Scaling animal impacts on dispersal and structure through space and time.

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Background

Animals disperse seeds, nutrients and microbes (collectively referred to as cargo hereafter), and they modify the physical structure of their ecosystem (Subalusky & Post, 2019). Scaling theory allows us to extrapolate these results from individual species to all species in an ecosystem over large distances and time periods (West et al., 1997). To scale movement of cargo across landscapes by animals, we use body mass scaling of metabolic rate, day range, population density, home range, gut passage time and animal lifetime (Doughty et al., 2013; Wolf et al., 2013). Scaling theory can predict how much food an individual animal needs to consume (metabolic rate) and how far it will move that food between consumption and defecation (multiply day range (how far an animal moves in a day) by food passage time) (Fig 1a). Scaling theory can also predict animal population density (individuals per km^2) which can allow us to scale movement of cargo from the individual animal to estimate the movement by all animals of that species (Fig 1b). Of course, individual animals will rarely move in a straight line and the movement of an individual can be characterized as a random walk (Fig 1a). The aggregate statistics of the movement of a population of animals can be described as Brownian motion (Okubo and Levin 2001) (Fig 1b). Therefore, we can calculate the movement of cargo across the landscape as a diffusivity of all the animals in the landscape using species range maps and those animal's body mass (Fig 1c) (Doughty et al., 2013; Wolf et al., 2013), since the scaling factors are all a function of body mass. Finally, we can predict animal mediated diffusivity of cargo at the global scale (Fig1d).

However, certain scaling factors are more predictable than others (i.e. predicting metabolic rate vs population density). For instance, metabolic rate scales very consistently with body mass across vast ranges, from microbes to whales (Kleiber's law) because metabolic scaling theory (MST) predicts this tight relationship based on constraints of how resources are transported through bodies (see chapters xxx and West et al 1997). Different theory predicts other scaling relationships such as home range which predicts larger animals need disproportionately more space to support themselves than smaller animals (Broekman et al., 2023). However, body mass predictability (r^2) of home range is lower than metabolic rate because the theory explaining home range does not go down to first principles but the theory explaining metabolic rate does. Scaling of movement of cargo combines scaling parameters with high r^2 (that go down to first MST principles like metabolic rate) to others with lower r^2 (like home range or population density) that are based in sound ecological theory, but not first principles and predictability is therefore lower than metabolic rate.

To test scaling models of animal mediated cargo movement, we first test mass-based scaling of seed dispersal as it is well studied. Seed dispersal is strongly body size dependent with larger terrestrial animals generally moving seeds further than smaller ones (Pires et al., 2018). This is predicted with scaling theory that combines gut passage time with day range models and is empirically validated. For instance, Asian elephants that disperse seeds an average of 1–2 km (Campos-Arceiz et al., 2008; Pires et al., 2018), and African forest elephants that move 88% of seeds more than 1 km and move 14% more than 10 km (Blake et al., 2009)). However, it is difficult to observe the ecological impacts of animal dispersal of seeds because trees are long lived, and thus, vegetation turn-over can be slow (and out of human time scale). In other words, if forest elephants are removed from a forest, it could take decades to observe the impact because of the long lives of trees. One broader way to consider the ecological impacts of megaherbivores (>1000kg) on seed dispersal is to consider megafauna extinctions in South America where all 15 megaherbivore species went extinct ~12,000 ybp (allowing sufficient time to see the full ecological implications). It has been hypothesized that many key fruit tree species in South America co-evolved with the now extinct megafauna (Janzen & Martin, 1982) and recent work has identified 103 such fruit tree species (Guimarães Jr. et al., 2008). One study used scaling theory and an individual based model to predict that tree species dispersed by these extinct megaherbivores would have a range contraction of ~31% following extinctions compared to an actual range contraction of ~26% using data from the Botanical Information and Ecology Network (Enquist et al., 2016) for 63 (of the 103 hypothesized) megafauna dispersed species (Doughty, Wolf, et al., 2016), which suggests mass based scaling of cargo is possible.

Scaling relationships can also be used to predict the movement of species that are carried by terrestrial vertebrate hosts, including single cell prokaryotes, eukaryotes, viruses, and macro-parasites. The movement of gut microbes and endo-parasites is governed by largely the same allometric scaling laws that determine the movement of seeds and nutrients, including gut passage time and day range. Whereas the dispersal of ectoparasites and skin microorganisms may be closer to the movement of seeds that hitchhike on the exterior of the host. Modelling microbes is often more difficult than nutrients as they are often part of a large, competing population that changes through time. The movement of cargo organisms likely impacts their evolution, especially those that have limited independent mobility when outside the host. Changing this dispersal would therefore alter these evolutionary processes and Doughty et al. (2020) estimate a global average 7-fold reduction in the dispersal of gut microbes and ectoparasites following the extinction of many of the largest host species during the Late Pleistocene and early Holocene (Doughty et al., 2020). Doughty et al. (2020) show that decreased host dispersal could lead to the aggregation of mutations in a simple, single-species gut microbe community, resulting in the development of different microbial strains through time. This divergence is similar to the evolution that occurs when a single species colonizes a new group of islands (MacArthur & Wilson, 1967), such as an ancestor to the Darwin's finches that speciated across the Galapagos Islands (PETREN et al., 2005). The genetic differences that build up in the various sections of the population, eventually lead to separate species on each island. In this comparison, the ocean between the islands is a physical barrier to population mixing, analogous to the reduced dispersal faced by microorganisms and ectoparasites with the extinction of their carrier species.

