Title: **Bottom-up effects of a megaherbivore alter plant growth and competition regimes, promoting vegetation heterogeneity**

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ABSTRACT:

1. Megaherbivores are known to strongly influence multiple ecological processes, but their bottom-up impacts on vegetation via nutrient redistribution remain poorly understood, particularly in mesic ecosystems. Here, we investigated how woody plant communities are influenced by large nutrient inputs in the form of dung deposited by Asia's largest herbivore, the Asian elephant (*Elephas maximus*), in the tropical forests of southern India.

2. We conducted field and mesocosm experiments on woody saplings to examine three mechanisms through which dung deposition by elephants can alter plant community assembly. Specifically, we tested if elephant dung input 1) creates hotspots of plant growth, and shapes plant communities by altering 2) the negative density-dependent effects of neighborhood competition, and 3) interference competition between plant functional types differing in nutrient limitation, namely nitrogen-fixers and non-nitrogen-fixers.

3. Our findings show that dung deposition by elephants can generate fine-scale spatial differences in woody sapling communities by creating local growth hotspots and altering competitive interactions. Notably, saplings receiving dung inputs were buffered against the negative density-dependent effects of neighborhood competition. Importantly, nitrogen-limited species, i.e., non-nitrogen-fixers outcompeted nitrogen-fixers when supplied with elephant dung. These bottom-up effects on plant growth and competition can be of substantially large magnitude, as we estimated that elephants in these forests create a total of 11000 such nutrient-rich sites /km^2/year, with each elephant redistributing ~130.29 kg N/year through this pathway and each site receiving 19.83 g N.

Synthesis: Our findings highlight the role of nutrient redistribution by megaherbivores as an underappreciated driver of species interactions that can alter plant communities at fine scales, effects that are widely distributed across megaherbivore habitats. Such bottom-up effects of

megaherbivores, along with their top-down effects, have important conservation implications and can help in restoring species interactions and spatial heterogeneity in plant communities in defaunated habitats.

INTRODUCTION

Large herbivores are integral to the functioning of many ecosystems as they regulate multiple ecosystem processes (Pringle et al., 2023). They have pronounced impacts on biodiversity through their effects on vegetation structure and composition (Jia et al., 2018; Van Der Plas et al., 2016), nutrient cycling (Augustine et al., 2003; Coetsee et al., 2023; Pastor et al., 2006; Villar et al., 2021) and fire regimes (Archibald & Hempson, 2016; Karp et al., 2024), in addition to downstream effects on other organisms (McCleery et al., 2024; Trepel et al., 2024). Worryingly, while ecosystems worldwide have become functionally degraded due to the body-size-downgrading of herbivore communities (Dirzo et al., 2014), our current understanding of their functional roles is strongly biased, both taxonomically and geographically (Pringle et al., 2023; Ripple et al., 2015; Sankaran & Ahrestani, 2016; Trepel et al., 2024). Such regional and taxonomic blind-spots are particularly evident for megaherbivores i.e., herbivores with >1000 kg body weight (Hyvarinen et al., 2021). Megaherbivores are thought to have disproportionate impacts on ecosystem functioning (Owen-Smith, 1988) and are considered keystone species (Malhi et al., 2016). Yet, empirical knowledge of their various ecological roles is scarce for most species (systematic review in Hyvarinen et al., 2021), which hinders a generalized understanding of the functional

importance of a very large body size (Pringle et al., 2023). This limitation impedes locally informed application of such knowledge in conservation, particularly in rewilding and restoration of ecological functions lost from defaunated ecosystems (Geremia et al., 2025; Ripple et al., 2015; Schmitz et al., 2023; Svenning et al., 2016).

The disproportionate ecological impacts of a very large body size stem from its association with unique functional traits among large herbivores (Owen-Smith, 1988; Pringle et al., 2023). For instance, the large daily forage requirement, generalist diet and destructive foraging behaviour of megaherbivores exert strong top-down control on plants, while their wide-ranging behaviour promotes long-distance transport of nutrients and seeds (Berzaghi et al., 2018; Malhi et al., 2016; Trepel et al., 2024). Being largely immune as adults to top-down control by non-human predators, megaherbivores are instead bottom-up limited by resource availability – this bottom-up limitation amplifies their effects on vegetation (Hyvarinen et al., 2021). In recent reviews, their ecological roles have been emphasized as so uniquely important for conservation that their per-capita impact cannot be compensated for by managing densities of smaller herbivores (Hyvarinen et al., 2021; Pringle et al., 2023).

Recent meta-analyses of herbivore exclosure experiments have concluded that megafauna alter the composition of plant communities (e.g. increase species evenness, Jia et al., 2018) and enhance spatial heterogeneity in vegetation and soil nutrients (Trepel et al., 2024). Such megafauna-induced changes in community composition and heterogeneity can arise via top-down (consumptive effects) and/or bottom-up (alteration of resource availability) regulatory pathways (Ferraro et al., 2024; Hobbs, 1996; Knapp et al., 1999; Pringle et al., 2023). Past studies on megaherbivores have predominantly focused on the top-down regulation of

vegetation through consumption and trampling, with most research concentrated in African savannas (Hyvarinen et al., 2021). In contrast, their bottom-up effects are poorly understood and have been studied primarily through the lens of seed dispersal (Campos-Arceiz & Blake, 2011). A critical bottom-up impact of megaherbivores is nutrient distribution and cycling (through dung, urine and carcasses, Wolf et al., 2013), but this function remains largely understudied for megaherbivores other than hippos and savanna elephants (Hyvarinen et al., 2021). Importantly, how nutrient redistribution by megaherbivores shapes plant communities is not well understood (Sitters & Olde Venterink, 2021).

Megaherbivores are strong agents of nutrient cycling as they return large amounts of nutrient-rich faeces and urine (Le Roux et al., 2020; Pastor et al., 2006; Wolf et al., 2013) and facilitate long-distance transport of nutrients, like “arteries” of ecosystems (Malhi et al., 2016; Wolf et al., 2013). The patchy deposition of nutrient-rich faeces by megaherbivores creates a heterogeneous matrix of nutrient availability (Afzal & Adams, 1992; Ferraro & Lienau, 2025; Le Roux et al., 2020), which in turn, can generate fine-scale mosaics of vegetation in multiple ways. These nutrient-mediated effects include changes in plant growth and survival (Tandalla et al., 2024), as well as modification of species interactions such as competition among plants (Van der Waal et al., 2009). For instance, herbivore dung can alter the competitive outcomes between species differing in nutrient limitation, thereby shaping community composition (Sitters & Olde Venterink, 2018, 2021). Because such responses are mediated by the quantity of nutrient inputs via dung (Sitters & Olde Venterink, 2021; Valdés-Correcher et al., 2019), megaherbivores are expected to exert disproportionate effects since they deposit large amounts of dung. However, empirical examinations of such bottom-up impacts remain scarce (Kalbitzer et al., 2019; Sitters & Olde Venterink, 2021). Therefore, our

study aimed to elucidate the mechanisms through which nutrient deposition by megaherbivores influences plant communities, using elephants as a model system.

