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Ecosystem engineers alter the evolution of seed size by impacting fertility and the understory light environment

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Abstract: It has been hypothesized that the extinction of the dinosaurs, and later the Pleistocene megafauna, created a darker forest subcanopy benefiting large-seeded plants. Larger seeds and their fruit, in turn, opened a dietary niche space for animals thus strongly shaping the ecology of the Cenozoic, including our fruit-eating primate ancestors. In this paper, we develop a mechanistic model where we replicate the conditions of tropical forests of the early Paleocene, with small animal body and small seed size, and the Holocene, with small animal body and large seed size. We first calibrate light levels in our model using stable carbon isotope ratios from fossil leaves and estimate a decrease of understory light of *c.* 90 μmol m^{-2} s^{-1} (a 19% decrease) from the Cretaceous to the Paleocene. Our model predicts a rapid increase in seed size during the Paleocene that eventually plateaued or declined slightly. Specifically, we find a dynamic feedback where increased animal sizes opened the understory causing negative feedback by increasing subcanopy light penetration that limited maximum seed size, matching the actual trend in angiosperm seed sizes in mid/high latitude ecosystems. Adding the ability of larger animals to increase ecosystem fertility to the model, further increased mean animal body size by 17% and mean seed size by 90%. Our model is a drastic simplification and there are many remaining uncertainties, but we show that ecological dynamics can explain seed size trends without adding external factors such as climate change.

Key words: ecosystem engineer, Cretaceous, Paleocene, evolution, body size, seed size.

THE world has gone through five mass extinction events and is currently going through a sixth (Barnosky *et al.* 2011). During such extinction events, large animals, which tend to have disproportionately greater ecosystem engineering effects, such as on vegetation structure and ecosystem fertility (Bakker *et al.* 2016; Doughty *et al.* 2016a) are replaced by smaller animals. Here we explore the evolutionary impacts of the loss of ecosystem engineering following the latest two extinction events, the dinosaur extinctions 66.02 Ma and the Pleistocene megafauna extinctions over the past 50 000 years. We begin with the evolutionary implications of the dinosaur extinctions and a hypothesis developed by Wing & Tiffney (1987). They hypothesized that large-bodied herbivores like dinosaurs would impact vegetation sufficiently that angiosperms during the Cretaceous were '*r*-selected' (small, fast growing and adapted to disturbance) and therefore had small seeds with few animal seed dispersers (Wing & Tiffney 1987). However, after the dinosaur extinctions, there was less forest disturbance and angiosperms became '*K*-selected' (large and slow growing) where both plant and animal size started small but gradually increased in size due to a coevolutionary relationship between seeds and their seed dispersers (Wing & Tiffney 1987). Eriksson *et al.* (2000) and Eriksson (2016) furthered this hypothesis by suggesting that plant species with large seeds were favoured post dinosaur extinction because without dinosaurs to disturb the forests, the understory light environment would be dark, which favoured bigger seed sizes (with larger energy reserves) due to their ability to grow taller to compete for light before requiring new photosynthates (Eriksson *et al.* 2000; Eriksson 2016). It is likely that the diversity of seed sizes, fruit sizes and fruit types expanded rapidly post dinosaur

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extinctions but possibly as early as 80 Ma then peaked *c.* 55–50 Ma, after which average seed size dropped. As seed size increased, the fleshy parts of the fruit also became more abundant (Eriksson 2016). A more recent review has found that this large post Paleocene increase in seed size may have been limited to angiosperms (not gymnosperms) and have been primarily limited to only mid to high latitude systems (Naware & Benson 2024).

Studies of animal extinctions and exclosure studies have many times demonstrated that large modern herbivores (e.g. African elephants) can transform their landscapes (Bakker *et al.* 2016). For example, in areas where all animals >5 kg were excluded from Kruger National Park, South Africa, aircraft data showed that woody cover increased *c.* 9% over *c.* 36 years (Asner *et al.* 2009; Davies & Asner 2019). This impact is mainly attributed to elephants, which can uproot >1500 trees/elephant/year (Duffy *et al.* 1999). At larger scales, the Pleistocene megafauna extinctions have also been shown to increase woody cover in several locations across the planet. For example, *Sporormiella* spores, indicative of megafauna presence, and present alongside pollen data, have been used to determine which came first: changing vegetation or megafauna extinctions (Gill *et al.* 2009). These spores show that vegetation change followed the extinction of the Pleistocene megafauna in North America (Gill *et al.* 2009) and Australia (Rule *et al.* 2012) rather than preceding it as had been previously thought. Similar results have been found in Siberia using DNA methods (Murchie *et al.* 2021). Following the extinctions, there were additional associated changes in the microbial communities (Murchie *et al.* 2023). One study found megaherbivore (>1000 kg) presence as an explanatory variable for indicating tree cover abundance in savanna ecosystems. With that result, they estimated that when the extinct megafauna were present in South America there would be lower woody cover with percentages similar to current African ecosystems (Doughty *et al.* 2016b). A similar result was found in another study showing that extinct megafauna can explain continental scale patterns in wood density, leaf size, spines and latex (Dantas & Pausas 2022).

Increases in the abundance of fleshy fruits led to an open dietary niche space and the evolution of many frugivore animal groups, including early primates (Sussman *et al.* 2013). However, much of the early diversification of angiosperms (*c.* 65–55 Ma) took place before the evolution of primates and other key frugivores such as birds or bats (Fleming & John Kress 2011; Eriksson 2016). Eriksson suggested that multituberculates (early mammals ranging in size from a mouse to a beaver, but now extinct) were the key seed dispersers in the post-K–Pg boundary rapid evolution phase of angiosperms. Recently, evidence has emerged indicating that birds may have consumed fruit earlier than we had previously known during this era (Hu *et al.* 2022). However, it is likely that many animal species began to disperse fruit at this time, because, as Janzen (1979) showed, most animal herbivore species will opportunistically consume figs (and probably most other fruit and seeds) with most animals being seed dispersers rather than seed predators (granivores). Since the start of the Cenozoic, consuming fleshy fruits has become an incredibly successful dietary strategy for many animals, while relying on animals as dispersal vectors (zoochory) has become similarly advantageous for plants. This mutualistic relationship has led 70–94% of woody species in tropical forests to be fleshy-fruited plants (Fleming *et al.* 1987) and most tropical animal species are at least partially frugivorous (Wilman *et al.* 2014; Jantz *et al.* 2024).

The rise in seed size may have opened evolutionary niche space for large bodied frugivores because larger animals can give a competitive advantage to large seeds by distributing them far from their mother tree and reducing density dependent mortality effects (the Janzen–Connell Effect) (Janzen 1970). For instance, forest elephants distribute 14% of the seeds they ingest >10 km (Blake *et al.* 2009) with similarly long distribution distances for many other large bodied, but now extinct animals (Pires *et al.* 2018). Defaunation of mainly larger bodied animals has led to a 60% decline in the ability of seeds to track climate change (Fricke *et al.* 2022). The passage through a megaherbivore gut creates large amounts of scarification of seed coats and increases germination (Rogers *et al.* 2021). Such relationships are likely to be widespread and Janzen & Martin (1982) suggested that many large fruits coevolved with now extinct large-bodied mammals. However, if there is a reciprocal relationship between large animals and large seeds, why have the 103 neotropical fruit tree species (Guimarães *et al.* 2008) that may have co-evolved with the now extinct Pleistocene megafauna not also gone extinct? Doughty *et al.* (2016c) found that these species had range declines of 26% and models suggest that they may eventually go extinct on timescales of *c.* 30 000 years (Doughty *et al.* 2016c). Range declines may have been greater except for some species (e.g. cacao/avocado) that found new human dispersers.

The loss of large-bodied dispersers may have also impacted seed sizes. For instance, a reduction in size distribution of the frugivores (such as toucans) reduced the seed size in a palm species (Galetti *et al.* 2013). There is currently a global positive relationship between fruit size and frugivore body size (Lim *et al.* 2020). Further back in time, during the early Cenozoic, there was also a rapid increase in mammal body size on every continent and across many different orders of animals that eventually leveled off after 25 million years (Smith *et al.* 2010). Increased fruit size may have been one small factor among many that contributed to the increased body sizes during this period since larger animals can competitively exclude smaller bodied animals from terrestrial resources (Abraham *et al.* 2023), and thus preferentially benefit from more fallen fruit resources. What drives maximum body sizes? Hypothesized reasons include 'pull factors' such as larger animals having lower relative energy requirements and longer ingesta passage rates, which allows them to use forage of lower quality and get more energy per unit of food ingested (Clauss *et al.* 2003). Alternately, a 'push factor' would be how large body size can help escape predation pressure (Owen-Smith 1988). Seed size and animal size eventually decoupled since seed size gradually decreased as animal size increased until early Miocene. This may be due to the diversification of megafauna diets after *c.* 40–50 Ma since the largest mammals became hindgut fermenters, adapted to large amounts of low-quality forage rather than energy rich fruits (Clauss *et al.* 2003).

