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Primates create seedling growth hotspots through pattern of dung deposition

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Abstract

Primates play important roles in tropical forests through seed dispersal and herbivory. They comprise a large part of the biomass of forest communities and tend to have clumped patterns of defecations (i.e. at favoured food trees or sleeping sites). Therefore, they may also play important roles in accelerating ecosystem nutrient cycling. Here we conduct a controlled growth experiment to quantify the effect of the addition of primate dung on the growth of both light-demanding and shade-tolerant seedlings over 1 year in Kibale National Park, Uganda. A mixed model analysis revealed that light-demanding species were affected by the natural dung treatment and plants with small initial size had accelerated growth, whereas there was no effect on plant growth for shade-tolerant species. The long-term implications of increased dung deposition on the local tree community are unclear as shade-tolerant species may only show an effect over the long-term and light-demanding species may only be able to take advantage of the increased growth if subsequently exposed to high light conditions, such as a treefall gap.

Résumé

Les primates jouent un rôle important dans les forêts tropicales par la dispersion des graines et le broutage. Ils constituent une grande partie de la biomasse des communautés forestières et ont tendance à grouper des modèles de défécations (c'est-à-dire sur des arbres alimentaires ou des sites aménagés pour dormir privilégiés). Par conséquent, ils peuvent également jouer un rôle important dans l'accélération du cycle des éléments nutritifs dans l'écosystème. Ici, nous effectuons une expérience de croissance contrôlée pour quantifier l'effet de l'ajout de bouse de primate dans la croissance simultanée d'exigences de lumière et tolérance de l'ombre plus d'un an dans le Parc national de Kibale, Ouganda. Une analyse de modèle mixte a révélé que les espèces exigeant de lumière sont affectées par le traitement naturel des excréments et que les plantes de taille initiale petite avaient une croissance accélérée, alors qu'il n'y avait aucun effet sur la croissance des espèces tolérantes à l'ombre. Les conséquences à long terme d'une augmentation de dépôts d'excréments sur la communauté d'arbre locale ne sont pas claires, car les espèces tolérantes à l'ombre ne peuvent montrer un effet sur long terme et les espèces exigeantes en lumière ne peuvent uniquement bénéficier de la croissance accrue si elles sont exposées ultérieurement dans des conditions de forte luminosité, tel qu'un vide de la chute des arbres.

KEYWORDSfertiliser, Kibale National Park, nutrient, *Ptilocolobus tephrosceles*, primate, red colobus, Uganda

1 | INTRODUCTION

It is well recognised that animals can play important roles in structuring plant communities (Power, 1997). There are several detailed studies that quantify these roles (e.g., for prairie dogs, *Cynomys* spp.; van Nimwegen, Kretzer, & Cully, 2008, sea otters, *Enhydra lutris*; Estes & Palmisano, 1974, or beavers *Castor canadensis*; Naiman, 1988). However, the role played by elephants (*Loxodonta africana*) is perhaps the best known (Dublin, Sinclair, & Mcglade, 1990; Laws, 1970; Stuart, Hatton, & Spencer, 1985), because they can shift forests to grasslands (Stuart et al., 1985) or prevent forests from recovering (Lawes & Chapman, 2006; Paul, Randle, Chapman, & Chapman, 2004).

Primates also play important roles in determining tropical forest structure and regeneration by acting as seed dispersers (Andresen, 2000; Effiom, Nunez-Iturr, Smith, Ottosson, & Olsson, 2013; Kaplin & Lambert, 2002). Their importance is demonstrated by the fact that primates constitute between 25% and 40% of the frugivore biomass in these forests and they defecate or spit out a large number of viable seeds (Chapman, 1995; Lambert & Garber, 1998; Wrangham, Chapman, & Chapman, 1994); reviewed by Chapman & Dunham, 2018). For example, in a single day, the individuals in the redtail monkey (*Cercopithecus ascanius*) population could potentially remove 24,492 fruits/km² and disperse their fruits (Lambert, 1999). In addition, the extensive herbivory of some folivorous primates can influence the forest community structure by retarding tree growth and increasing mortality for specific tree species (Chapman, Bonnell, Gogarten et al., 2013; Chapman, Bonnell, Sengupta, Goldberg, & Rothman, 2013).