Elephants, the world's largest herbivores, are often referred to as "ecosystem engineers" or "megagardeners" due to their large impacts on ecosystem processes (Campos-Arceiz & Blake, 2011; Poulsen et al., 2018). Existing knowledge on their ecological roles largely derives from studies on the African savanna elephant (Guldemond et al., 2017; for example, Sukumar, 2003 pp. 223-252) that occupies arid and semi-arid open habitats. In contrast, the African forest (*Loxodonta cyclotis*) and Asian elephants remain understudied, with research primarily focused on their role as seed dispersers (Campos-Arceiz & Blake, 2011; Sekar et al., 2017; but see Berzaghi et al., 2023; Blake, 2002; Omeja et al., 2014; Sivasubramaniyan & Sivaganesan, 1996). Studying these two species can elucidate the impacts of megaherbivores in wetter niches, a key gap identified in Hyvarinen et al.'s systematic review (2021). Currently, the impacts of nutrient distribution by elephants on vegetation are poorly understood for all three species. Experimental manipulation of dung input can reveal its effects on vegetation (Sitters & Olde Venterink, 2021; Valdés-Correcher et al., 2019), but to our knowledge, only one such study exists. Interestingly, this study by Kalbitzer et al. (2019) did not find growth-enhancing effects of elephant dung on plants in central African rainforests. Given the lack of other field experiments, there is a need to further evaluate the supposedly large bottom-up impacts of elephants on vegetation.

Here, we conducted field and ex-situ mesocosm experiments manipulating elephant dung input to woody saplings in the tropical forests of southern India to understand bottom-up regulation of vegetation by megaherbivores. We hypothesized that elephants create fine-scale

differences in nutrient availability through dung deposition, which in turn, alters plant growth and competition regimes, with implications for local heterogeneity in vegetation (Fig 1). We tested three predictions linked to the distinct mechanistic responses by plants. First, we expected dung-deposition sites to act as growth hotspots compared to adjacent control sites (*Prediction 1*). Second, we predicted that such nutrient input via dung provides a localized buffer against the negative density-dependent effects of neighborhood competition (also known as scramble competition) (*Prediction 2*). We then examined how dung input affects competitive balance between plant functional types (PFT) differing in nutrient limitation (inter-PFT interference competition). To this end, we chose nitrogen-fixing (N-fixers) and non-nitrogen-fixing (non-N-fixers) woody plants; these two PFTs present an excellent contrast model as they clearly differ in nutrient-limitation (Vitousek & Howarth, 1991). Non-N-fixers are limited by nitrogen availability and thus benefit more from external nitrogen inputs (Tandalla et al., 2024; Varma et al., 2018). While a previous study showed that herbivore dung alters tree-grass coexistence by shaping competition between grasses and woody N-fixers, such impacts on the competition between woody non-N-fixers and woody N-fixers remain unknown (Sitters & Olde Venterink, 2021). We predicted that woody non-N-fixers, being nitrogen-limited, would outcompete N-fixers when supplied with nitrogen-rich dung (*Prediction 3*). Finally, to understand the overall magnitude of these bottom-up effects, we estimated the annual cycling of nitrogen and production of such nutrient-rich sites by elephants.

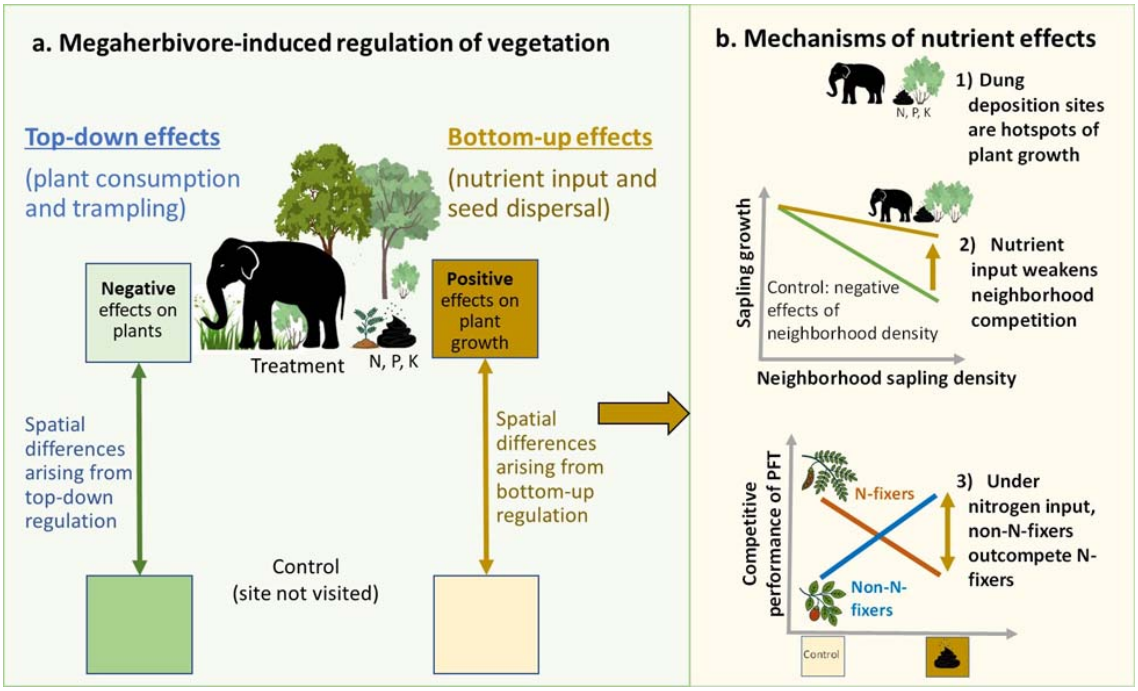

Figure 1. a) Top-down and bottom-up effects of megaherbivores as distinct regulatory pathways that enhance local heterogeneity in vegetation, b) Hypothesized mechanisms through which nutrient input via dung deposition can create fine-scale differences in vegetation.

METHODOLOGY

We conducted this study in and around the tropical forests of Nagarahole National Park (henceforth called Nagarahole). Tropical moist deciduous forests, tropical dry deciduous forests and teak plantations are the major vegetation types in the park, where mean annual rainfall ranges from ~1000-1500 mm, temperature ranges from ~10 □ in winter to ~35 □ in summer, and the soil is loamy, clay-loamy and deep (Reddy et al., 2016).

Field experiment on woody plant growth and neighborhood competition

To examine if elephant dung deposition creates spatial differences in plant growth and neighborhood competition, we selected 19 experimental sites in September 2021 in different locations in the park, representing a range of ecological conditions spanning the three forest types. These sites were at least 2km apart from each other and were in randomly selected 2km x 2km cells. At each location, we established two pairs of plots, 20m apart; each pair consisted of a control and a dung treatment plot ($1m^2$) that were 10m apart. We first sampled plots to quantify the initial state of the vegetation before applying the dung treatment. All woody individuals ≥30cm tall with girths less than 10cm (henceforth called saplings) in plots were marked with uniquely numbered aluminum tags, and their girth at 10cm aboveground measured using an INSIZE 1112-150 digital caliper (0.01mm resolution). We also measured their height up to 1m using a scale (saplings taller than 1m were categorized into 1-2m or >2m bins). In addition, we estimated the cover of grasses, forbs and shrubs in plots, as these could potentially compete with saplings.

After the initial vegetation inventory, we experimentally added dung to one plot (henceforth called treatment plot) in each pair. The treatment involved placement of an entire pile (5-10kg) of fresh dung in each plot. We collected dung piles from fresh (or overnight) defecations by adult wild elephants and transferred them to the treatment plot on the same day. We re-sampled the girth and height of marked saplings after ~6 months during April and May 2023. We also noted the status (dead/alive) of saplings; in case of saplings with multiple stems, if the main stem had died and only the smaller stem(s) survived, we classified it as ‘partially dead’. The total duration between the initial and final measurements was 162 days

on average, but varied due to logistics (143-215 days). One site burned in a forest fire, leaving us with 18 sites or 36 plot-pairs.