The Wing and Tiffney hypothesis depends on dinosaurs having large impacts on forest structure, which has increasing empirical evidence. There are many studies showing dinosaurs occupying forest environments and displaying herd behaviour. For instance, Shillito & Davies (2019) studied 85 Lower Cretaceous (Berriasian–Valanginian) dinosaur footprints from 13 morphotypes from the Ashdown Formation of East Sussex, southern England. The dinosaurs tracks were grouped in a way that suggested herding behaviour because there were few tracks away from the main route (Shillito & Davies 2019). The vegetation of these floodplains included ferns, lycopods and gymnosperms. Gymnosperms with diameters greater than 35 cm and signs of dense roots were found near the tracks as were dinosaur footprints within 5 cm of fossilized plants >10 cm. Many current megaherbivores (e.g. elephants, giraffes, white rhinos) also form herds, walk along trails and impact vegetation structure (Berzaghi *et al.* 2023; Wang *et al.* 2023; Keany *et al.* 2024). It is hypothesized that dinosaurs also impacted forest structure across various habitats, but more records are found in floodplains because they are good for sedimentological preservation (McCarthy *et al.* 1998).

The hypothesis that large dinosaurs may have impacted forest structure is based on observations that compared plant diversity and structure across the K–Pg boundary in Colombia (Carvalho *et al.* 2021). They found several lines of evidence of more open forest understories in vegetation before the extinction of the dinosaurs and that closed-canopy tropical forests seem to appear for the first time shortly after the K–Pg extinction event. For instance, leaf vein length per area (VLA) post extinctions showed values similar to modern multi-stratal rainforests. Further, Graham *et al.* (2019) found that Cretaceous forests had stable carbon isotope ratios ($\delta^{13}C$) indicating an open canopy that promoted mixing of respired and atmospheric CO_2 and a small light gradient between the understory and the canopy (Graham *et al.* 2019). These independent lines of evidence suggest a more heavily vegetated forest understory with low light levels after the dinosaur extinctions (see Graham *et al.* (2019) for a more complete discussion of this).

We have also learned much about the understory tropical forest light environment. Seedling height in forest understories is a linear function of seed size with the smallest seeds leading to sapling heights after germination of *c.* 1 cm and the biggest seeds saplings of *c.* 36 cm with larger seeds surviving better in a dark understory and with each increase in $\mu mol\ m^{-2}\ s^{-1}$ of light survivorship increased by *c.* 0.5% (Baraloto *et al.* 2005). Trees can produce more small seeds than big ones, but seedling survival is a linear function of seed size so after accounting for similar energy expenditure per tree for seeds there is often not an advantage to many small seeds vs few big ones (Baraloto *et al.* 2005). Dinosaurs may have had similar impacts on forest light dynamics as humans do through selective logging of tropical forests and Fauset *et al.* (2017) developed a model in which vertical light levels were predicted as a function of logging intensity. Light levels can vary with 16, 9 or 2% of the top of canopy light in the bottom 1 m of tropical forest canopy in three different forests (Montgomery 2004). Overall, this detailed understanding of the understory light environment can help to parameterize models testing the Eriksson hypothesis (Eriksson 2016).

Another potential feedback in this process is how large animals are disproportionately important for fertilizing ecosystems since soil fertility impacts tree growth and fruit abundance. For instance in the Brazilian Amazon, a fivefold increase in soil phosphorus led to a fourfold increase in fruit abundance at the community scale (Doughty *et al.* 2014). Recent work has suggested that large animals are disproportionately important for diffusing nutrients across the landscape with a scaling exponent of 1.17 (a scaling exponent of 1 would indicate all animals are of equal importance on a weight basis) (Doughty *et al.* 2013; Wolf *et al.* 2013). This was tested empirically by comparing fossilized plants (coal records) between the Carboniferous (prior to the evolution of tetrapod animals) and the Cretaceous (with the largest terrestrial animals ever) which found increased Cretaceous concentrations of plant-important rock-derived nutrients (136%) and decreased spatial heterogeneity (22%) (Doughty 2017). Therefore, large animals can spread both seeds (Pires *et al.* 2018) and fertility (Doughty *et al.* 2016a) efficiently across the landscape. These results are especially interesting given the rapid increase in mammal body size following the dinosaur extinctions, which may be due to niche filling (Smith *et al.* 2010).

In this paper, we explore the transition from a bottom-up controlled system (light environment impacts seed size which impacts animal dynamics) to a system kept in equilibrium by the bottom-up (light environment) and top-down (animal disturbance and dispersal) control on seed size. Once animals have become big enough to engineer their ecosystems, only top-down control by human hunting, asteroid impacts or volcanic eruptions will reduce size again. If the top-down (large animal) disturbance control on vegetation and hence the light environment is maintained, seed size will eventually decrease as long as the animal sizes keep increasing. We show a conceptual diagram of these ideas in Figure 1. The extinction of the dinosaurs created a 'blank slate' on which these interactions could start from scratch. In fact, mass extinction events generally may allow us to test how the ecosystem engineering effects of animals affect evolution. However, because these relationships involve complex feedbacks, a mechanistic model parameterized with detailed understory light dynamics data is useful to test the hypotheses developed by Wing & Tiffney (1987) and Eriksson (2016).

We test the following two hypotheses:

H1: Detailed understory light and seed dynamics can explain how seed size developed and eventually stabilized over millions of years following the dinosaur extinctions.

H2: The impact of animal body size on fertility increases maximum seed sizes in ecosystems.

METHOD

Model

To understand the long-term interactions between angiosperm seed size, animal size and the understory light environment, we created an individual based model using Matlab v2022a (Mathworks) with a grid size of 50 × 50 cells (also tested at 100 × 100). Each grid cell was assigned an initial animal bodyweight of 1 kg and a seed size of

