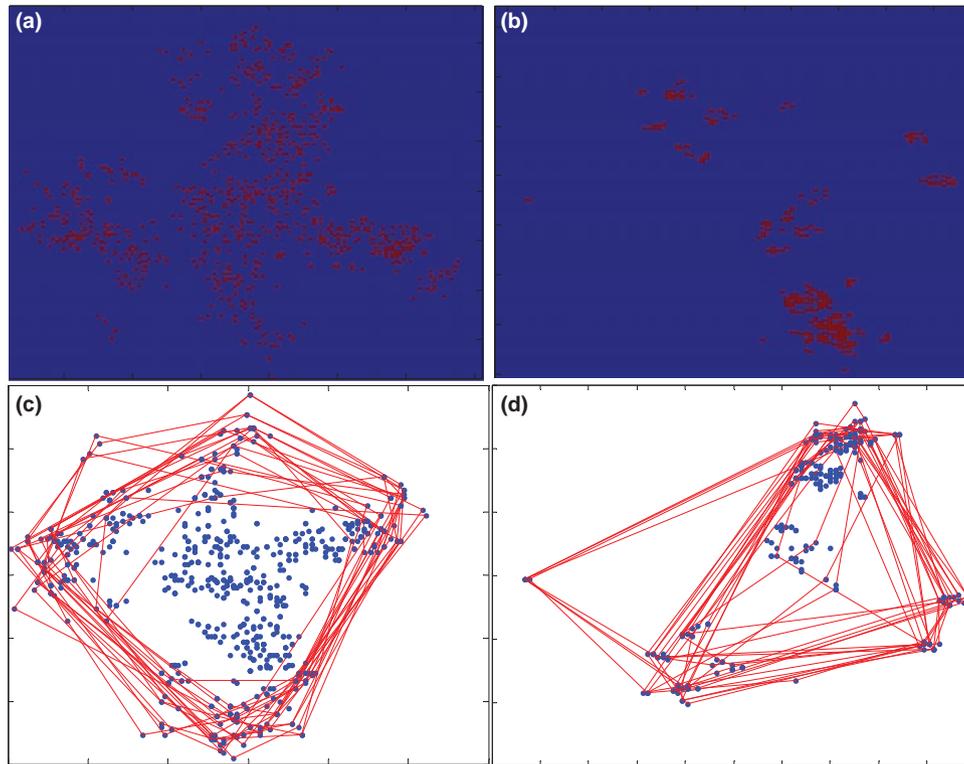


Figure 4. (a) Distribution of a 2 g seeded species with megafauna present, and (b) the distribution of that same species 10 000 yr (1000 model time steps) after the extinction of the large animals but assuming small animals can distribute the seeds. (c and d) 5% of the pixels from (a) and (b) randomly sampled with a convex hull drawn 20 separate times around this subset of data. We repeat 20 times to show the stochasticity involved in estimating species area using the convex hull approach.

in large-seeded fruit species is likely larger than is shown in Table 1. Finally, we found that when we continued to run the model, the tree species were predicted to eventually go extinct with a mean extinction time ($n = 5$) in our scenario of 26 600 yr following the disperser extinctions (Fig. 5).

Carbon estimates

As a thought experiment, we now roughly estimate how the reduction of range of these species may have affected Amazonia forest carbon storage. If we assume no correlation between species range and seed size prior to the extinctions, then the extinctions decreased the population of large-seeded fruit trees by $\sim 50\%$ (based on our modelled value of 54% from the previous paragraph). If we further assume large-seeded fruit trees today comprise $\sim 8\%$ of all trees in the Amazon basin (based on the current proportion of large-seeded fruit trees in BIEN), but in the past they accounted for 12% of the trees (50% greater than 8%), and if we further assume that the 4% (range 2–6%) of missing large-seeded fruit trees (mean wood density $- 0.67 \pm 0.02 \text{ g cm}^{-3}$) were replaced by trees with the lightest wind-dispersed seeds (mean wood density $- 0.49 \pm 0.09 \text{ g cm}^{-3}$), then the mean carbon content in the Amazon (assuming an average forest biomass of 289 Mg ha^{-1}) would decrease by $1.5 \pm 0.7\%$. We found the mean wood density for wind dispersed seeds ($0.49 \pm 0.09 \text{ g cm}^{-3}$) by looking at the wood density of the smallest seeded ($< 0.03 \text{ g seeds}$) trees since these trees would be most likely to fill empty gaps.