Scaling theory can also help us to predict how large animal browsing, movement, and destruction impacts vegetation structure and carbon cycling. Megaherbivores (>1000 kg) large body size and selective feeding behavior determines plant species compositions, opening up the understory in dense forests and increase vegetation openness in savanna/forest systems (Bakker et al., 2016). Specifically, African elephants are known to cause significant damage to understory vegetation both in the open savannas and dense tropical forests. For example, an exclosure study in Kruger that removed all animals greater than 5 kg found ~9% more trees over ~36 years and most of the change was due to elephants (Asner & Levick, 2012; Davies & Asner, 2019). Another study followed reintroduced African savanna elephants across five nature reserves between 1927 - 2003 and found that elephants promote a semi-open ecosystem (Gordon et al., 2023). Many other large species show similar, but lesser, impacts on vegetation (Bakker et al., 2016). Doughty et al 2016 used scaling theory and statistical modelling to predict that the extinction of South American megafauna would have increased total woody cover in South America savannas by ~ 29% resulting in similar openness to African savannas (Doughty, Faurby, et al., 2016). In high latitude ecosystems such landscape changes following megafauna extinctions may even have affected global climate (Doughty et al., 2010).

African forest elephants (*Loxodonta cyclotis*) are also known to be significant drivers of tropical forest structure by trampling, upheaving, and ingesting vegetation. Consistent destruction of small sapling numbers and large sapling diversity allows large trees to succeed, while clearing out the understory (Terborgh et al., 2016). Unlike the Amazon, African rainforests have less diversity in the understory, but higher diversity of large trees that dominate the canopy layer, which points to the substantial impact of megaherbivores on forest structure (Terborgh et al., 2016). Furthermore, the changes in vegetation structure from elephant disturbance have significant effects on carbon stocks. The Ecosystem Demography (ED) model was used to estimate that, if elephants were to become extinct in African tropical forests, aboveground biomass would be reduced by 7% (Berzaghi et al., 2019) mainly due to their preferential browsing on leaves from low wood density species and their propensity to disperse large seeds of trees with high wood density (Berzaghi et al., 2023). With tropical forests storing a significant percentage of global carbon, the ecological importance of forest elephants could be substantial, however additional research on their specific impact is needed. Forest elephants may impact forest structure like a light version of logging which could increase biodiversity (Malhi et al., 2022). Future research could use scaling theory to predict the accumulated impact of all animal species on structure.

In addition to scaling seed and pathogen dispersal by megaherbivores, scaling laws have also been used to predict animal mediated elemental transport in an ecosystem. Wolf et al 2013 combined the scaling coefficients of metabolic rate, day range, population density, home range, gut passage time and animal lifetime to predict movement of elements through both bodies (corpses) and feces. They found a superlinear (>1) scaling coefficient of 1.17 for nutrient movement through feces, indicating that larger animals are disproportionately important to the spread of nutrients. Furthermore, movement of elements through feces was two orders of magnitude more important than through bodies. This scaling framework was used to predict that total phosphorus concentrations in the Amazon basin decreased by ~50% following the megafaunal extinctions (Doughty et al., 2013) and that global (marine and terrestrial) animal mediated nutrient diffusion capacity was reduced by >90% following direct and indirect anthropogenic extinctions and population reductions (Doughty, Roman, et al., 2016). We have gained confidence in these model outputs comparing fossilized plant (coal) element concentrations across the US which found more, and more evenly distributed bio-important elements in the Cretaceous (with the biggest animals through Earth history) compared to the Carboniferous (with few large animals) (Doughty, 2017).

This prior work (e.g. Doughty et al 2013 and 2016) focused on simple mass-based scaling relationships to make predictions for global regions (with many data gaps) or for extinct animals (of which often little is known beyond body mass). However, to predict nutrient movement for existing, more data rich species at local scales, scaling theory can be modified to fit nuances of specific systems with, for instance, gap filling of missing data. For example, Hempson et al. (2017) parameterized the nutrient movement model from Doughty et al. (2016) with species specific population abundance data instead of only using scaling relationships and found far more dramatic declines in nutrient transport since the late-Pleistocene than originally calculated by Doughty et al. (2016) (Hempson et al., 2017). Abraham et al. (2021) further improved the nutrient transport model by using scaling theory and empirical data to calculate gut passage time which had previously been estimated (Demment & Van Soest, 1985). The simple mass-based scaling of gut passage time was less accurate than models that included important features such as gut physiology (e.g. ruminants vs hindgut fermenters) among other features like foraging strategy, morphology and phylogeny (Abraham et al., 2021). Therefore, whilst mass-based scaling relationships provide a foundational platform, more sophisticated characterization of nutrient transport using species specific data is required at local scales (Ellis-Soto et al., 2021).

One way to address the shortcomings of mass-based scaling relationships is through individual/agent-based models (I/ABMs), techniques for modelling an ecosystem service at the resolution of the individual. Agent-based models, which can resolve such individual-scale heterogeneity, provide one option. Ferraro et al. (2022) demonstrate how this suite of models can improve upon the one species, one nutrient model (Ferraro et al., 2022). Abraham et al. (2022) extend the agent based model approach and provide a number of suggestions of how future nutrient dispersal models can increase accuracy at finer resolutions (Abraham et al., 2022). Another benefit of ABM's is that mass-based scaling is usually based on average mature individuals, but in an ABM or other mechanistic model, we can also account for age, health (disease, parasites, injury), gender, pregnancy, season (temperature + NPP), and predation risk.