Ex-situ mesocosm experiment on inter-PFT competition

To examine if dung input affected the competitive dynamics between nitrogen-fixers and non-fixers, we set up a semi-natural mesocosm experiment at a site ~3km from the southeastern boundary of Nagarahole, in September-October 2022. The site had naturally regrowing vegetation with an overstory of deciduous trees and a dense understory. At the site, we enclosed a flat rectangular area ~600m^2 using a wire mesh (one-inch gap). We further covered the enclosure with a plastic net to prevent the entry of birds and mammals or falling tree branches while retaining the effects of sunlight and canopy. We selected seedlings (8-10 weeks) of native N-fixing (*Dalbergia latifolia*, *Pterocarpus marsupium*, *Butea monosperma*, *Acacia ferruginea*) and non-N-fixing tree species (*Terminalia tomentosa*, *Anogeissus latifolia*, *Tectonia grandis*, *Zizyphus oenoplia*, *Cassia fistula*, *Terminalia bellirica* and *Syzigium cumini*). These seedlings were obtained from nearby forestry nurseries (Tithimati, Beechanahalli) where seeds collected from natural forests were germinated for plantation/restoration purposes. For *Anogeissus latifolia* and *Zizyphus oenoplia*, which are widespread in this landscape but were not available in nurseries, we collected similar sized seedlings from vegetation outside the park boundary. Together, these species represent >50% of the naturally occurring community of tree seedlings in Nagarahole forests (based on data in Gautam et al., 2019). We used a total of 132 seedlings in this experiment. Seedlings were grown in large, rectangular pots (~18” length, 12” width, 11” depth, i.e., with top surface area of 0.14 m^2) with local soil from uncultivated land adjacent to the park’s border. Pebbles and plant debris in soils were first removed, after which the soil was mixed with sand in a 2:1

ratio to ensure water percolation and prevent clogging. Pots were then filled with this soil-sand mix up to ~90% of their heights (~16kg), and planted with two seedlings, as described below.

We planted two seedlings of comparable size ~10 inches apart in each pot to examine how elephant dung input influences seedling competition. We created two competition scenarios for each PFT: i) inter-PFT or mixture competition, i.e., competition between one N-fixer and one non-N-fixer seedling, and ii) monoculture or intraspecific competition, i.e., competition within each PFT. This resulted in two types of monocultures, one each for N-fixers and non-N-fixers. We maintained two sets of each monoculture and mixture regime pots, one being the control while the other received dung treatments, in each block (n=11 blocks of six pots containing two seedlings each). The dung treatment involved placing 500g (wet weight, ~2/3rd of a bolus) of fresh elephant dung between the two seedlings. Since we were interested in inter-PFT competition, we ensured a balanced sample size for each PFT (N=66); however, the competition design resulted in twice the number of seedlings under monoculture than the mixture (inter-PFT) competition. Replication at the species level was limited by logistical constraints (availability of seedlings in nurseries, soil requirements for large pots, and space). At the seedling level, this experiment had a 2 (treatment) × 2 (PFT) × 2 (competition type) design. All pots were watered 2-3 times a week. After the experiment ended in April 2022 (after ~5-6 months), all saplings were harvested for dry biomass measurements. We separated shoots from roots (at the soil mark) to quantify shoot and root biomass separately. Any soil sticking to the saplings was brushed off, after which the saplings were dried in an oven at 60 °C for 60 hours and their dry weight measured in the laboratory. We obtained final sapling biomass by adding root and shoot biomass.

Statistical analyses of field experiment data

Our analysis of the field experiment was based on all saplings alive at the end of the experiment (N=418 saplings in 18 plot-pairs). We calculated the following variables for sapling girth and height: absolute change and relative growth rate (RGR); RGR measures growth rate relative to an individual's initial size and was calculated as ln [(initial size) – ln (final size)]/duration of experiment. In the case of height, since we had measured height only up to 1m, we excluded all saplings whose initial and final height was >1m. RGR_{height} was calculated for this subset of 308 saplings.

We used general linear mixed effects models or LMMs (*lmer*, using the *R* package *lmerTest* Kuznetsova et al., 2017)) to first examine if RGR_{girth} differed between dung treatment and control plots. In these models, we included treatment (dung/control), initial sapling girth , sapling density and forest type as fixed effects and species and site (or plot-pair) as random effects. Random effects were excluded if they explained negligible variance and resulted in model singularity. All continuous predictors were standardized (mean = 0, standard deviation = 1) to make their effect sizes comparable. Further, we included the three-way and two-way interactions involving dung treatment, sapling density and initial girth, since one of our objectives was to examine if elephant dung mediates neighborhood competition which could depend on the focal sapling's size-dependent nutrient requirements. A positive effect of the interaction involving dung treatment and sapling density would suggest that dung treatment buffers saplings against negative-density dependence. We compulsorily included the full three-way interaction between treatment, sapling density and size, as these interactions with treatment were of our *apriori* interest. If outliers violated model assumptions of LMMs, we used robust LMMs which downweigh extreme outliers (using *lmer* function in *robustlmm*

package, Koller, 2016). We similarly modeled absolute change in girth (mm), where we included standardized total duration (between final and initial measurement day) as an additional fixed effect. While we initially included grass cover, forb cover and shrub cover as additional fixed effects in our models, none of these variables had a significant effect on any response variable; thus, they were removed from all models for simplicity.

Similar to the modelling of RGR_{girth}, we also modelled RGR_{height} based on the subset of 308 saplings mentioned earlier. Here, initial height was included in place of the fixed effect of initial girth.

Statistical analyses of mesocosm experiment data

To examine how dung treatment affects inter-PFT competition between N-fixers and non-N-fixers, we analyzed the final sapling biomass data in two ways. First, we tested the effect of elephant dung on final sapling biomass, using an LMM containing the fixed effects arising from a full interaction between treatment (control/dung), PFT (N-fixer/non-N-fixer) and competition type (mixture/monoculture). To account for any variation due to initial size, initial girth (standardized, mean = 0, SD = 1) was included as a fixed effect, while species identity and block were used as random effects. To infer the effect of elephant dung on the competitive ability of each PFT, we considered the estimated effect (from LMM) of dung treatment on sapling biomass under inter-PFT competition. Second, we obtained the relative competitive strength (RCS) of each PFT, using sapling total biomass as

$$Relative\ competitive\ strength = \frac{performance\ under\ inter\text{-}PFT\ competition}{performance\ under\ intraspecific\ competition} \qquad \textit{Equation 2}$$

A PFT's is considered a better competitor under inter-PFT competition if its RCS exceeds 1.0 or if it reduces the RCS of the competing PFT (Sitters & Olde Venterink, 2021). To examine this, we used LMMs to model RCS as a function of the fixed effects arising from a full interaction between treatment (control/dung) and PFT (N-fixer/non-N-fixer). We also accounted for the variation in RCS due to the initial size differences between the saplings being compared (girth in mixture pot/girth in monoculture pot, fixed effect) and the random effects of species identity. Further, we included mixture pot ID as a random effect because for the focal sapling of each PFT competing in each mixture pot (i.e. inter-PFT competition pot), two RCS values were obtained due to its comparison with the two conspecific saplings in the corresponding monoculture pot. We inferred a PFT's competitive ability in two ways. We first obtained the estimated marginal means from the LMM (using *emmeans*) for each group in the treatment × PFT interaction to test if each PFT's RCS was significantly different from the null expectation of 1.0 (which implies similar performance in inter-PFT and conspecific competition). We checked if each PFT's "RCS>1.0 or not" status changed from control to dung treatment conditions. Second, we examined the estimated effects (i.e., slope estimates) in the LMM to test if dung treatment significantly shifted the RCS value of the PFTs, compared to control conditions.