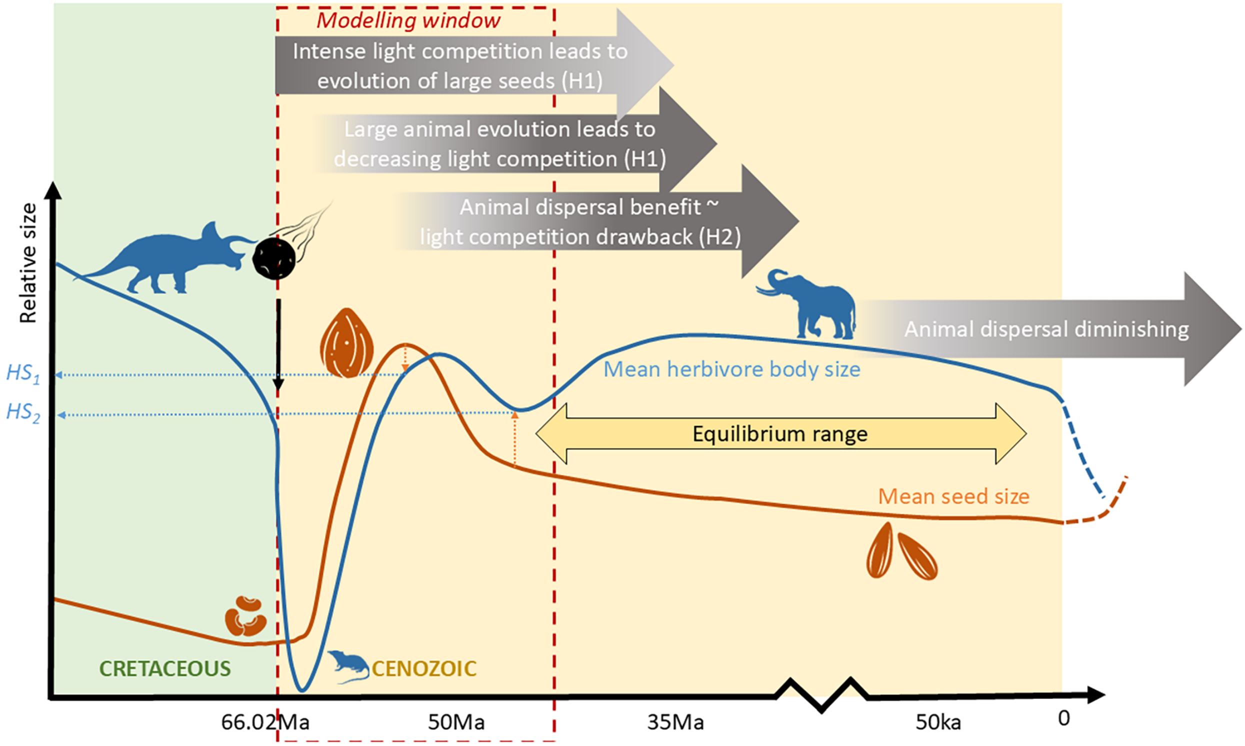

FIG. 1. Conceptual diagram of our hypotheses. Following the extinction of dinosaur megafauna 66.02 Ma, light competition for saplings increased tremendously leading to the evolution of large seeds able to establish taller saplings before relying on photosynthesis for energy (orange curve). Feeding on large fruit/seeds as concentrated energy sources opened the niche for large mammal evolution (blue curve). When animals reach a particular herbivore size (HS_1), animal disturbance leads to decreased light competition driving a decrease in seed size. When megafauna disturbance decreased to a certain level, the herbivore size will show a local minimum (HS_2) after which a dynamic equilibrium state with smaller fluctuations in seed will establish in our model. In reality, megafauna eventually diversified away from relying on large seeds for energy (e.g. proliferation of hindgut fermentation), and therefore their sizes started increasing again to reach a maximum sizes >10 000 kg around the Oligocene–Miocene transition. Animal sizes started decreasing substantially in the late Quaternary due to hunting and climate change, which may lead to renewed evolutionary pressure on large seed development (dashed lines) depending on continued human modification of the light environment. Silhouettes from Phylopic (http://phylopic.org: triceratops, elephant (CC0 1.0); shrew (Sarah Werning; CC BY 3.0)) and the Noun Project (https://thenounproject.com: meteor (Alex Muravev), small, intermediate and large seed icons (Soetarman Atmodjo, ji-na seo and Royyan Wijaya, respectively), all CC BY-3.0).

0.038 g to simulate the small seeds and animals present in the aftermath of the dinosaur extinction event (Smith *et al.* 2010; Eriksson 2016). We focus on fleshy reproductive organs such as angiosperm fruits not gymnosperm seeds because the fruit surrounding angiosperm seeds will attract dispersers more often. At each timestep, animal/seed mass is assigned based on randomly choosing a value within a distribution with a mean based on the animal/seed size from the prior timestep and a normally distributed standard deviation of 2/3 for plants/animals (also as 1% of body weight in a sensitivity study) with lower mass truncated at 0.038 g for seeds and 0.03 kg for animals (but no upper threshold). Trees can produce more small seeds than big ones, but seedling survival is a linear function of seed size (Baraloto *et al.* 2005). Therefore, assuming the same energy input per tree into seed mass regardless of seed size, increased numbers of seeds do not increase survivability (or vice versa) and we do not change number of seeds in each grid cell at each iteration. Based on the seed size for each grid cell, we calculate how tall the seedling (between 1 cm and no upper limit) will become based on the following equation (Baraloto *et al.* 2005) based on eight tropical trees species:

$$\text{Plant height (cm)} = 18.9 + 5.2 \times \log_n(\text{seed size}) \qquad (1)$$

Where plant height is measured in cm, and seed size in g ($r^2 = 0.95$, $p < 0.0001$). Next, we calculate understory light environment at the height of that seedling. To do this, we estimate the vertical light environment under a disturbance gradient using the results of a logging experiment from Brazil (Fauset *et al.* 2017) with the following equation:

$$T(H) = \alpha + \exp(k_z \times H) \qquad (2)$$

Where T is light transmission as a percentage of the top of canopy irradiance (2000 μmol m^{-2} s^{-1}) at height Z, α is T at 1 metre, and k_z is an extinction coefficient based on height above the ground (H). Fauset *et al.* (2017) used values of 2.5/6.2 for a and 0.190/0.213 for k_z for intact/selective logged forests. We used these same values but adapted them for animal induced disturbance. Since the Cretaceous understory was very open (Carvalho *et al.* 2021), we assumed animals reaching the size of sauropods (*c.* 10 000 kg; a median including several dinosaur size classes, not just the biggest) would mimic the impact of a ‘light logging’ event.

We explore this in Figure 2 using data from Ehleringer *et al.* (1986) relating light environment to δ^{13}C isotope ratios (Ehleringer *et al.* 1986). On this graph, we added the minimum δ^{13}C values from a Cretaceous forest compared to the minimum from a Paleocene forest (Graham *et al.* 2019). We justify using the minimum because it is unknown which part of the canopy the fossil leaves were from, but the understory will always be the darkest and that is the part of the forest of interest for our study. When we place the minimum values from each site into our equation, we estimate a change in light levels of 89.9 μmol m^{-2} s^{-1} (a 19% decrease from the Cretaceous to the early Paleocene) (Fig. 2). We therefore estimate the structural impact of an animal with a size of 10 kg in a grid cell using the coefficients of an unlogged forest (2.5/0.19) and an animal with a size of 10 000 kg with the coefficients of a selectively logged forest (6.2/0.213) with linear interpolation in between. For the fine scale light differences at the bottom metre of the canopy, we used data from Montgomery (2004) who found that light transmittance decreased from 16 to 9 to 2% in light in three tropical forests in Brazil, Panama and Peru between about 0 and 1 m height above ground surface (Montgomery 2004). Therefore, 1 m light levels are calculated using Equation 2 and below this, light decreases linearly to the ground by an additional 16% (also 2% and 9%). In a sensitivity study, we test all of these values and we also run a dynamic change model in which the larger the mean body size the more open the bottom metre is (toward 16%).

We then calculate the likelihood of sapling survival based on the height of the seedling and the light level at that height. Baraloto *et al.* (2005) found a significant positive relationship between light and survivorship for eight tree species that represent a range of seed sizes with a standardized regression coefficient of 0.14 after 5 years for all species (Baraloto *et al.* 2005). An increase in survivorship of 0.14 when light changed from 1.3% (50%) to 4.1% (95%) of full sun (assuming top of canopy maximum of 2000 μmol m^{-2} s^{-1}) means understory species ability to survive increased by 14% per 28 μmol m^{-2} s^{-1} increase or 0.5% per μmol m^{-2} s^{-1} increase. The light compensation point for photosynthesis can vary between species but one study found that it averages *c.* 10 μmol m^{-2} s^{-1} (Craine & Reich 2005), and Equation 3 gives 0% survival at 10 μmol m^{-2} s^{-1} and below:

$$\text{Survival} = (0.5 \times (\text{light level} - 10))/100 \qquad (3)$$

In a sensitivity study, we use a non-linear equation which will increase survival more greatly as lower light levels are increased:

$$\text{Survival} = (18.62 \times \log(\text{light level} - 10) - 15.61)/100 \qquad (4)$$

At each timestep, the seed will replace the seed size of the previous iteration if survival is greater than a random number between 0 and 1; if not, the old seed size will remain. As understory light levels increase, we assume that the more numerous smaller seeds will begin to outcompete the bigger seeds with a 50% chance of a 5-fold decrease in seed size between light levels of 75 and 100 μmol m^{-2} s^{-1}, a 75% chance of a 10-fold decrease in seed size between 100 and 150 μmol m^{-2} s^{-1}, and a 95% chance 20-fold decrease in seed size above 150 μmol m^{-2} s^{-1} (varied in a sensitivity study; Table 1).