Another way to address the shortcomings is incorporating the agent-based model approach as cohorts (representing several individuals at once, sharing the same traits and state parameter values), into larger earth system models. For instance, scaling theory and the cohort approach has now been incorporated into animal based general ecosystem models like the Madingley model which is a global, process-based model that simulates the interactions between all animal species in an ecosystem (Harfoot et al., 2014). By simulating simplified animal cohorts, rather than individuals (like the I/ABMs), Madingley can simulate larger-scale processes like the landscape of fear where predators influence herbivore behavior. This allows for a more detailed and realistic representation of the system being modeled and thus accounts for the variability in metabolic rates, providing a powerful tool to challenge metabolic scaling theory's assumptions. It can be used to simulate the impact of many parameters on individual cohorts' metabolic rates and on ecosystem-level metabolic rates. Such a model has been used to show that continued loss of large animals globally could lead to a 44% reduction in terrestrial heterotrophic biomass, a 18% decline in metabolism, and a 92% decline in fertility (Enquist et al., 2020). Future directions in Madingley could rely on more scaling relationships not currently included (e.g. amount of sleep scales to -0.25), but in Madingley all cohorts are active for 0.5 day.

Overall, significant progress has been made in using scaling theory to predict animal impacts on their environment at global scales and over tens of thousands of years. There are advantages and disadvantages to this approach. As we have seen, using scaling theory to predict nutrient movement at the local scale without taking advantage of available, species-specific data can lead to low accuracy. However, scaling theory provides the fundamental framework for helping us calculate to within an order of magnitude whether the megafauna extinctions impacted cargo movement or vegetation structure. Another advantage to scaling theory is that because it is tied to physics first principles (West et al., 1997), we can attempt to extend it over even greater scales across time and space. For instance, MST initially was utilized only for mammals, but has since been extended to sub-microbial levels (chapter xxx) and at broader astrobiological scales (chapter xxx). Now we attempt to build on this approach and suggest future ways to scale our previous results over even greater periods of space and time.

Future directions - Scaling over space and time

The main premise of our work is that scaling theory suggests that larger animals are disproportionately important for movement of cargo and changing vegetation structure. Before we move on to scaling our results over space and time, we wanted to revisit some of the data from Wolf et al 2013 and Abraham et al. 2021 to verify that the nutrient diffusion coefficients do scale super-linearly (>1). We test this by calculating the coefficients using several methods including: leave one datapoint out and varying the data randomly by ±20%. In figure one, we show a histogram distribution of the coefficients for the key parameters in our models including: nutrient diffusion, metabolic rate, home range, day range, population density, and lifetime (Fig 2a-f). The nutrient distribution parameter remained superlinear (with one exception) and we further noted possible underestimates to our nutrient diffusion coefficient due to an unusually low metabolic rate coefficient of 0.72 (compared with the typical 0.75) which would underestimate large herbivore consumption (e,g. predicting elephants consuming ~10 kg/day versus actual ~30kg/day of dry matter). New mass-based scaling of gut passage time (GPT) from Abraham et al 2021 gives a scaling coefficient of 0.21 versus our previous modelled value 0.26 (Fig 2g)(Demment & Van Soest, 1985). Combining new coefficients for GPT and metabolic rate gives a superlinear scaling coefficient of 1.15, but foregut fermenters have a lower coefficient (0.06 vs 0.17 hindgut, 0.24 simple, and 0.11 ruminant) taking the total nutrient diffusion coefficient down to linear (=1) (Fig 2h). Future work should expand this dataset further (for example, new datasets of home range include over 75 thousand home range observations (Broekman et al., 2023)) and we encourage work to link the superlinear scaling of nutrient movement to the fundamental precepts of MST. However, overall, we remain confident of the superlinear scaling for most animal mediated cargo.

Now that we have gained more confidence in the superlinear scaling coefficients, we extrapolate our work over longer periods of Earth's history using body size distributions over the past 250 million years (O'Gorman & Hone, 2012) to predict potential planetary nutrient diffusion capacity following methodology developed in Doughty et al 2013 (Fig 3). In prior work, potential nutrient movement over a similar period was calculated based on the largest single species of the era (Doughty 2017). Here we calculate nutrient distribution by all animal species (not just the biggest) during each period. This is important because a distribution with more, smaller species could have greater diffusion potential than a distribution with fewer, bigger species. We find nutrient diffusion is more homogeneous over the past 300 million years than was previously reported (Doughty 2017), but still peaks in the Mesozoic. As a percentage, nutrient movement peaks during the late Jurassic (800% of current) followed by late Cretaceous (~500% of current) (Fig 3 bottom). This is initially surprising as the Mesozoic has fewer total number of species than the Cenozoic (Fig 3 top), but it reinforces the importance of overall body size versus total number of species on nutrient distribution potential.

Potential nutrient movement does not translate directly into actual nutrient movement because this is dependent on soil substrate variations. However, previous work suggests time periods with larger body sized animals do increase nutrient availability because the Cretaceous (with larger bodied animals) had increased concentrations (136%) and decreased spatial heterogeneity (22%) of plant-important rock-derived nutrients than the carboniferous (with smaller bodied animals)

(Doughty 2017). Taphonomic bias, which means it is harder to find older, smaller fossils than newer, bigger ones, may account for fewer smaller species during the Mesozoic period. However, Gorman and Hone 2012 suggest the Mesozoic body size distributions were not due to taphonomic bias, but instead due to the unique ecology of egg laying dinosaurs where smaller herbivore niches were filled by smaller versions of bigger dinosaurs instead of different species. Overall, we suggest future verifications of these scaling results against other coal elemental records for different time periods and regions following Doughty 2017.