Quantifying nitrogen redistribution by elephants

To understand the broader implications of our experiments, we estimated annual rates of nitrogen redistribution per km^2 by elephants in Nagarahole following an earlier approach to quantify carbon stocks in elephant dung (Sandhage□Hofmann et al., 2021) as follows:

$$\text{Nitrogen (kg km} - 2\,\text{y} - 1) \;=$$

$$\text{avg. wet weight of dung pile (kg)} \;\times\; \text{dry weight as proportion} \;\times\; \text{N\% in dung (mg/g)} \;\times$$

$$\text{dung deposition rates (day} - 1) \;\times\; \text{elephant density (km} - 2) \;\times\; 365 \text{ (days)}$$

Equation 1

We obtained average wet weight by measuring whole fresh dung piles (N=42) in the field. To estimate dry weight, we collected ~200-400g of sample for each dung pile, sun dried them initially, and then dried them further in the lab at 60° C for ~60 hours. We then weighed them to obtain dry weight as a fraction of the original wet weight. Nitrogen content in elephant dung was quantified for three seasons using LecoCN analyzer in a parallel study on elephant diet (Gautam et al., 2024), to which we added data from another season (Table S4). Elephant density in Nagarahole and dung deposition rates of Asian elephants were taken from previous studies.

RESULTS

<u>Field experiment</u>: *Elephant dung increases sapling growth and alters neighborhood competition*

Spatial differences in sapling growth in response to dung deposition were clearly evident, supporting *Prediction 1*. The girth of saplings treated with dung increased on average by 16% — a relative increase of >40% over the 9% increase in the control plots 10m away (Fig. 2). Accordingly, the robust LMMs showed that dung addition enhanced RGR_{girth} by 37% relative

to control saplings (Table 1). Importantly, there was a significant effect of the dung treatment × sapling density × sapling size interaction (Fig. 3). While larger saplings in control plots expectedly showed a steep decline in RGR_{girth} with increasing sapling density, those receiving the dung treatment were buffered against the negative density-dependent effects, consistent with *Prediction 2*. The robust LMMs of the absolute change in girth (84% greater increase in absolute girth) in response to dung addition mirrored responses in the case of RGR_{girth} (Fig. S1a, SI Table S1). In contrast, the robust LMMs of RGR_{height} revealed no effect of dung treatment or its interaction with density and size (Fig. S1b, Table S2).

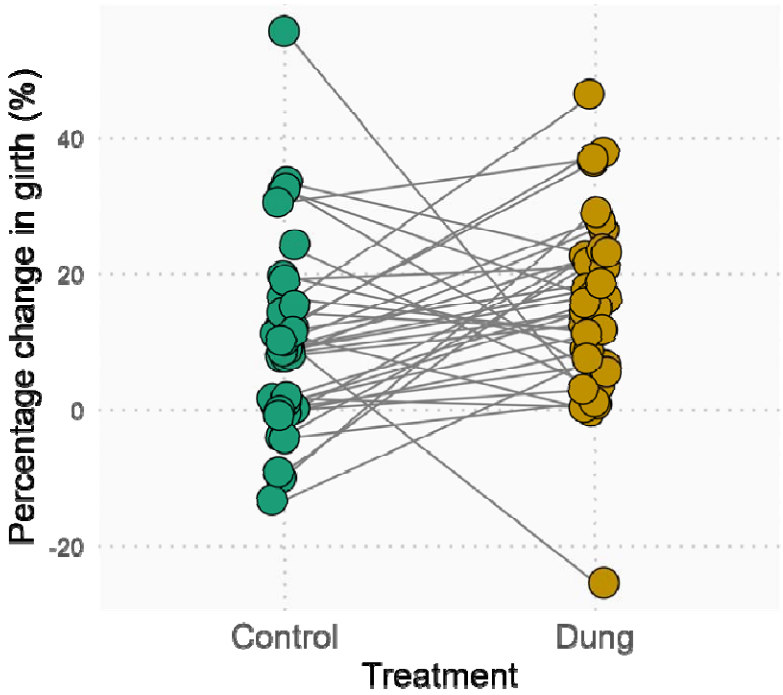

Figure 2: Observed within-plot mean (averaged across all individuals) percentage change in girth of saplings relative to their initial girth, in 36 paired plots of the field experiment. An increased growth in response to dung treatment is evident in the majority of pairs, relative to control plots 10m away.