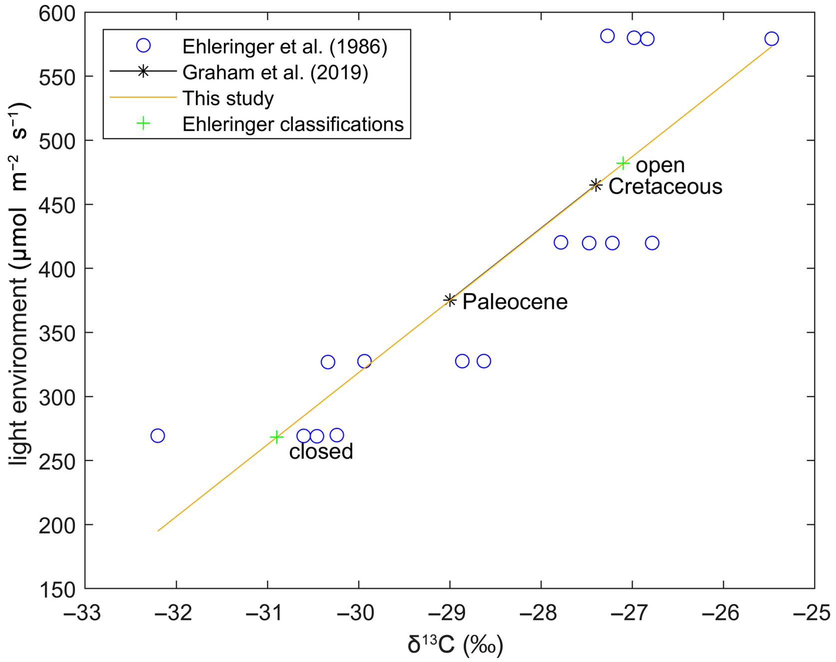

FIG. 2. The δ^{13}C values (‰) (*x* axis) from four plant species in blue circles vs the understory light environment (*y* axis) using data originally from Ehleringer *et al.* (1986). On this graph, we fit a linear model and using that model estimated understory light levels for isotopic data from the Cretaceous and the Palaeogene (black stars). We also show forest classifications of ‘open’ and ‘closed’ (green +) from Ehleringer *et al.* (1986).

Larger animals will competitively exclude smaller animals for access to terrestrial resources (Abraham *et al.* 2023) and based on this, in our model, we allow larger bodied animals primary access to fruit (Gautier-Hion *et al.* 1985). We allow for the evolution of larger bodied animals in the model over time to replicate the dramatic increase in animal body size of the Paleocene (Smith *et al.* 2010). The edibility of the seeds by frugivores is based on oesophagus size, which we assume is linearly related to animal size with the equation (Doughty *et al.* 2016b):

$$\text{Oesophagus size (cm)} = 0.0027 \times \text{M} + 1.734 \tag{5}$$

where M is body mass (in kg). If the seed in the grid cell is too small then it is ill suited for that animal and, in the cell, the animal will be replaced by a smaller one (if seed is between 3 and 6 times smaller than the throat, the current animal will be replaced by an animal 4.5 times smaller, between 6 and 12 times size of throat, an animal 9 times smaller, and less than 12 times the size of the throat, an animal 20 times smaller). If the seed size is too big to be consumed, then we assume that it will not succeed and will be replaced by the average seed size of all touching pixels. We estimate mammal movement of seeds using equations from Wolf *et al.* (2013):

$$\text{Day range (km/day)} = 0.453 \times \text{M}^{0.368} \tag{6}$$

$$\text{Passage time (days)} = 0.29 \times \text{M}^{0.26} \tag{7}$$

$$\text{Linear distance moved (km)} = \text{Day range} \times \text{passage time} \tag{8}$$

Based on the above equations, we separate animal size into three categories (below 5 kg, between 5 and 50 kg, and above 50 kg; these numbers are varied in a sensitivity study in Table 2). Animals the size of 5 kg or less access only the grid cell they are in. Between the sizes of 5 and 50 kg animals can access neighbouring grid cells (3×3) and above 50 kg can access 5×5 grid cells. We assume each grid cell is *c.* 0.25 km^2, or the approximate maximum distance across which a 5 kg mammal could spread a seed (0.5 km). The animal will spread the seeds into the neighbouring cells (with 75% probability, varied in a sensitivity study; Table 2) if the seed can fit in the animal’s throat but is not less than 3–12 times (explained above) smaller than can fit since such small seed/fruit may not interest large animals. If the animal replaces the seed in the grid cell, it will also replace any smaller (but not bigger) animal present in the grid cell. This replicates how larger bodied animals will often competitively access resources at preferential times over smaller bodied animals (Abraham *et al.* 2023). The understory light environment is based on the size of the animal in the grid cell following Equation 2. An animal is less likely to disperse

TABLE 1. Plant coefficient sensitivity studies: percentage change in model results for 500–1000 averaged time steps for mean seed size and understory light environment when individual parameters are changed.

Parameter changed	Seed size	Light environment
No light dynamics[1]	−100	−36
Light penetration (2% or 16%)[2]	−10/10	0/−1
Dynamic change on[3]	−25	−4
Non-linear[4]	4	1
Eqn 1: Seed size to plant height ratio (3 or 7)[5]	−20/2	−4/−1
Eqn 2: Extinction prediction parameter, k_z (0.000023 or 0.00000023)[6]	−14/−7	1/−3
Eqn 2: Extinction prediction parameter, a (0.000037 or 0.0037)	347/−95	−26/118
Grid size 100 × 100[7]	19	6

[1] Remove the ability of bigger seeds to access more light.

[2] Change light penetration of the bottom metre of the forest from 2 to 16%.

[3] Dynamic change turned on; a dynamic change model where the larger the mean body size the more open the bottom metre is (from 2% toward 16%).

[4] We use a non-linear equation (Eqn 4) which will increase survival more greatly as lower light levels are increased.

[5] Change slope of Eqn 1 (Baraloto *et al.* 2005), dictating seed size to plant height ratio from 3 to 7.

[6] Change parameters k_z and α in Eqn 2 (Fauset *et al.* 2017) from 0.00000023 to 0.000023 and from 0.0037 to 0.000037 respectively.

[7] Increase grid size from 50 × 50.

a seed further away (i.e. 2 grid cells vs 1), but nearby cells will have higher density dependent seed mortality, and therefore, our model gives seeds in both near and far pixels the same success probability (75% but varied in a sensitivity study; Table 2). We recognize the key role of birds in dispersing seeds, but the focus of this study is only mammal frugivores.

Fertility

We then explored the implications of how changing animal body size could impact fertility. Larger body size can increase fertility at continental scales over millions of years (Doughty 2017). Here we expand that work to show nutrient diffusion capacity for the last 100 million years in greater detail. We first calculate nutrient diffusion capacity (Doughty *et al.* 2013; Wolf *et al.* 2013) for the last 100 million years based on the largest bodied animal in each time period using data from (Smith *et al.* 2010; Benson *et al.* 2014). We then compare this to coal (fossilized leaves) chemistry data from COALQUAL (CQ20166334750) (Palmer *et al.* 2015) for three time periods: the Cretaceous (N = 680), Cretaceous–Tertiary (N = 4), and the Palaeogene–Neogene (labelled Tertiary in COALQUAL) (N = 911) for the critical plant nutrients P, K, Mg and S as a ratio following the methodology from Doughty (2017). K is excluded due to its absorption during clay formation (Kumari & Mohan 2021), hence concentrations of K in coal cannot be expected to show good correlation with general plant availability. Cretaceous–Tertiary coal is mainly from the Chuckanut Formation which began *c.* 54 Ma. We compare these data to aluminium content, a proxy for abiotic rock weathering. We use the exact data and methodology from Doughty (2017).

We then explore how the relationship between body size and fertility might impact seed and understory light dynamics. To do this, in our model we make fertility an

TABLE 2. Animal coefficient sensitivity studies: model results for averaged time steps 500–1000 for mean seed size and mean understory light environment changing one parameter from our standard parameterization (averaged over three simulations) with the percentage change in the model result.

Parameter changed	Seed size	Light environment
No animal spread of seeds[1]	−98	−36
Seed swallowability slope (0.00027 or 0.027)[2]	−89/5394	−23/−15
Ratio of cells animals can spread seeds (0.95 or 0.5)[3]	−4/−15	0/−3
Seed size too small to be consumed (6 or 30 g)[4]	22/72	−12/−32
Animal size threshold to spread seeds (2 or 20 kg)[5]	4/6	1/−1
With fertility[6]	90	6
Mid-Cretaceous start[7]	−100	49
Future forests (151 or 1 µmol m^{-2} s^{-1})[8]	−60/−9	71/−2

[1] We remove the ability of animals to move seeds into neighbouring cells.

[2] Change the slope in Eqn 4 for seed swallowability from 0.0027.