Our final goal for this chapter is to demonstrate the use of remote sensing techniques to scale animal impacts on their landscape over large spatial scales (Fig 4). Nutrients moved by animals that are limiting in an ecosystem (like phosphorus in tropical regions) will be absorbed into canopy top leaves that are observable from aircraft or satellites. Forests or grasslands with more nutrients in their leaves, like nitrogen or phosphorus, will reflect light in a different way and the nutrient concentrations can be measured with aircraft or satellites carrying hyperspectral (many band) sensors (Asner et al., 2016). For example, Asner et al 2016 predicted plant canopy nutrient biogeochemistry for the entire country of Peru by combining hyperspectral data from aircraft and satellites (Asner et al., 2016). In theory, we can predict where leaves will have higher nutrient concentrations based on which animal populations are present (following animal nutrient modelling from Doughty et al 2013). We can then validate such models by observing trends in canopy biogeochemistry as predicted with hyperspectral remote sensing techniques (following Asner et al 2016) (Fig 4 right).

Above we described how large animals impact forest structure, which could be measured with lidar (light detection and ranging). Lidar shoots a laser into a forest and based on the amount and timing of the return energy, can be used to predict forest structure. For example, aircraft lidar was used to show that regions with large animals had ~9% fewer trees (Asner and Levick 2012). A more recent study found that lidar can detect forest elephant trails in a dense tropical forest (Keany et al 2024). Since, there is now satellite lidar for measuring forest structure (GEDI-Dubayah et al 2020), we propose to use scaling theory to predict large animal impacts on forest structure and then to validate these estimates using either aircraft or satellite lidar to measure vegetation structure (Fig 4 left).

Finally, vertical forest stratification can lead to more species coexistence in species-rich regions like tropical forests and climate change could drive arboreal species away from the warmer top canopy towards the ground (Oliveira and Scheffers 2019). Since forest elephants may impact vertical forest structure (Keany et al 2024) we propose, in Fig 4b, to use a spaceborne thermal sensor to observe how structural impacts from elephants may influence thermal heterogeneity at broad spatial scales. Increasing vertical forest heterogeneity could allow more thermal niche space to allow arboreal animals to better acclimate to climate change.

Conclusions

Scaling theory allows us to predict animal impacts on seed distribution, zoogeochemistry, pathogen movement, and vegetation structure over space and time. Here we have both reviewed this literature and suggested future directions to scale such work over space and time and apply it to such disparate fields as ecosystem ecology, paleontology and remote sensing.

Figures

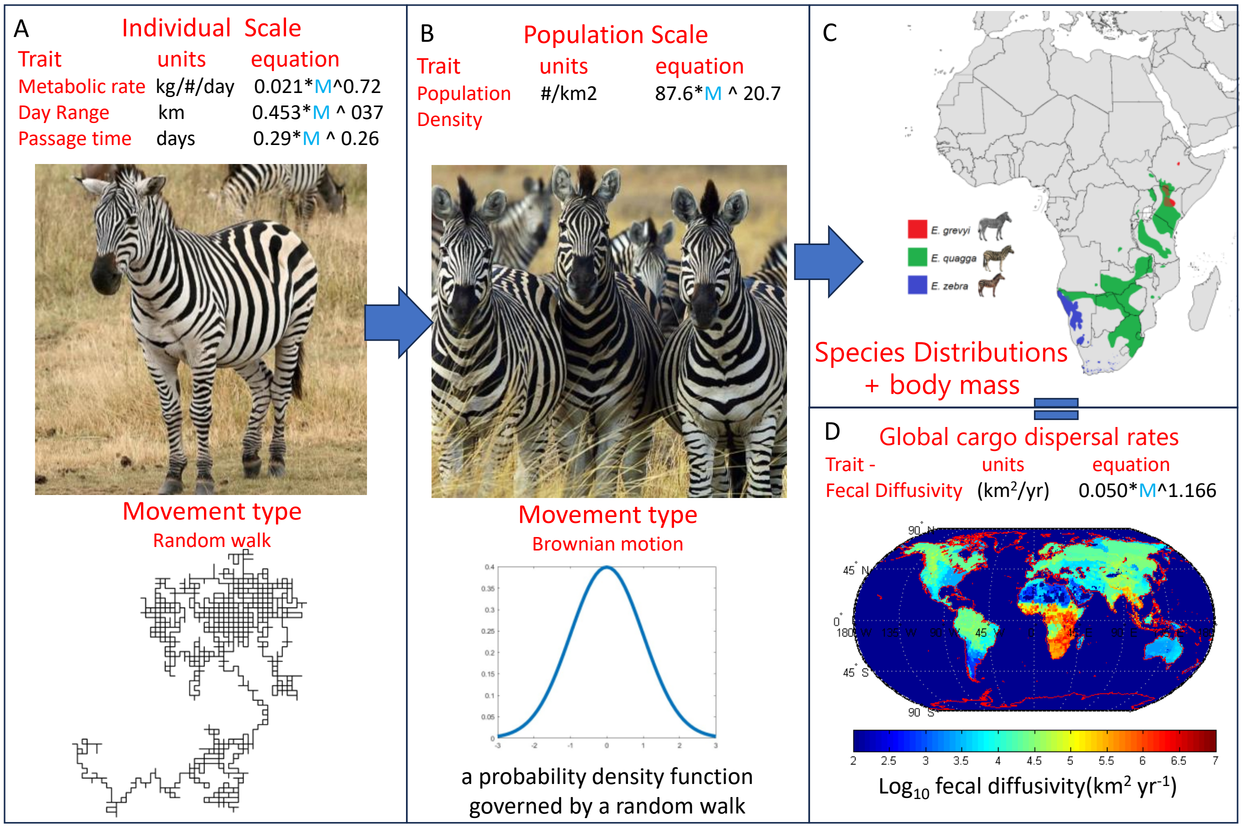

Fig 1 – A schematic overview to calculate cargo dispersal rates. Individual scale (A) is aggregated to the population scale (B). Random walk movement at the individual scale is simplified into Brownian motion diffusivity at the population scale. Population scale dynamics are combined with species body mass and range maps (C) to estimate global cargo dispersal rates for all species (D).