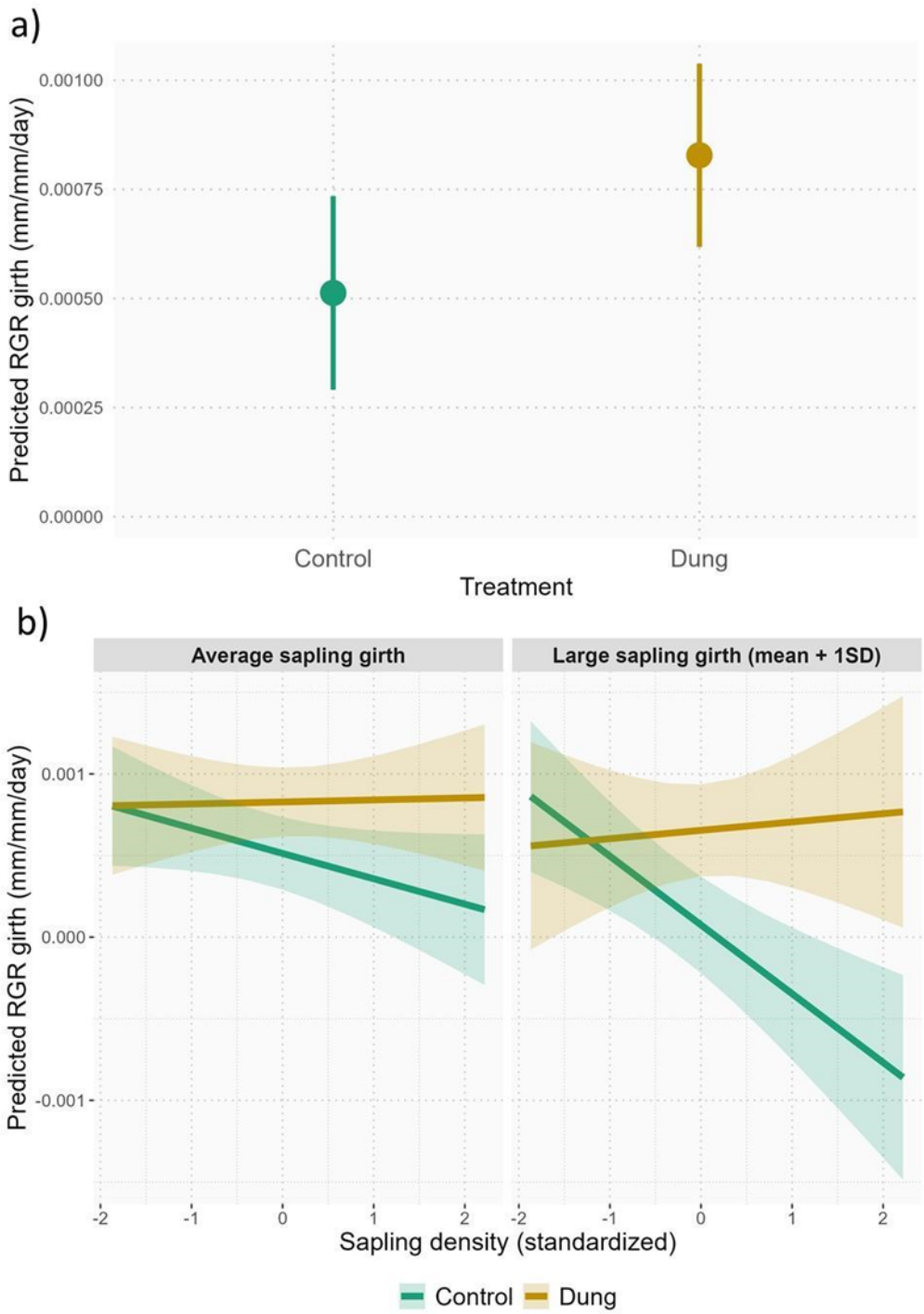

Figure 3: Predicted RGR_{girth} under dung treatment and control. a) main effect of dung input: dung deposition sites are growth hotspots. b) 3-way interaction between dung, sapling density and size: dung treatment buffers against the strong negative density dependence seen under

control conditions. Left and right panels represent effects at average sapling size and at larger sapling size (mean + 1SD), respectively. Error bars represent 95% confidence intervals.

Table 1: Robust LMMs showing RGR in sapling girth increasing with dung input, with this effect being especially evident for larger saplings at higher sapling density. Terms of interest are marked blue and significant effects marked bold (based on 95% CIs).

	Estimate	S.E.	CI lower	CI upper
Intercept (reference: control)	**0.00051**	**0.00011**	**0.00029**	**0.00073**
Treatment (Dung)	**0.00032**	**0.00013**	**0.00007**	**0.00056**
Sapling density	-0.00016	0.00009	-0.00033	0.00001
Initial girth	**-0.00044**	**0.00010**	**-0.00063**	**-0.00025**
Forest type – MDF	-0.00016	0.00014	-0.00042	0.00011
Forest type – Teak	**-0.00066**	**0.00023**	**-0.00110**	**-0.00021**
Treatment (Dung) × Sapling density	0.00017	0.00013	-0.00008	0.00042
Treatment (Dung) × Initial girth	**0.00026**	**0.00013**	**0.00001**	**0.00052**
Sapling density × Initial girth	**-0.00027**	**0.00008**	**-0.00043**	**-0.00011**
Treatment (Dung) × Sapling density × Initial girth	**0.00030**	**0.00014**	**0.00003**	**0.00058**

<u>Ex-situ mesocosm experiment</u>: *Non-N-fixers outcompete N-fixers under dung input*

Both analyses, of final sapling biomass and relative competitive strength (RCS), suggested that elephant dung affected inter-PFT competition, supporting *Prediction 3*. When in inter-PFT competition, N-fixers and non-N-fixers had similar biomass under control conditions (Figure 4a, Table 2). In contrast, dung addition resulted in non-nitrogen fixers accumulating over twice the biomass as nitrogen-fixers (non-N-fixers: mean=21.79, 95% C.I. = 17.07—26.50; N-fixers: mean=8.99, 95% C.I. = 3.66—14.30) (group-wise means in Table S3).

In the absence of dung input (i.e., control conditions), N-fixers performed better under inter-PFT competition with non-N-fixers than under intra-specific competition (mean RCS= 2.42, P=0.019, null RCS=1.0) (Figure 4b, Table 3a). In contrast, such better performance under inter-PFT competition did not hold when dung was added. The non-N-fixers showed similar performance under inter-PFT and intraspecific competition in both control condition or dung treatment (RCS did not differ from 1.0), although under dung treatment they appeared to perform better under inter-PFT competition (mean RCS =1.81, P=0.093). The estimated effects in LMMs showed that dung treatment appeared to substantially increase the RCS of non-N-fixers (i.e., improved performance under inter-PFT vis-à-vis intraspecific competition) compared to control conditions, although this effect was statistically not significant ($\text{estimate}_{\text{dung}}$ = 1.294, P=0.053, Figure 4b, Table 3b). Further, dung treatment appeared to

reduce the RCS of N-fixers, but not significantly (estimate$_{dung}$ = -0.673, P=0.232).‗ ‘