Discussion

It has been hypothesized for some time that large-seeded fruit species should experience range reduction or even extinction following the extinction of their dispersers (Janzen and Martin 1982, Guimaraes et al. 2008, Blake et al. 2009), although this idea has been contentious (Howe 1985). Until recently, our ability to test this hypothesis has been hampered by the lack of information on the distributions of tropical trees. In this paper, we provide quantitative support for this hypothesis on

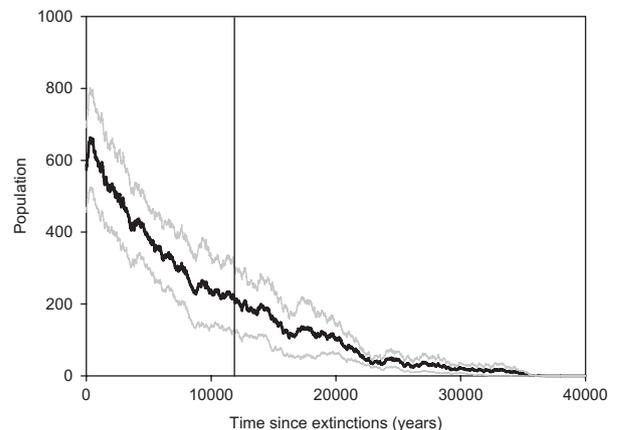


Figure 5. Mean (black) \pm SE (grey) of five simulations from Fig. 4 showing the longer-term gap dynamics in process. Vertical line is approximately current day, 12 000 yr post extinction. Mean time to extinction for the five simulations was $26\,600 \pm 390$ yr.

an Amazon basin scale. We further demonstrate a mathematical argument that supports the empirical result based on scaling theory and highlight why our quantitative estimates of species ranges are likely to underestimate the actual changes in species abundance and range. Finally, we demonstrate that this range reduction may have had impacts not only on species range and occupancy, but may have reduced the carbon content of Amazonian forests.

However, our sensitivity study shows that our results can vary depending on the parameters chosen. The biggest uncertainty of our results was model choice for estimating range distribution since the convex-hull and Maxent models gave different numbers, with Maxent tending to predict smaller ranges. We are confident that we can better answer our question of interest using the convex hull methodology because few assumptions are required and it is unlikely to predict the presence of a species far outside of its observed range (although as we show, it may be sensitive to outliers). However, the size of the hull depends on the number of trees sampled and recorded, itself a very stochastic process that we explore in detail with our simulations (Supplementary material Appendix 1, Fig. A2). Under recommendation from the BIEN group, we chose species with at least five independent occurrences. Species with fewer coordinates and smaller ranges are not likely to be well measured by the convex hull methodology because they are more sensitive to outliers, even though they are the species that are likely to have seen the largest range reduction. However, mean predicted range size increases as the threshold increases (Supplementary material Appendix 1, Fig. A2). Since we compare all groups using the same threshold (5), this should not bias our results. Finally, our results vary depending on our choice of megafauna-distributed plant species (Supplementary material Appendix 1, Table A3 vs Table A4). Our more conservative species list only has 6 species and is too small a sample size to evaluate our question. To have confidence in our results, we must have confidence in the tree species that likely coevolved with the megafauna. However, there is not yet wide agreement on a definitive list of megafauna distributed fruits. The sensitivity study of our model results demonstrate that better data are still needed for further confidence in the model. For instance, fruit consumption, a term that is not well quantified, can have a large impact on our results (Supplementary material Appendix 1, Fig. A1). Overall, our sensitivity study demonstrates that some caution is still necessary in the interpretation of both our empirical and model results (Supplementary material Appendix 1, Table A1 and A2). However, we hope that we have put forward a methodology that can be repeated when better data becomes available in the future.

Both Table 1, showing that the mean range size of megafauna-distributed fruit is significantly smaller than other animal distributed fruit, and Fig. 1, showing the negative correlation of species range with seed size supports the notion that the extinction of the megafauna reduced effective dispersal of large-seeded species likely distributed by megafauna. In addition, our simple mathematical model provided a second, independent test of the hypothesis, demonstrating that large animals play a dominant role in the seed-dispersal process. Our model estimated that the loss of the megafauna reduced the seed dispersal effectiveness of large seeds by > 95%. As an example, the model estimates that the

loss of megafauna would reduce the dispersal potential of a 2 g seed from ~ 10% traveling further than 10 km to only 10% travelling more than 2 km.

Based on the above predicted decrease in dispersal abilities, we used a simple gap dynamics model to predict how total species range may have decreased following the Late Pleistocene extinctions. It is important to use such a model because of the long timescale necessary to see a change in species composition. Previous research that looked for the impact of elephant removal on tree biodiversity did not take long-generation times for forest transitions into account, and predictably found no evidence that vegetation composition changed following loss of elephants (Hawthorne and Parren 2000), however, other analyses suggest that the loss of dispersers has an almost immediate impact on seedling recruitment (Terborgh et al. 2008). In our example, mean dispersal distance has dropped from 5 km to 1 km following the megafauna extinctions. This decreased dispersal distance reduced the likelihood of the seed finding itself in an open gap, eventually leading to a slow decrease in abundance. If no dispersers were available, extinction would have been much quicker. In South America, enough time has elapsed since the megafauna removal (~ 12 500–8000 ybp) for the effects of megafaunal extinctions to manifest. Our model simulations indicate that range reduction is a very slow process and that even in South America where the extinctions happened > 10 000 yr (100 tree generations in our model), we may not yet have seen the full reduction in range due to the extinctions. Our model predicts greater clumpiness of species following the extinctions, range reductions, followed eventually by tree extinction > 25 000 yr post animal extinction (but highly dependent on a range of parameters). However, this is, by necessity, a simple model and there are many complications that we are not taking into account. For instance, a recent study found that megafauna extinctions may have led to selection for smaller seed size in some species (Galetti et al. 2013).