[3] Change the probability of larger animals spreading seeds into outer cells from 95 to 50%.

[4] Change seed size too small to be consumed by animals between 6 and 30 g.

[5] Change the animal size threshold to spread to other cells between 2 and 20 kg.

[6] Turn on larger animals increasing fertility.

[7] Start simulation with large animals (10 000 kg) and small seeds.

[8] Start simulation with small animals (10 kg) but different understory light environment (1 or 151 µmol m^{-2} s^{-1}).

increasing function of average body size and then fertility can impact seed size because seed standard deviation is a function of fertility. We varied seed standard deviation between 1 and 2; as the mean body size increased towards 5000 kg the seed standard deviation moved closer to 2. Increased mean body size increases fertility which allows seed size to potentially get bigger but does not preferentially choose bigger seeds. We acknowledge that there is little empirical data to support the direct relationship between fertility and standard deviation of seed size, but fertility generally increases fruit abundance with, for instance, a fivefold increase in soil phosphorus, leading to a fourfold increase in fruit abundance (Doughty *et al.* 2014).

Simulations

With the above described model, we simulate three scenarios: Early Paleocene where we start with animal size = 1 kg, seed size = 0.038 g, light environment = 1 μmol m^{-2} s^{-1}; future scenario 1 where we start with animal size = 10 kg, seed size = 100 g, light environment = 1 μmol m^{-2} s^{-1}; and future scenario 2 where we start with animal size = 10 kg, seed size = 100 g, light environment = 150 μmol m^{-2} s^{-1}.

To test why seed size may have differed across the K–Pg boundary between low and higher latitude ecosystems, we add a temporal climate variability aspect to our model. In our model, in mid to high latitude systems (Naware & Benson 2024), on even time steps the standard deviation of potential seed size is three, and on odd steps it is 1. For low latitude systems, the standard deviation (SD) is always 2. This replicates the greater variability inherent in mid/high latitude systems which might vary between good years (SD = 3) and bad, more conservative years (SD = 1).

Datasets

We used isotopic data from Ehleringer *et al.* (1986) and from Graham *et al.* (2019) to predict understory light differences. We used data from Baraloto *et al.* (2005) to establish relationships between seed size, height and survivability under different light conditions. We used results from Fauset *et al.* (2017) to predict vertical light profiles along a disturbance gradient and results from Montgomery (2004) to predict light profiles in the bottom metre of the canopy. We used data from COALQUAL (CQ20166334750) (Palmer *et al.* 2015) to show elemental differences between time periods following the methodology from Doughty (2017).

RESULTS

Variation in carbon isotope ratio values ($\delta^{13}C$) along an irradiance gradient (Ehleringer *et al.* 1986) showed a significant ($p < 0.001$) positive relationship ($r^2 = 0.75$) (Fig. 2) where light levels increased by 56 μmol m^{-2} s^{-1} per unit increase in $\delta^{13}C$. We used this linear relationship to estimate the change in understory light levels between a Cretaceous and a Paleocene forest (Graham *et al.* 2019) and found that the lowest light leaves (which we estimate to be the understory) in the Cretaceous forests had 89.9 μmol m^{-2} s^{-1} more light (a 19% decrease from the Cretaceous to the Paleocene) than Paleocene forests (Fig. 2). The Ehleringer *et al.* (1986) study also classified forests as 'open' or 'closed' and we adding these classifications to Figure 2 shows that the $\delta^{13}C$ levels of the Cretaceous are close to the 'open' forest type and the Paleocene forests are closer to the 'closed' forest type (Fig. 2). We then compared those estimates of changing light levels to our model that uses animal body size to determine the understory light environment. We found that switching between a forest with a maximum animal size of 10 kg to one with a 10 000 kg animal will increase understory light levels by 75 μmol m^{-2} s^{-1} at *c.* 1 m elevation above the surface, slightly lower than the 89.9 μmol m^{-2} s^{-1} estimated in Figure 2. Our model further estimates that sapling survivorship will increase by 0.5% per μmol m^{-2} s^{-1} increase in light (Baraloto *et al.* 2005) and a light level increase of 75 μmol m^{-2} s^{-1} will increase seedling survivorship by 37.5%.

We used a seed size of 0.038 g (varied in Fig. 3) to begin our simulations (the smallest seed size in the Baraloto *et al.* (2005) dataset) which will lead to a sapling height of *c.* 1 cm that can access 56 μmol m^{-2} s^{-1} light in a dense understory (animal size 10 kg). A seed size of 28 g will lead to a sapling height of 36 cm (Baraloto *et al.* 2005) which can access 63 μmol m^{-2} s^{-1} of light. Therefore, increasing seed size from 0.038 to 28 g in a dense understory will increase light available by 7 μmol m^{-2} s^{-1} and increase survivability of that sapling by 3.5% (Fig. 3). This result depends on the understory light changes in the bottom metre of the canopy where light levels can change by 2, 9 and 16% over the bottom metre (between 1.7 and 0.7 m) which will change light accessed by changing seed size between 0.038 and 28 g by 1, 4 and 7 μmol m^{-2} s^{-1} respectively (Table 1).

Animal driven movement of seeds is a function of animal day range and gut length both of which can be predicted with body size (although individual species can vary quite substantially in this relationship) (Abraham *et al.* 2021). For instance, on average, we might expect a 5 kg animal to linearly move a seed 0.36 km, a 50 kg animal will move a seed 1.5 km and a 500 kg animal will

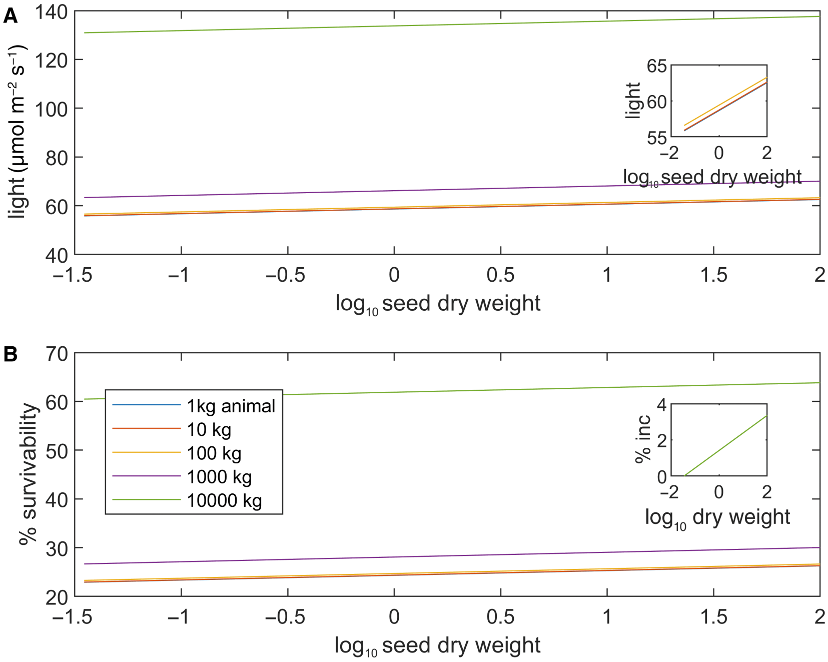

FIG. 3. A, the relationship between $\log_{10}$ seed dry weight and predicted understory light environment at the sapling height as a function of largest body sized animal (kg) in the ecosystem; the inset is an enlargement of animal sizes 1–100 kg. B, the relationship between $\log_{10}$ seed dry weight and predicted survivability at the sapling height as a function of largest body sized animal in the ecosystem; the inset shows the change in survivability based on $\log_{10}$ seed dry weight.

move a seed 6.5 km following Equations 6–8. Because our model is gridded, it is difficult to approximate this behaviour exactly, but we instead used size thresholds (<5 kg, between 5 and 50, and greater than 50 kg) that can allow animal access to different numbers of cells (we modified these thresholds in a sensitivity study starting with 2 and 20 kg; Table 2). As animals reach 50 kg, they can access 25 grid cells (5 × 5) and in each, they can spread larger seeds (with a probability of 75% varied between 50 and 95% in Table 2). However, as body size and larger seeds spread, so does an understory light environment that diminishes the competitive advantage of the larger seeds. For instance, as animal size exceeds 3500 kg, light into the understory begins to exceed 75 μmol m^{-2} s^{-1} for even the smallest saplings (1 cm tall) which then compete effectively with the larger seeds thus diminishing the large seeds' advantage. At an animal size of 1 kg (our simulation starting point), a seed size of 0.038 g will have access to light levels of 56 μmol m^{-2} s^{-1} compared to 131 μmol m^{-2} s^{-1} with a seed size of 0.038 g if an animal 10 000 kg is present, which will increase survivorship by 38% but reduce the competitive advantage of the larger seeds (a 75% chance of a 10-fold decrease in seed size).