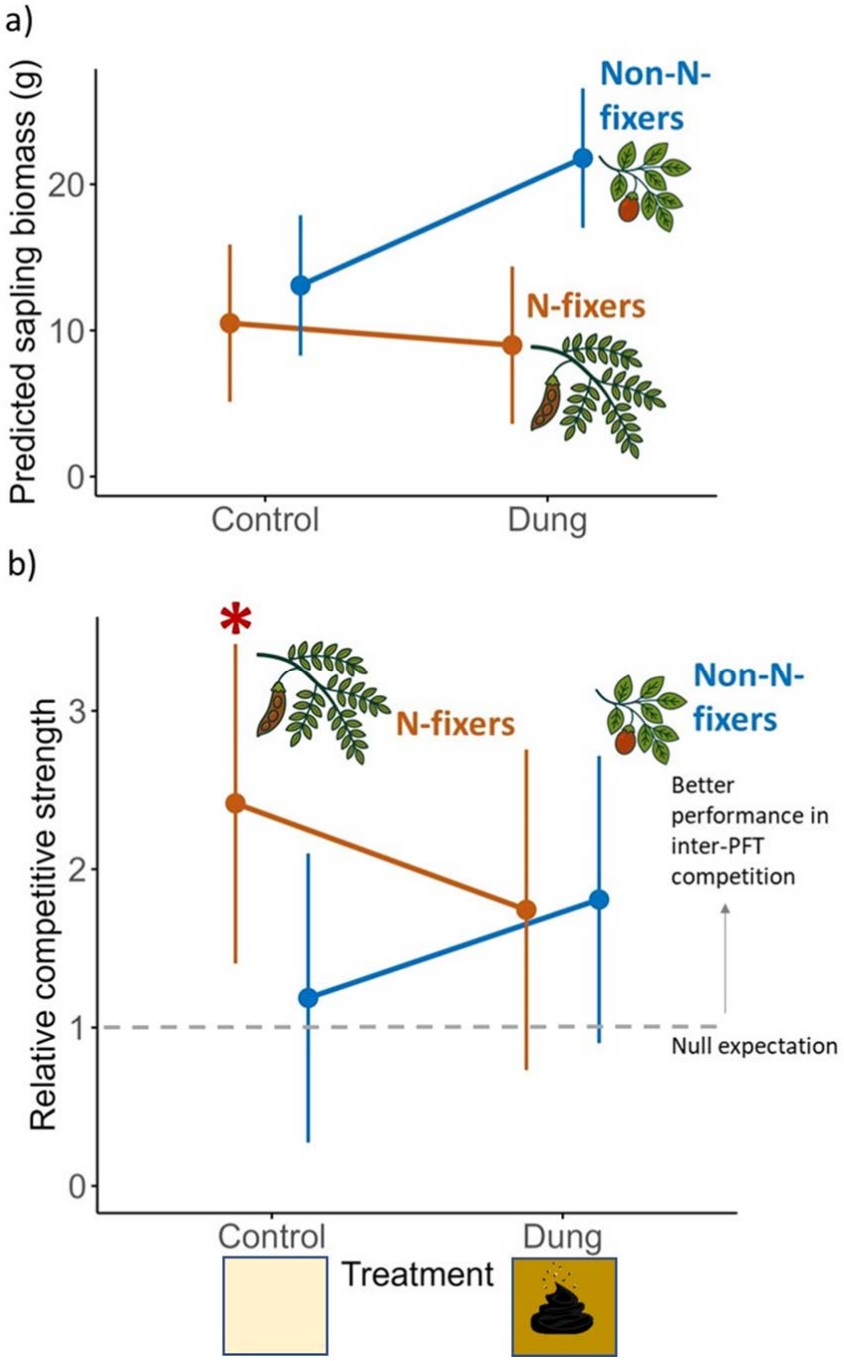

Figure 4: Outcomes of inter-PFT competition between N-fixers and non-N-fixers in the mesocosm experiment. a) Predicted total sapling biomass under inter-PFT competition (based on robust LMM): when supplied with dung, non-N-fixers outcompete N-fixers under mixture competition. b) Predicted relative competitive strength (RCS, based on LMM): RCS is

significantly >1.0 for N-fixers under control, dung treatment did not significantly change the RCS of either PFT. RCS = performance under inter-PFT competition / intraspecific competition. Error bars represent 95% confidence intervals around estimated means.

Table 2: Robust LMM of total sapling biomass under control and dung treatment, and under monoculture and mixture (i.e., inter-PFT) competition in the mesocosm experiment. Terms of *a priori* interest are marked blue and effects different from 0 are marked bold.

	Estimate	SE	Lower CI	Upper CI
Intercept (reference: control, N-fixer, monoculture)	**8.017**	**2.341**	**3.429**	**12.604**
Treatment (Dung)	0.013	1.955	-3.818	3.844
Competition type (Mix)	2.479	2.395	-2.215	7.173
PFT (Non-N-fixer)	**5.955**	**2.978**	**0.119**	**11.791**
Initial girth (standardized)	**2.155**	**0.719**	**0.745**	**3.564**
Treatment (Dung) × Competition type (Mix)	-1.520	3.384	-8.152	5.112
Treatment (Dung) × PFT (Non-N-fixer)	0.494	2.789	-4.973	5.962
PFT (Non-N-fixer) × Competition type (Mix)	-3.371	3.385	-10.005	3.263
Treatment (Dung) × Competition type (Mix) × PFT (Non-N-fixer)	**9.725**	**4.796**	**0.326**	**19.125**

Table 3: Results from the LMM of relative competitive strength (RCS). a) Estimated mean RCS: only N-fixers had RCS>1.0 (null expectation), b) LMM summarizing the effect sizes: non-N-fixers increased their RCS under dung treatment but not significantly (rows of interest are marked in blue). Rows with P<0.05 are marked in bold.

a) Estimated mean RCS of PFTs

Treatment: PFT	Mean	95% CI	Null	SE	df	*t*	*P*
Control: N-fixer	**2.42**	**1.28 - 3.56**	**1**	**0.52**	**11.4**	**2.722**	**0.019**
Dung: N-fixer	1.74	0.61 - 2.88	1	0.52	11.5	1.430	0.180
Control: Non-N-fixer	1.19	0.22 - 2.15	1	0.468	23.7	0.399	0.693
Dung: Non-N-fixer	1.81	0.85 - 2.76	1	0.463	24.2	1.747	0.093

b) LMM summary	Estimate	SE	df	*t*	*P*
Intercept (reference category: Control, N-fixers)	**2.416**	**0.509**	**15.849**	**4.751**	**<0.001**
Standardized initial size ratio	0.208	0.200	75.096	1.041	0.301
Treatment (Dung)	-0.673	0.553	35.273	-1.217	0.232
PFT (Non-N-fixer)	-1.229	0.610	14.775	-2.014	0.063

Treatment (Dung) × PFT (non-N-fixer)	1.294	0.654	60.190	1.978	0.052

The overall magnitude of nitrogen redistribution

We estimated that elephants annually produce 11038 such nutrient-rich patches/ km^2 on average in these tropical forests, amounting to an annual cycling of 218.88 kg N/km^2 through this pathway alone (Table S4). On a per capita basis, each adult elephant redistributes ~130.29 kg N/year throughout its home range by creating 6570 dung sites/year (Table S4). Elephant dung piles are fertility hotspot as their nitrogen content (annual average = 0.971%) is substantially higher than the upper soil layers in this landscape's deciduous forests (0.14 to 0.31%; Mani et al., 2018, 0.40% in Swamy and Proctor, 1994; 0.26% in Ramachandra et al., 2012).

DISCUSSION

The impact of megaherbivores on vegetation through large-scale redistribution of nutrients has been poorly documented (Sitters & Olde Venterink, 2021), especially in mesic regions (Hyvarinen et al., 2021). Our experiments offer important insights into the bottom-up effects of megaherbivores. We found that elephant dung deposition sites 1) act as hotspots of plant growth, 2) weaken the negative effects of neighborhood competition, and 3) shift the competitive balance between plant functional types (PFTs) differing in nutrient limitation, by favoring non-N-fixers over N-fixers. Importantly, 4) the magnitude of such effects is substantial; we estimate that elephants create >11000 nutrient-rich sites annually in these mesic tropical forests. These findings highlight the role of megaherbivores as modifiers of species interactions key to plant community assembly, and as promoters of fine-scale vegetation heterogeneity across their vast home ranges.

Elephant dung deposition creates hotspots of plant growth

We found that the large inputs of nitrogen (~19.83g N, Table S4) make elephant dung deposition sites hotspots for plant growth. Elephant dung treatment strongly enhanced growth in the girth of woody saplings compared to adjacent control plots. However, this growth-enhancing effect was not evident for plant height, possibly because height responses may take longer to manifest than girth (eg. Noyer et al., 2019; Seymour et al., 2022), potentially reflecting preferential allocation to bark thickening before height as a strategy to reduce mortality (eg. from fire Lawes et al., 2011). Such potentially delayed effects on height could explain why the only previous experiment of this nature could not detect growth-enhancing effects of elephant dung in central Africa's rainforests (Kalbitzer et al., 2019). Kalbitzer et al. analyzed height, and not girth, and did not find growth-enhancing effects of elephant dung

one year after the experimental dung input. However, shade-tolerant saplings in their study enhanced leaf production, suggesting that the allocation of this productivity to increases in shoot length may be delayed but potentially detectable with longer monitoring.