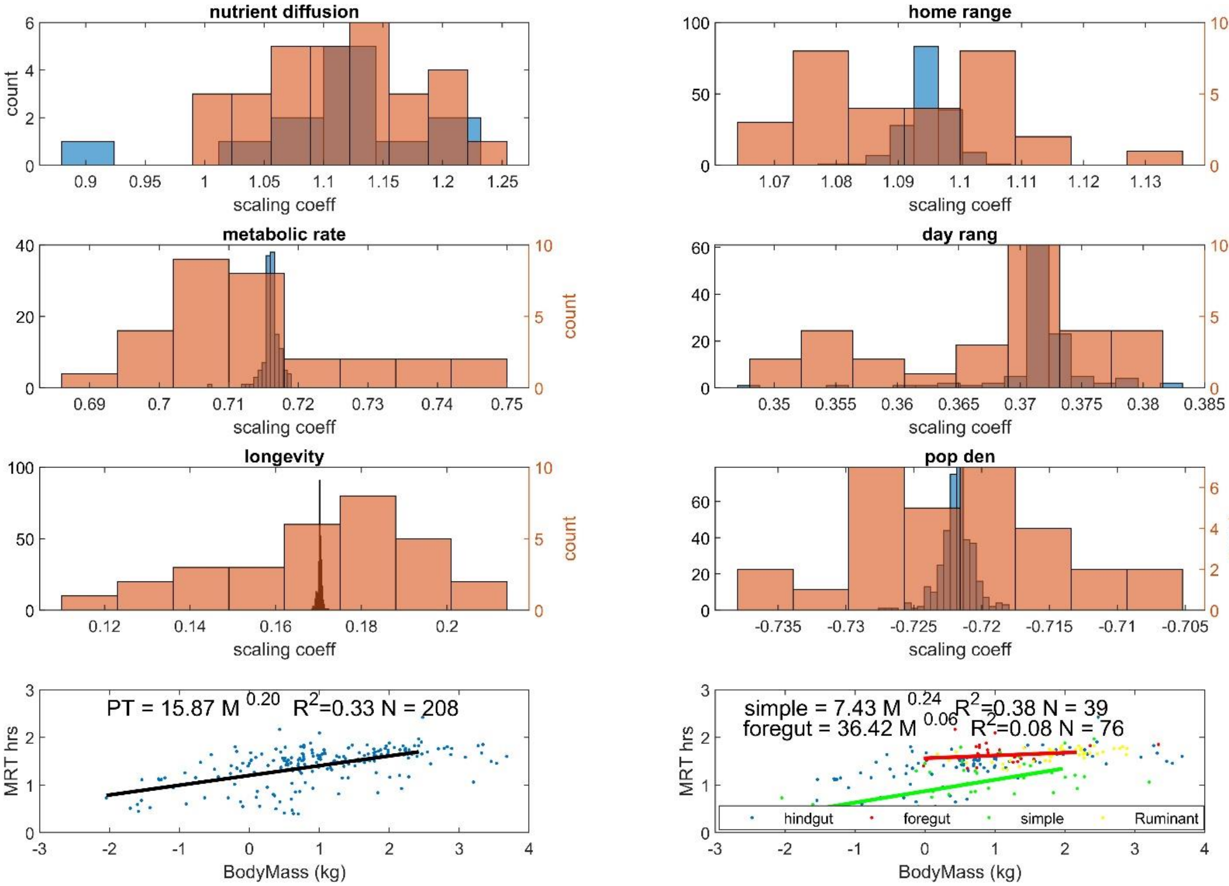

Fig 2 - Histograms for scaling coefficients for nutrient diffusion, home range, metabolic rate, day range, animal lifetime, and population density using data from Wolf et al 2013 and Abraham et al. 2021 with a leave one datapoint out methodology (blue) and adding a random 20% error to each datapoint (orange). Bottom row shows log10 mean gut retention time in hours for all animals (left) and separated by gut type (right). We show linear regressions and statistics for all mammals (left) and separated by gut type (simple=green, foregut=red).