We then simulated the post dinosaur extinction environment starting with small seeds (0.038 g) and body sizes (1 kg) (Fig. 4). Seeds can get either bigger or smaller at each timestep, but initially, the dark understory gives a competitive advantage to larger seeds (when this competitive advantage is removed seeds do not get bigger; Table 1). Larger fruits are consumed by larger bodied animals that can swallow larger seeds. We find a linear increase in seed size and understory light environment until the understory light environment starts to exceed an average of *c.* 75 μmol m^{-2} s^{-1} light when large animal size exceeds *c.* 3500 kg (Fig. 4). This then leads to a decrease in the success of large seeds as smaller seeds start to outcompete them. This causes an asymptote in body size as larger animals begin to be outcompeted by smaller animals due to the smaller seeds. This further reduces the large animal impact on understory light environment which shifts the competitive advantage back towards the larger seeds. We start to see a cyclical pattern in seed size going from small to large and back again. Figure 4 shows grid average and maximum, but the spatial patterns (Fig. 5) of the final grid show spatial dynamics as well. For instance, once animal size exceeds 3500 kg there are spatial areas where small animals and small seeds exist alongside patches of large animals with large seeds and many dynamic changes between them. Plotting animal size vs seed size (Fig. 5C) shows that seed size changed first, demonstrating seed size driving the dynamic.

Our simulation shows similar patterns to actual seed size for the Cenozoic in Figure 6 which shows data from Smith *et al.* (2009), Eriksson (2016) and Naware &

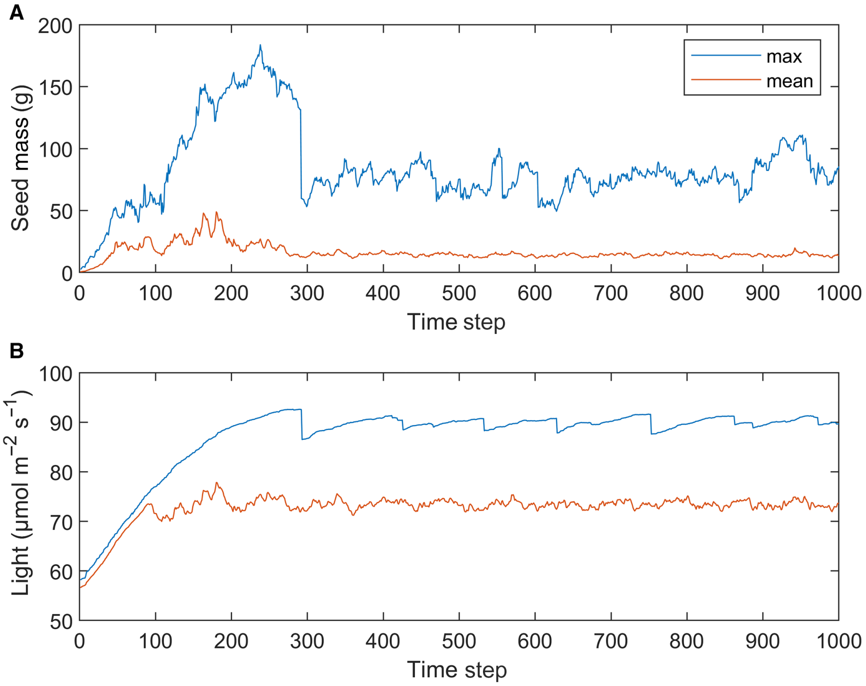

FIG. 4. A, seed size as grid mean (red) and maximum (blue). B, understory light environment as grid mean (red) and maximum (blue). Starting with animal size of 1 kg and seed size 0.038 g.

Benson (2024). Figure 6 shows several orders of magnitude increases in both seed and mammal body size over the first few million years of the Paleocene (but not for gymnosperms). Seed size started at *c.* 0.2 mm^3 at *c.* 67 Ma (overlapping with the K–Pg extinction event) and then peaked at *c.* 52 Ma at 107 mm^3, a three order of magnitude increase over 15 million years. Mammal body size showed similar rapid growth with the largest mammal at 3 kg *c.* 70 Ma but growing to *c.* 5000 kg *c.* 43 Ma, a similar order of magnitude increase to seed size over *c.* 17 million years. Seed size peaked at *c.* 52 Ma and then declined, while mammal body size increased more incrementally by increasing to 14 000 kg *c.* 30 Ma and then decreasing to *c.* 6000 kg *c.* 5 Ma. This is a similar fluctuation pattern to what we see in our simulations for seed sizes (Fig. 4). We then tested whether the increased temporal variability inherent in mid/high latitude systems could impact this result (to better understand the Naware & Benson 2024 results) and found that increased temporal variability (common to mid/high latitudes) slightly, but significantly ($p < 0.001$), did increase mean seed size (14.5 g vs 15.8 g) relative to more stable systems.

We make a number of assumptions in our model that we tested in sensitivity studies (Table 1 for plant coefficients; Table 2 for animal coefficients). Removing the ability of larger seeds to benefit from increased light resulted in no size increase in seeds. Reducing the light transmission in the bottom metre from 16% to 9% reduced mean seed size by 10% because a denser understory increases the competitive advantage of large seeds which also increases the competitive advantage of the largest seed consumers. Allowing larger animals to have a dynamic larger impact on the lowest understory light levels reduced animal size by 14% and seed size by 25%. Likewise, increasing the slope of the seed size from Equation 1 (Baraloto *et al.* 2005) to sapling height from 5 to 7 reduces seed size by 20% because taller saplings reduces the benefit of larger seeds. Increasing the value of α (transmission at 1 m above ground) in Equation 2 (Faucet *et al.* 2019) from 0.00037 to 0.0037 greatly increases the understory light environment by >100% and thus reduces seed size by 95%. Overall, it seems robust that increasing light levels at the lowest levels of the canopy reduce predicted seed size. Removing the ability of larger animals to spread larger seeds resulted in no size increase in seeds (Table 2). Increasing the point when seed size is too small to be consumed and thus for animals to spread seeds, from 3 to 30 increased seed size by 72% because the bigger animals could outcompete smaller animals for seeds more often. Increasing the slope (Eqn 4) of the animal's ability to swallow seeds by an order of magnitude greatly increasing seed size (5394%). Reducing the likelihood that animals can spread seeds into outer cells from 75 to 50% reduced seed size by 15%. Increasing the animal size threshold to spread seeds from 5/50 to 20/200 kg had only a minor impact on seed size. Hence, the model