Elephants modify ecological interactions key to plant community assembly

We found that nutrient inputs via dung can locally alter plant competition in two ways. First, elephant dung can buffer saplings against neighborhood competition or negative density-dependence. This was especially evident in the case of large saplings whose growth (both RGR and absolute growth in girth) under control conditions declined sharply with sapling density. In contrast, dung addition resulted in a near consistent ecological release from neighborhood competition for all sapling sizes (see slopes in Fig 3b, Fig S1). Since larger saplings have greater nutrient requirements, their dung-mediated release from neighborhood competition suggests that nutrient input from dung is substantial. Second, our mesocosm experiment revealed that dung can modify the outcome of interference competition between PFTs differing in nutrient limitation. Non-N-fixers accumulated more biomass and outcompeted N-fixers when amended with dung but not otherwise. That elephant dung favored non-N-fixers was also evident in the analyses of relative competitive strength (RCS), although less clearly. The otherwise better performance of N-fixers under control conditions (RCS>1.0) did not hold in the presence of dung, which implies net gains for non-N-fixers under dung input. Dung input also substantially increased the RCS of non-N-fixers, although this effect was statistically inconclusive. Herbivore dung has been previously shown to alter the competitive balance between grasses and woody N-fixers in African savannas (Sitters & Olde Venterink, 2021). Taken together, these findings suggest that such bottom-up effects of

herbivores can be critical in regulating the abundance of different plant types, including woody N-fixers, non-fixers and grasses.

Dung-mediated differences in local competitive outcomes can determine which saplings succeed in transitioning to the recruitment stage, thereby influencing community composition. Our findings indicate that dung deposition can locally accelerate competitive exclusion along at least two axes: size and nutrient limitation among PFTs. First, although larger saplings were negatively affected by neighborhood density under control conditions, they were buffered against neighborhood competition in the presence of dung (Fig. 3b, Fig. S1). This similarity in RGR between large and small saplings, even at high densities, suggests that herbivores can reinforce or even amplify existing size differences through their dung inputs. Such dung-mediated ecological release from competition can reinforce the beginners' advantage to larger saplings (for example, taller understory plants have advantage in light competition), thus potentially excluding smaller saplings. Second, along the nutrient-limitation axis, herbivore dung addition is likely to favor nutrient-limited PFTs. In our mesocosm experiment, nitrogen-rich dung shifted the competitive balance between non-N-fixers and N-fixers (Fig 4), suggesting that dung deposition could bring about fine-scale spatial differences in the relative abundances of these two PFTs, favoring non-N-fixers. It must be noted that the observed effects on inter-PFT competition may be an underestimate as we used only <10% (500g) of the amount of an average elephant defecation (6.88 kg) in our treatments. Importantly, such effects on the coexistence among plant species may be widespread along other PFT axes of nutrient limitation, for example, fast- vs- slow-growing and shade-tolerant vs. light-demanding species. Localized competitive exclusion along these axes could thus change plant communities in multiple ways. Such dung-mediated gains by

large, nutrient-limited plants can potentially explain the increases in species evenness often reported in herbivore presence (Jia et al., 2018).

Conservation implications

Our study has implications for understanding how defaunation may impact ecosystem functioning through effects on species interactions shaping plant communities. (Poulsen et al. (2018) speculated that the loss of nutrient cycling associated with megaherbivores would result in a loss of the light-demanding species as they are more nutrient-limited. While we did not focus on the light-demanding/shade-tolerant distinction, our experiment suggests that elephant dung indeed favors nutrient-limited PFTs (non-N-fixers) and thus elephant presence can substantially shift the composition of plant communities, possibly even at the landscape scale through cumulative effects of numerous temporary growth hotspots generated over multiple years. Nevertheless, we note the contradictory finding where elephant dung had small positive effects on shade-tolerant species that are less nutrient limited, although these results were based only on leaf production (Kalbitzer et al., 2019). In addition to the effects at the landscape level, we propose that enhanced fine-scale heterogeneity in community composition is another key consequence of such nutrient redistribution by megaherbivores. The large-scale annual production of nutrient hotspots by elephants (totally >11000/km^2/year in Nagarahole) likely amplifies vegetation heterogeneity through fine-scale differences in growth and competition, which is in line with earlier findings that herbivore dung deposition increases soil heterogeneity (Afzal & Adams, 1992; Ferraro & Lienau, 2025; Hobbs, 1996). Importantly, the functional importance of megaherbivores is underscored by the fact that vegetation responses intensify with the amount of dung input (Valdés-Correcher et al., 2019),

which is exceptionally large in the case of megaherbivores. Thus, protecting megaherbivore populations is critical to conserving such important functional roles.

Future directions and Conclusion

Our experiments open several possibilities to further understand bottom-up effects of megaherbivores. As these dung sites are temporary nutrient hotspots, they would only induce short-term spatial differences in plant growth. To what extent these pulses of altered growth trajectories shape the recruitment fate to mature stages can only be understood through longer-term studies, or models that consider such pulsed nutrient effects on plant growth and competition. Second, we encourage investigations on inter-PFT competition along other axes of differentiation, including fast- vs slow-growth and shade-tolerant vs light-demanding species. Third, stoichiometric ratios of different growth-limiting elements in dung can be important for plant growth and interactions. Megaherbivores have high phosphorous requirements and thus their faeces tend to be P-depleted i.e., with high N:P ratios (Le Roux et al., 2020) that could favour non-N-fixers over N-fixers (Sitters & Olde Venterink, 2021).

In conclusion, our study highlights large-scale nutrient redistribution by megaherbivores as an underappreciated driver of plant growth and species interactions that generate fine-scale vegetation heterogeneity. Such functional roles of megafauna remain understudied in the mesic tropics (Hyvarinen et al., 2021), particularly in South and Southeast Asia (Sankaran & Ahrestani, 2016). These regions have faced extensive defaunation and deforestation in both modern and prehistoric times (Svenning et al., 2016). Localized restoration efforts in such ecosystems could benefit from a mechanistic understanding of herbivore impacts (eg.

Geremia et al., 2025), including the relative impacts of top-down and bottom-up regulation. Our findings suggest that large herbivore rewilding could benefit conservation actions by restoring species interactions and fine-scale vegetation heterogeneity. We call for further investigations to advance a more comprehensive understanding of herbivore functions in these understudied ecosystems.

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AUTHOR CONTRIBUTIONS

HG: funding acquisition, conceptualization and research design, fieldwork and laboratory analyses, formal statistical analyses, writing the first draft, review and editing; MT: fieldwork; MS: conceptualization and research design, review and editing. All authors read and approved the manuscript for submission.