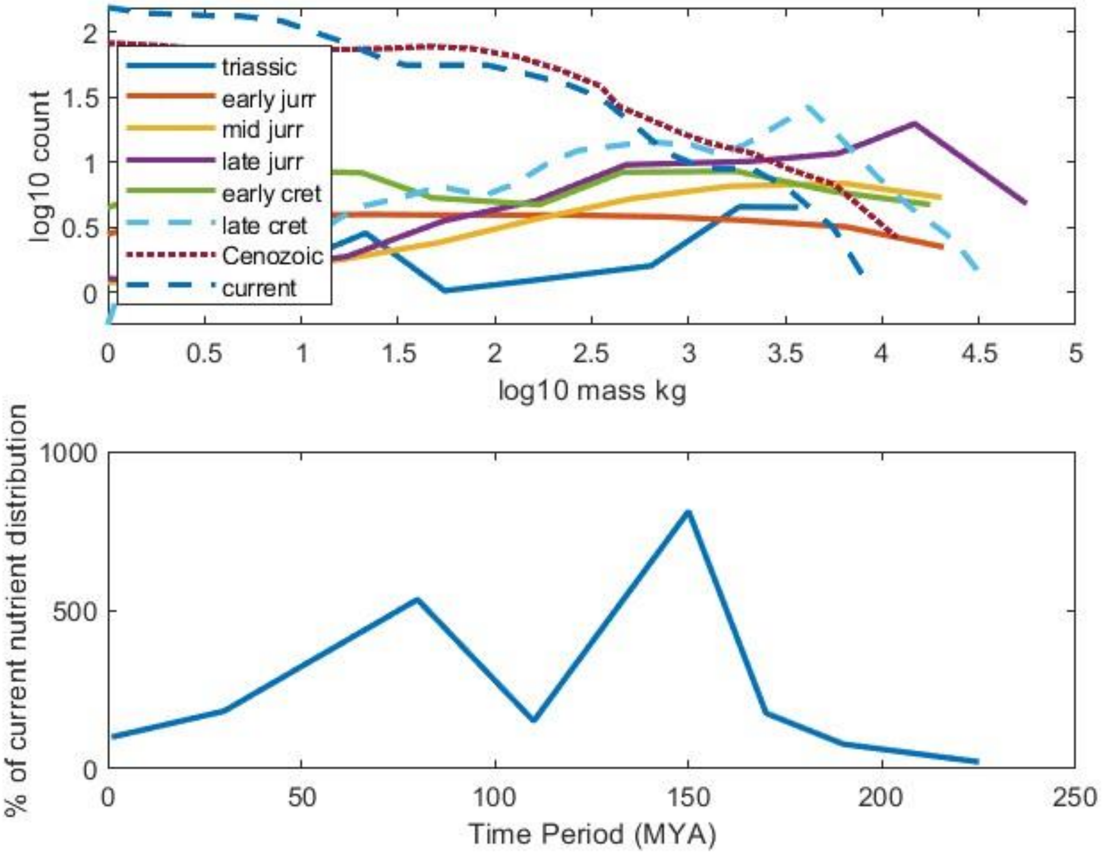

Fig 3 - (top) Body size distributions of number of animal species for eight distinct periods in Earth's history recreated from (Gorman and Hone 2012). (bottom) Calculated nutrient diffusion potential for each time period from species distributions shown above as a percentage of current nutrient diffusion following methodology from Doughty et al 2013.