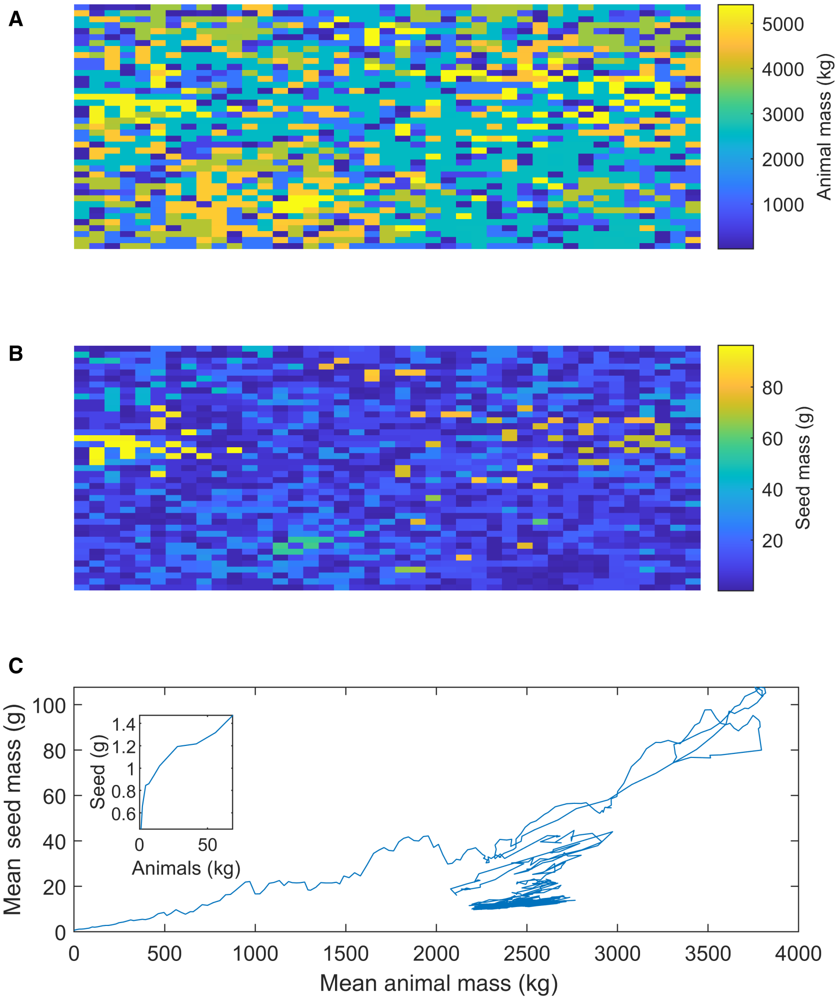

FIG. 5. The spatial dynamics in a 50 × 50 grid of animal mass (A) and seed mass (B) where we start with animal mass of 1 kg, seed mass 0.038 g at the end of a simulation. C, plot of mean animal mass vs seed mass for one run for the first 10 steps (inset) and the full 1000 steps.

is sensitive to the assumed animal impacts, strengthening the hypothesized relationship between animal and seed size mediated by light.

We then explored the implications of how changing animal body size could impact fertility, seed growth and understory light environment (Fig. 7). Following Doughty (2017), we present our results relative to a Cretaceous value of 1 for the bio-important elements, Ca, Mg, S and P (mean ± standard deviation) compared with the non-bio-important element Al. We assume that Al will represent abiotic elemental movement or weathering rate. For full justification of this methodology please see Doughty (2017). We find that the averaged ratio of the bio-important elements decreases to 0.52 ± 0.31 during the Cretaceous–Tertiary and 0.82 ± 0.15 during the Tertiary compared to the Cretaceous values (Fig. 7). Aluminium, which is not transported biotically but is reflective of abiotic movement, increases to 1.43 during the Cretaceous–Tertiary and then to 1.15 during the Palaeogene–Neogene. This result suggests that smaller mean body size reduced the availability of elements important for biology relative to baseline weathering and compares well to our animal diffusion capacity based on declines in body size which decrease to 0.49 *c.* 54 Ma and 0.87 *c.* 30 Ma compared to the Cretaceous animal diffusion capacity (Fig. 7). We then incorporated fertility into our simulations by allowing more fertile cells to have a higher seed standard deviation, following the logic that more fertile regions have higher fruit abundance in wet years (but not dry years). Comparing these simulations with our standard model, we found mean seed size increased by *c.* 90%. Therefore, adding the ability of animals to fertilize the landscape increased maximum seed size.

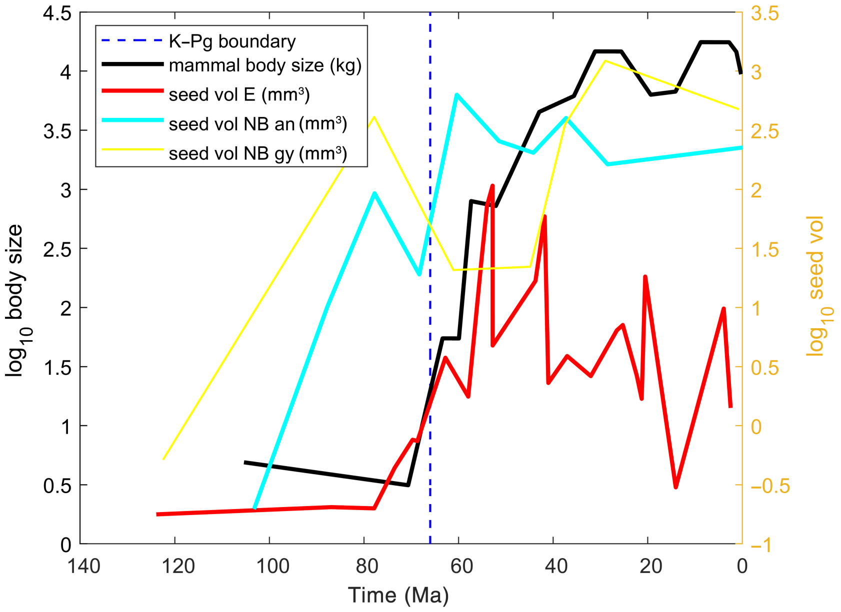

FIG. 6. Log_{10} maximum mammal body mass from Smith *et al.* (2010) (black) and $\log_{10}$ average seed volume from Eriksson (2016) (red; E), Naware & Benson (2024) angiosperms (cyan; NB an) and gymnosperms (yellow; NB gy). The blue vertical stippled line is the K–Pg boundary.

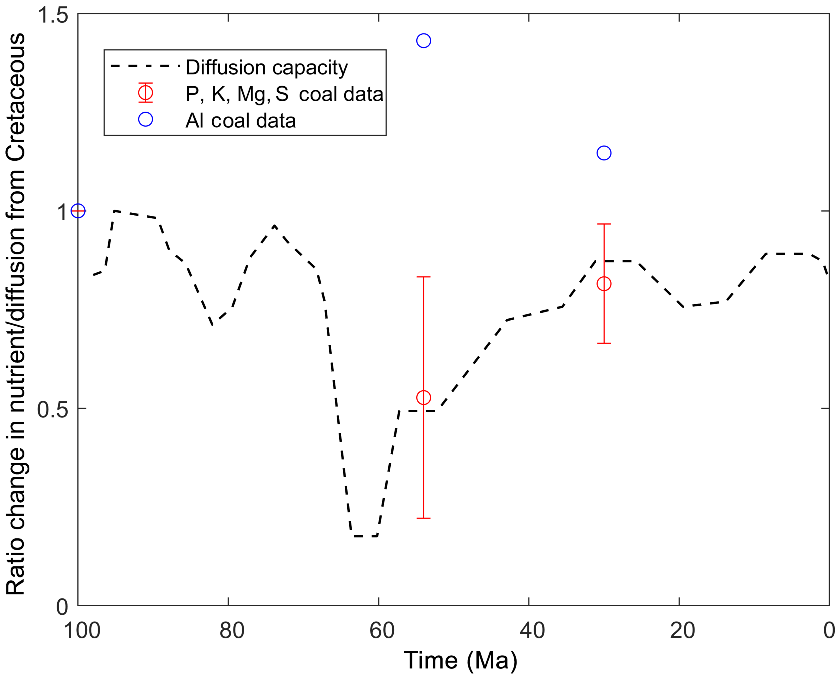

FIG. 7. Estimated availability of bio-important nutrients from the mid-Cretaceous into the Cenozoic for nutrient diffusion capacity based on the largest animal size from each period. Data from COALQUAL (CQ20166334750) for three time periods (Cretaceous (N = 680); Cretaceous–Tertiary (N = 4); and Palaeogene–Neogene (N = 911)) for the critical plant nutrients P, K, Mg and S as a ratio following the methodology of Doughty (2017). K is excluded due to its absorption during clay formation (Kumari & Mohan 2021), hence concentrations of K in coal cannot be expected to show good correlation with general plant availability. The standard deviation is the ratio differences between P, K, Mg and S. Blue dots are aluminium, a proxy for abiotic rock weathering.

Given the order of magnitude decline in body size over the last 50 000 years, our current forests have small mean animal size but large seed size which is a remnant of an era when larger animals existed (Janzen & Martin 1982). We simulated this scenario by starting with a body size of 10 kg and seed size of 100 g but ran two possible simulations, one with understory light at 1 μmol m^{-2} s^{-1} and another that started at 151 μmol m^{-2} s^{-1}. The low light scenario simulates the forest with no large animal impact while the high light scenario simulates humans selectively logging the forest. Another interpretation for the two scenarios is the world as if people went extinct vs a future where people selectively log forests into the distant future. Both scenarios take longer to reach steady state (*c.* 3000 model steps) but in the scenario with light levels at 151 μmol m^{-2} s^{-1}, seed sizes were *c.* 60% lower than baseline simulations; starting at 1 μmol m^{-2} s^{-1} resulted in seed sizes ending up close to the baseline (Table 2).