Using data from our simulated model, we can gauge the difference between range reduction as predicted by the convex hull methodology and actual species population reductions. This is because we estimate that, as species distributions become clumpier, their populations decrease by more than their range size. Our model simulations predict an average range reduction of ~ 31% following the extinctions after 10 000 yr, but an average population reduction of 54% (Fig. 4). Therefore, we are also confident that the reduction predicted with our BIEN dataset is likely underestimating the actual species population reduction.

Our model demonstrates that increased seed dispersal distance by megafauna benefited big-seeded fruits but became a liability once the megafauna went extinct. Our simple model may need future refinement because it does not account for differences in dispersal effectiveness of different animal species. For instance, tapirs are more efficient digesters of seeds than are elephants, leading to greater seed mortality (Campos-Arceiz et al. 2012), although New World tapirs are good dispersers (Fragoso 1997, Fragoso and Huffman 2000). While the model does not do a good job accounting for scatter-hoarding and thieving rodents (Jansen et al. 2012), dispersal distances of small-bodied rodents are at least an order of magnitude smaller than large megafauna. Also, extant sloths have particularly low metabolic rates. Many of the extinct species were within the same super-order Xenarthra, and we may therefore overestimate movement

of these animals by basing their movement on modern species with higher metabolisms.

Few data exist with which to corroborate our inferences. However, the northern Republic of Congo, where elephants and other megafauna still occur, offers pertinent insights into the validity of our conclusions. Blake et al. (2009) found that tree species only dispersed by elephants are less aggregated than would be expected by chance. Furthermore, they found that, similarly, decay in space is tightly correlated with dispersal mode, with elephant dispersed trees having wider, less aggregated distribution of big-seeded fruit trees than trees with seeds dispersed by wind, gravity, or smaller animals. They further predict based on their results that loss of elephants and large-bodied dispersers would lead to recruitment failure of large, animal-dispersed trees, and lead to a regeneration of abiotic-dispersed trees, supporting our findings in South America.

Our results suggest that the loss of megafauna has strong implications for the ability of today's Amazon forest to sequester carbon. Since we estimate that wood density increased with seed size (Fig. 2) for animal-dispersed species, as a thought experiment, we estimated that the reduction of range of these species may have reduced Amazon forest carbon content by $4.2 \pm 2.1 \text{ Mg ha}^{-1}$. This suggests that with megafauna, South American forests may have been previously populated with trees with denser wood and higher carbon content. It has been noted that African forests that still contain much of their original megafauna, have larger trees and more biomass than Neotropical forests that have lost their megafauna. For instance, mean aboveground biomass is 396 Mg ha^{-1} in Africa versus 289 Mg biomass in the Amazon, with more, larger, and denser trees in Africa (Lewis et al. 2013, Malhi et al. 2013). This may be due to floristic differences or due to elephants reducing the understory of the forest and allowing big trees to grow bigger (Terborgh et al. <<http://onlinelibrary.wiley.com/doi/10.1111/ecog.01641/abstract>>, <<http://onlinelibrary.wiley.com/doi/10.1111/ecog.01643/abstract>>). However, are bigger-seeded trees with higher wood density partially responsible for the increased biomass in African forests? We estimate that the reduction of large seeded fruit trees would have reduced wood density in the Amazon basin (assuming the seed sizes had similar frequency distributions before the extinctions) and therefore reduced total carbon content of the basin by $\sim 1.5 \pm 0.7\%$. Still, our estimated effect on wood density is too small to account for the large differences between African and South American forests and there are other mechanisms at work, such as the removal of the understory by megafauna allowing increased access of big trees to water and nutrients.

In conclusion, we find some empirical and theoretical support in the Amazon region for the controversial 'anachronism' theory of Janzen and Martin (1982) that the Late Pleistocene–early Holocene megafauna extinctions led to loss of dispersal ability and subsequent range declines in large-seeded tree species adapted to dispersed by large-bodied frugivores. This not only has strong implications for ecosystem function and biodiversity conservation, but also may have reduced the ability of the Amazon to sequester carbon. Our model simulations suggest that we may not yet have seen the full impact of the past extinctions on these processes. Forests globally are currently undergoing major defaunation (Dirzo et al. 2014) with multiple negative effects, with forest elephants and other large-bodied species

most vulnerable (Maisels et al. 2013, Ripple et al. 2015) and with strong declines in the remaining relatively large-bodied species throughout much of Amazonia (Peres and Palacios 2007). This study highlights how the implications of defaunation may go beyond traditional biodiversity conservation and toward the stability of the global ecosystem.

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Supplementary material (Appendix ECOG-01587 at <www.ecography.org/readers/appendix>). Appendix 1.