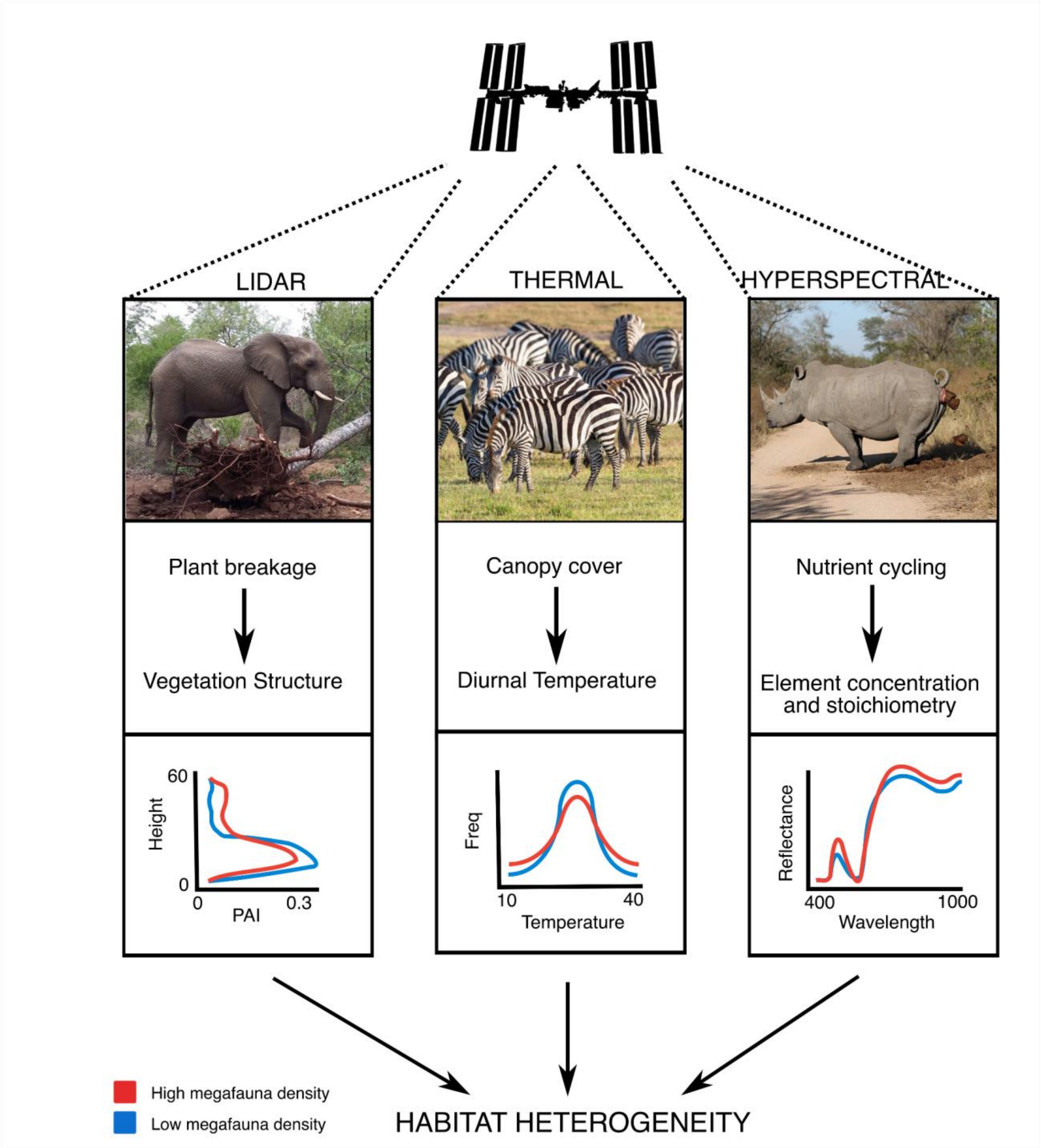

Fig 4 - Potential impacts of low (blue) and high (red) megafauna density on structure (left), temperature (middle), and biogeochemistry (right) as seen from space by three current instruments (lidar, thermal, and hyperspectral).

References

Abraham, A. J., Prys-Jones, T. O., De Cuyper, A., Ridenour, C., Hempson, G. P., Hocking, T., et al. (2021). Improved estimation of gut passage time considerably affects trait-based dispersal models. *Functional Ecology*, *35*(4), 860–869. https://doi.org/https://doi.org/10.1111/1365-2435.13726

Abraham, A. J., Duvall, E., Ferraro, K., Webster, A. B., Doughty, C. E., le Roux, E., & Ellis-Soto, D. (2022). Understanding anthropogenic impacts on zoogeochemistry is essential for ecological restoration. *Restoration Ecology*, *n/a*(n/a), e13778. https://doi.org/https://doi.org/10.1111/rec.13778

Asner, G. P., & Levick, S. R. (2012). Landscape-scale effects of herbivores on treefall in African savannas. *Ecology Letters*. https://doi.org/10.1111/j.1461-0248.2012.01842.x

Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., & Vaughn, N. (2016). Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1604863113

Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W. M., Sandom, C. J., Asner, G. P., & Svenning, J. C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1502545112

Berzaghi, F., Longo, M., Ciais, P., Blake, S., Bretagnolle, F., Vieira, S., et al. (2019). Carbon stocks in central African forests enhanced by elephant disturbance. *Nature Geoscience*, *12*(9), 725–729. https://doi.org/10.1038/s41561-019-0395-6

Berzaghi, F., Bretagnolle, F., Durand-Bessart, C., & Blake, S. (2023). Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. *Proceedings of the National Academy of Sciences*, *120*(5), e2201832120. https://doi.org/10.1073/pnas.2201832120

Blake, S., Deem, S. L., Mossimbo, E., Maisels, F., & Walsh, P. (2009). Forest Elephants: Tree Planters of the Congo. *Biotropica*, *41*(4), 459–468. https://doi.org/https://doi.org/10.1111/j.1744-7429.2009.00512.x

Broekman, M. J. E., Hoeks, S., Freriks, R., Langendoen, M. M., Runge, K. M., Savenco, E., et al. (2023). HomeRange: A global database of mammalian home ranges. *Global Ecology and Biogeography*, *32*(2), 198–205. https://doi.org/https://doi.org/10.1111/geb.13625

Campos-Arceiz, A., Larrinaga, A. R., Weerasinghe, U. R., Takatsuki, S., Pastorini, J., Leimgruber, P., et al. (2008). BEHAVIOR RATHER THAN DIET MEDIATES SEASONAL DIFFERENCES IN SEED DISPERSAL BY ASIAN ELEPHANTS. *Ecology*, *89*(10), 2684–2691. https://doi.org/https://doi.org/10.1890/07-1573.1

Davies, A. B., & Asner, G. P. (2019). Elephants limit aboveground carbon gains in African savannas. *Global Change Biology*, *25*(4), 1368–1382. https://doi.org/https://doi.org/10.1111/gcb.14585

Demment, M. W., & Van Soest, P. J. (1985). A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. *The American Naturalist*, *125*(5), 641–672. https://doi.org/10.1086/284369

Doughty, C. E. (2017). Herbivores increase the global availability of nutrients over millions of years. *Nature Ecology & Evolution*, *1*(12), 1820–1827. https://doi.org/10.1038/s41559-017-0341-1

Doughty, C. E., Wolf, A., & Field, C. B. (2010). Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming? *Geophysical Research Letters*, *37*(15). https://doi.org/https://doi.org/10.1029/2010GL043985

Doughty, C. E., Wolf, A., & Malhi, Y. (2013). The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience*, *6*(9), 761–764. https://doi.org/10.1038/ngeo1895

Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., et al. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences*, *113*(4), 868–873. https://doi.org/10.1073/pnas.1502549112

Doughty, C. E., Wolf, A., Morueta-Holme, N., Jørgensen, P. M., Sandel, B., Violle, C., et al. (2016). Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography*, *39*(2), 194–203. https://doi.org/https://doi.org/10.1111/ecog.01587

Doughty, C. E., Faurby, S., & Svenning, J. C. (2016). The impact of the megafauna extinctions on savanna woody cover in South America. *Ecography*. https://doi.org/10.1111/ecog.01593

Doughty, C. E., Prys-Jones, T. O., Faurby, S., Abraham, A. J., Hepp, C., Leshyk, V., et al. (2020). Megafauna decline have reduced pathogen dispersal which may have increased emergent infectious diseases. *Ecography*, *43*(8), 1107–1117. https://doi.org/https://doi.org/10.1111/ecog.05209