DISCUSSION

Large animals are ecosystem engineers that can impact forest structure and increase the amount of energy that can arrive in the subcanopy of a forest. In this paper, we create a mechanistic model to test hypotheses developed previously (Wing & Tiffney 1987; Eriksson 2016) that the change in the understory light environment impacted the trajectory of the evolution of plants and their seed sizes in the Cenozoic. Our model suggests that the initial dark understory at the start of the Cenozoic (Fig. 2) led to increased seed size (Fig. 4). However, we suggest an additional, negative feedback on this process. Animal size increased rapidly during this same period thus opening the understory, reducing the competitive advantage of large seeds/fruits and consequently decreasing the advantage of the large animals. Adding this additional negative feedback helps our results match the data better where there is a rapid increase in seed size followed by an upper limit on seed size (Figs 4, 6).

We have confidence in our model results because it matches the data shown in Figure 6. In Figure 6, data from the past 100 million years shows mammal mass increases from 3 to *c.* 4500 kg over 27 million years and seed volume increases from 0.4 to 72 mm^3 over 19 million years following the K–Pg dinosaur extinction. We do not specifically define the timesteps of the model but consider them akin to evolutionary time of many tree generations (*c.* 10 000 years/timestep), so a 1000 step simulation would approximate *c.* 10 million years. Therefore, the rate of change in seed mass over time from Galetti *et al.* (2013) was $((11.4 - 10.8\text{ g})/10.8\text{ g})/100\text{ years} = 6 \times 10^{-4}$ g/year vs the rate of change in seed mass over time from our model at $((200 - 0.038\text{ g})/0.038\text{ g})/10\,000\,000\text{ years} = 5 \times 10^{-4}$ g/year (Fig. 4) vs the rate of change in seed volume over time from Eriksson at $((72 - 0.4\text{ mm}^3)/0.4\text{ mm}^3)/19\,000\,000\text{years} = 1 \times 10^{-5}$ mm^3/year (Fig. 6). Overall, our model compares well to Galetti *et al.* (2013) and the actual seed size changes during the Cenozoic.

Seed size decreased close to the end of the Eocene (*c.* 33 Ma) (Fig. 6). An emergent property of our model can explain these decreases in seed size without outside forcing because large animals increase the understory light environment. However, during this period there were also large changes in global climate that could drive a reduction in seed size. A cooler, drier world decreased the extent of tropical forests (Morley 2011) and led to more open, patchier landscapes (Graham 1999). In addition, many groups of smaller, flying frugivores evolved during this period since flight is an advantage to access resources in a patchy landscape (Fleming & John Kress 2011; Eriksson 2016). Such small flying frugivores could distribute smaller seeds farther than larger terrestrial animals, potentially increasing the advantage of the smaller seeds that evolved during this period. These climatic and biodiversity changes could also affect seed size.

Our model also better replicates the greater variability in seed size vs animal size from Figure 6. Large animals' bigger home range adds connectivity to ecosystems (and our model) which can homogenize the landscape once they become dominant, and hence explains the lower variability in mean animal mass vs seed mass. This also explains the decrease in seed size following the peak since seed size is more prone to greater peaks and troughs in the model. A time series for seed size through the Oligocene specifically in tropical forests could help to resolve this question.

Recent evidence has shown that more energy flows through semi-open logged rainforests compared to closed-canopy old-growth forests which increases the productivity of both plants and animals in the logged forests (Malhi *et al.* 2022). More energy in the understory both increases understory plant growth but also the palatability of this forage as it selects for fast growing species with fewer defence compounds. At evolutionary timescales, this dynamic will give a competitive advantage to larger animals capable of consuming forage of lower nutritional value than fruits, such as leaves (a feedback not currently incorporated into our model). This is another potential explanation for the divergence in seed and animal sizes towards the end of the Eocene as larger animals had a competitive advantage in low quality forage and would not have been as dependent on fruit. Evidence is mounting that many ecosystems were more open, light-rich and disturbance-adapted before humans took over the landscapes, and mega-herbivores remain a prime candidate as a main disturbance agent (Pearce *et al.* 2023, 2024). Our study confirms the importance of including large herbivore-driven ecological dynamics into models to correctly understand long-term processes leading to our current vegetation structure and composition.

Recent results by Naware & Benson (2024) show an increase in seed size in low latitudes but not at high latitudes and we used our model to investigate whether the greater climate variability inherent to high/mid latitudes relative to low latitude could impact those results (Naware & Benson 2024). In mid/high latitude systems, each time step varied between a narrow distribution of seed sizes (SD = 1) and a wide distribution (SD = 3), while in low latitude systems, the distribution was always the same (SD = 2). We found that greater temporal variability led to a small, but significant increase in seed size and understory light environment which matches the direction of the Naware & Benson (2024) results of little change in angiosperm seed size across the K–Pg boundary in low latitude systems but a change in mid/high latitude systems. Trees in low latitude systems in our model always have a semiconservative strategy, while trees in mid/high latitudes with more variable climates will have conservative strategies (holding on to resources) in bad years and liberal strategies (allocating resources) in good years. The model results suggest that the trees with liberal strategies are rewarded with seeds spread widely while the trees with the conservative strategy are simply replaced. Thus, the pace of change for seed size and light environment is faster where variability is greater. However, the difference in our model results is small relative to what was found by Naware & Benson (2024), and there are probably many other explanations for these results (for example, the Erikson hypothesis may be wrong). More broadly, a simple mechanistic model like ours can quickly and easily suggest empirical datasets to find and test. For instance, in this case our results suggest that datasets relating climate variability and seed size distribution could be useful in addressing this question in the future.

Large animals may increase the dispersal of limited nutrients across the landscape, thus making them more available (Wolf *et al.* 2013; Doughty *et al.* 2016a; Enquist *et al.* 2020). Here we use the data and methods from Doughty (2017) (i.e. looking at plant nutrient distributions in coal deposits) to show that fertility dropped by half after the dinosaur extinctions and then recovered to *c.* 80% of the fertility of the Cretaceous during the mid-Cenozoic (Fig. 7). We integrated increased fertility with body size into our model by making the standard deviation of the seed size a function of total animal size. The increased proxy fertility allowed for (but did not mandate) larger seeds. The outcome of adding fertility was to increase the upper limit attained for seeds by 90%. More fertile soils increase fruit abundance (Doughty *et al.* 2014) leading to ‘fruiting lawns’ (Villar *et al.* 2021), but it is not clear over evolutionary time whether more fertile soils would lead to larger seeds and fruits. However, if larger seeds are more successful than small seeds, then evolution will be in this direction. Yet, without further data this relationship is still speculative.

Over the last 50 000 years there has been another drastic decrease in mean body size that rivals that of the extinction of the dinosaurs. For instance, the mean size of animals >10 kg throughout South America dropped from 843 to 81 kg, with similar trends across the planet (Barnosky *et al.* 2004; Doughty *et al.* 2013). Our model suggests that over periods of millions of years, similar long-term ecological dynamics will occur as less subcanopy light eventually encourages larger seeds and bigger bodied animals (Table 2). However, humans have taken over certain roles of the now extinct megafauna (Doughty 2013) such as our own propensity to remove trees, and human induced selective logging may increase the understory light environments and therefore reduce evolutionary pressure for bigger animals in forest ecosystems to re-evolve. Under this scenario, our model suggests that future seed and body size could be reduced by *c.* 60% (Table 2). It is clearly extremely speculative to predict human behaviour into the distant future, but our two scenarios may represent two endmember scenarios for humanity – human extinction or long-term sustainable extraction of resources.

CONCLUSION

In this paper we have explored the hypotheses of Wing, Tiffney and Erikson about relationships between animal sizes, light levels and seed size by developing a mechanistic model which predicts a Paleocene rapid increase in seed size that eventually plateaued or declined. The dynamics presented in this model would also function moving forward in time since over the past 50 000 years, we have experienced another order of magnitude decline in wild animal body size in most ecosystems.

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Author contributions. CED, JAK, AJA conceived of the study. CED wrote the first draft, wrote the model and did the analysis. JAK created Figure 1. All authors reviewed and edited the manuscript.

DATA ARCHIVING STATEMENT

All code and data to make all figures is available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.931zcrjw4.

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