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SUPPLEMENTARY INFORMATION

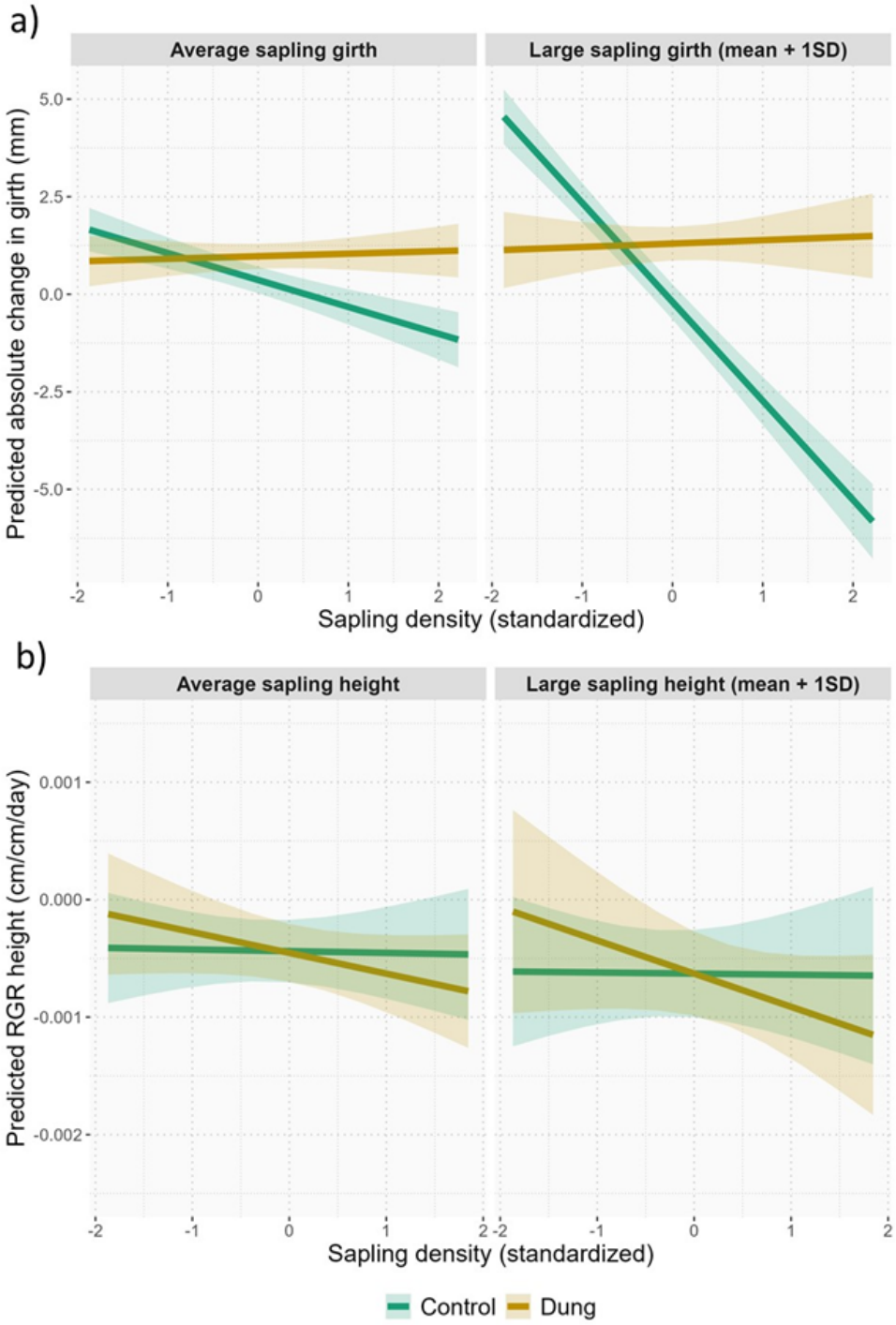

Figure S1. Size-dependent effect of neighborhood competition on sapling growth under dung treatment and control conditions. The buffering provided by dung input against negative

density dependence for larger saplings is evident for a) absolute change in girth, while b) RGR_{height} does not show any main effect of dung treatment or interaction.

Table S1: Robust LMM of absolute change in girth (mm) showing clear positive effects of elephant dung input on growth of sapling girth.

	Estimate	SE	CI lower	CI upper
(Intercept)	**0.366**	**0.173**	**0.028**	**0.704**
Treatment (Dung)	**0.608**	**0.193**	**0.229**	**0.987**
Sapling density	**-0.689**	**0.133**	**-0.95**	**-0.429**
Initial girth	**-0.561**	**0.148**	**-0.85**	**-0.271**
Duration	0.017	0.113	-0.204	0.238
Forest type – MDF	0.021	0.211	-0.392	0.435
Forest type – Teak	-0.465	0.385	-1.219	0.289
Treatment (Dung) × Sapling density	**0.755**	**0.197**	**0.369**	**1.14**
Treatment (Dung) × Initial girth	**0.885**	**0.198**	**0.497**	**1.273**
Sapling density × Initial girth	**-1.847**	**0.125**	**-2.093**	**-1.602**
Treatment (Dung) × Sapling density × Initial girth	**1.87**	**0.211**	**1.455**	**2.284**

Table S2: Robust LMMs showing RGR_{height} being not affected by dung input. Terms of interest are marked blue and significant effects marked bold (based on 95% CIs).

	Estimate	S.E.	CI lower	CI upper
(Intercept)	**-0.00044**	**0.00014**	**-0.0007**	**-0.00017**
Treatment (Dung)	-0.00001	0.00016	-0.00032	0.00029
Sapling density	-0.00001	0.00012	-0.00025	0.00022
Initial height	-0.00019	0.00012	-0.00042	0.00004
Forest type – MDF	0.00022	0.00017	-0.00011	0.00054
Forest type – Teak	**0.00078**	**0.00028**	**0.00023**	**0.00134**
Treatment (Dung) × Sapling density	-0.00016	0.00017	-0.00049	0.00017
Treatment (Dung) × Initial height	0.00001	0.00017	-0.00032	0.00034
Sapling density × Initial height	0.00001	0.00012	-0.00022	0.00023
Treatment (Dung) × Sapling density × Initial height	-0.00011	0.00018	-0.00046	0.00024

Table S3: Estimated mean biomass for different group in the treatment x competition type x PFT. The rows of interest for the effect of dung on inter-PFT competition are marked in blue. Means were obtained from LMMs using *emmeans*.

Treatment	Competition type	PFT	Mean	SE	Lower 95% CI	Upper 95% CI
Control	Monoculture	N-fixer	8.02	2.34	3.43	12.6
Dung	Monoculture	N-fixer	8.03	2.34	3.44	12.6
Control	Mixture	N-fixer	10.5	2.72	5.17	15.8
Dung	Mixture	N-fixer	8.99	2.72	3.66	14.3
Control	Monoculture	Non-N-fixer	13.97	1.97	10.12	17.8
Dung	Monoculture	Non-N-fixer	14.48	1.96	10.64	18.3
Control	Mixture	Non-N-fixer	13.08	2.42	8.33	17.8
Dung	Mixture	Non-N-fixer	21.79	2.41	17.07	26.5

Table S4: Quantification of annual nitrogen redistribution via dung deposition by elephants in Nagarahole National Park, southern India. N% was averaged from N% quantified at every 3 months: October 2022 (1.151%), January 2023 (1.027%), April 2023 (0.738) based on Gautam et al. 2024, and August 2023 (0.967%) quantified in this study. Estimates of elephant density (~1.68/km^2) in Nagarahole were obtained from the Karnataka Elephant Survey 2010 (Baskaran and Sukumar 2011[1]). We used 18/day as the daily defecation rate as reported for Mudumalai in this landscape (Santosh and Sukumar 1995[2]) as well as another study with a large sample size (Hedges 2012 pp. 82[3]).

Variable	Mean (SD, N)	Source
Nitrogen % in dung	0.9707 (4 seasons, 113 samples)	Gautam et al. 2024 and this study
Wet weight of a dung pile (kg)	6.881 (2.333, 42)	This study
Proportion of dry mass in dung	0.297 (0.031, 29)	This study
Defecation rate (day^{-1})	18	Santosh and Sukumar 1995, Hedges 2012, pp.82
Elephant density (km^{-2})	1.68	Baskaran and Sukumar 2011
Total annual dung deposition sites (km^{-2})	11038	-
N deposited at each defecation site	19.831g	This study
Total annual N deposition (kg km^{-2})	218.882	This study

Per capita annual N deposition (throughout the range)	130.287	This study
Per capita production of dung sites (throughout the range)	6570	-

[1]Baskaran, N., Sukumar, R., 2011. Karnataka Elephant Census 2010. Technical Report submitted to Karnataka Forest Department – March 2011. Asian Nature Conservation Foundation and Centre for Ecological Sciences, Bangalore, Karnataka.

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