Dubayah, R., Blair, J. B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., et al. (2020). The Global Ecosystem Dynamics Investigation: High-resolution laser ranging of the Earth's forests and topography. *Science of Remote Sensing*. https://doi.org/10.1016/j.srs.2020.100002

Ellis-Soto, D., Ferraro, K. M., Rizzuto, M., Briggs, E., Monk, J. D., & Schmitz, O. J. (2021). A methodological roadmap to quantify animal-vectored spatial ecosystem subsidies. *Journal of Animal Ecology*, *90*(7), 1605–1622. https://doi.org/https://doi.org/10.1111/1365-2656.13538

Enquist, B. J., Condit, R., Peet, R. K., Schildhauer, M., & Thiers, B. M. (2016). Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ Preprints*, *4*, e2615v2. https://doi.org/10.7287/peerj.preprints.2615v2

Enquist, B. J., Abraham, A. J., Harfoot, M. B. J., Malhi, Y., & Doughty, C. E. (2020). The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, *11*(1), 699. https://doi.org/10.1038/s41467-020-14369-y

Ferraro, K. M., Schmitz, O. J., & McCary, M. A. (2022). Effects of ungulate density and sociality on landscape heterogeneity: a mechanistic modeling approach. *Ecography*, *2022*(2). https://doi.org/https://doi.org/10.1111/ecog.06039

Gordon, C. E., Greve, M., Henley, M., Bedetti, A., Allin, P., & Svenning, J.-C. (2023). Elephant rewilding affects landscape openness and fauna habitat across a 92-year period. *Ecological Applications*, *n/a*(n/a), e2810. https://doi.org/https://doi.org/10.1002/eap.2810

Guimarães Jr., P. R., Galetti, M., & Jordano, P. (2008). Seed Dispersal Anachronisms: Rethinking the Fruits Extinct Megafauna Ate. *PLOS ONE*, *3*(3), e1745. Retrieved from https://doi.org/10.1371/journal.pone.0001745

Harfoot, M. B. J., Newbold, T., Tittensor, D. P., Emmott, S., Hutton, J., Lyutsarev, V., et al. (2014). Emergent Global Patterns of Ecosystem Structure and Function from a Mechanistic General Ecosystem Model. *PLoS Biology*. https://doi.org/10.1371/journal.pbio.1001841

Hempson, G. P., Archibald, S., & Bond, W. J. (2017). The consequences of replacing wildlife with livestock in Africa. *Scientific Reports, 7*(1), 17196. https://doi.org/10.1038/s41598-017-17348-4

Janzen, D. H., & Martin, P. S. (1982). Neotropical Anachronisms: The Fruits the Gomphotheres Ate. *Science*, *215*(4528), 19–27. https://doi.org/10.1126/science.215.4528.19

Keany, J.M., Burns, P., Abraham, A.J., Jantz, P., Makaga, L., Saatchi, S., Maisels, F., Abernethy, K. and Doughty, C.E. (2024), Using multiscale lidar to determine variation in canopy structure from African forest elephant trails. Remote Sens Ecol Conserv. https://doi.org/10.1002/rse2.395

MacArthur, R. H., & Wilson, E. O. (1967). *The Theory of Island Biogeography*. Princeton: University of Princeton Press.

Malhi, Y., Riutta, T., Wearn, O. R., Deere, N. J., Mitchell, S. L., Bernard, H., et al. (2022). Logged tropical forests have amplified and diverse ecosystem energetics. *Nature*, *612*(7941), 707–713. https://doi.org/10.1038/s41586-022-05523-1

Oliveira, B.F., Scheffers, B.R., 2019. Vertical stratification influences global patterns of biodiversity. Ecography 42, 249–249. https://doi.org/10.1111/ecog.03636

O'Gorman, E. J., & Hone, D. W. E. (2012). Body Size Distribution of the Dinosaurs. *PLOS ONE*, *7*(12), e51925. Retrieved from https://doi.org/10.1371/journal.pone.0051925

Okubo A, Levin SA (2001) Diffusion and ecological problems : modern perspectives 2nd Ed. New York: Springer. 467 p.

PETREN, K., GRANT, P. R., GRANT, B. R., & KELLER, L. F. (2005). Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. *Molecular Ecology*, *14*(10), 2943–2957. https://doi.org/https://doi.org/10.1111/j.1365-294X.2005.02632.x

Pires, M. M., Guimarães, P. R., Galetti, M., & Jordano, P. (2018). Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. *Ecography*, *41*(1), 153–163. https://doi.org/https://doi.org/10.1111/ecog.03163

Schaefer, H.M., Schmidt, V., Wesenberg, J., 2002. Vertical stratification and caloric content of the standing fruit crop in a tropical lowland forest. Biotropica 34, 244–253. https://doi.org/10.1111/j.1744-7429.2002.tb00535.x

Subalusky, A. L., & Post, D. M. (2019). Context dependency of animal resource subsidies. *Biological Reviews*, *94*(2), 517–538. https://doi.org/https://doi.org/10.1111/brv.12465

Terborgh, J., Davenport, L. C., Niangadouma, R., Dimoto, E., Mouandza, J. C., Scholtz, O., & Jaen, M. R. (2016). Megafaunal influences on tree recruitment in African equatorial forests. *Ecography*, *39*(2), 180–186. https://doi.org/https://doi.org/10.1111/ecog.01641

West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*. https://doi.org/10.1126/science.276.5309.122

Wolf, A., Doughty, C. E., & Malhi, Y. (2013). Lateral Diffusion of Nutrients by Mammalian Herbivores in Terrestrial Ecosystems. *PLOS ONE*, *8*(8), e71352. Retrieved from https://doi.org/10.1371/journal.pone.0071352