Given the biomass of folivorous and frugivorous primates and the amount of food they eat daily, primates produce large amounts of dung. This suggests that primates may also play an important role in nutrient cycling—a topic that has rarely been studied (Feeley, 2005; Pouvelle, Feer, & Ponge, 2008; Stevenson & Guzmán-Caro, 2010). In general, large animals are thought to play an important role in accelerating ecosystem biogeochemical cycling (Ripple et al., 2015). Nutrients that would have been locked in mature leaves, taking months or years to fall to the forest floor and decompose, are liberated for use through animal consumption, digestion, defecation and urination. On the other hand, nutrients in fruits will not be liberated much faster than if they were not eaten. Both folivorous and frugivorous primates will however change the spatial distribution of nutrients. Many species of primates use one or a few sleeping sites at fixed locations (Anderson, 1984; Chapman, Chapman, & McLaughlin, 1989; Neves, Feer, Salmon, Chateil, & Ponge, 2010) and at these sites large amounts of dung are deposited daily (Chapman, 1989; Lieberman, Hall, Swaine, & Lieberman, 1979). Furthermore, while travelling a group will typically follow arboreal pathways (Di Fiore & Suarez, 2007), which will therefore receive substantial amounts of dung.

Receiving input from dung is important because in tropical rainforests available nutrients are recycled quickly back into plant materials, and soils are therefore usually poor in nutrients (Sugihara, Shibata, Ze, Araki, & Funakawa, 2015). Plant growth is therefore nutrient limited, and the addition of nitrogen (N), phosphorus (P), and

potassium (K) can increase seedling growth (Santiago et al., 2012). As a result, sites receiving substantial amounts of dung may represent “hotspots” for seedling growth. Primates may often create such hotspots. For example, howler monkeys (*Alouatta palliata*), who have a mixed diet of fruits and leaves, produce dung that contained 1.8%–2.1% N and 0.3%–0.4% P (based on dry mass measurements; Milton, Soest, & Robertson, 1980; Nagy & Milton, 1979). The N and P levels will be a function of the species, and their diet, but in general, dung contains much greater concentrations of nutrients than leaf litter (~1% N and 0.04% P for tropical moist forests; Vitousek & Sanford 1986). Thus, primate dung is expected to be an important natural fertiliser.

Our objective was to conduct a controlled growth experiment to quantify the effect of the addition of primate dung on the growth of seedlings over one year in Kibale National Park, Uganda. However, plant species have different resource allocations (Zanne & Chapman, 2005; Zanne, Chapman, & Kitajima, 2005) and recruitment strategies (Coley, 1983). For example, light-demanding species are better adapted to recruit in gaps and thus use new resources mainly for growth, while shade-tolerant seedlings tend to slowly build their way to the canopy over years or decades and invest more in their roots and defensive mechanism (e.g., plant toxins) so they are not disrupted by herbivory in their slow climb (Grubb, 1977; Richards, 1996; Wright, 2002). Furthermore, these different strategies might vary depending on the size of the plant (e.g., a small plant might invest more resources into growth than a larger plant). Therefore, we tested for differences in the effect of primate dung addition between light-demanding and shade-tolerant species while controlling for initial size; we expected light-demanding species to have a greater increase in height, and gain more new leaves compared to shade-tolerant species.

2 | METHODS

2.1 | Study design

The study was conducted between April 2016 and May 2017 in Kibale National Park (795 km²; 0°13′–0° 41′N and 30°19′–30°32′E) in western Uganda near the foothills of the Rwenzori Mountains. Kibale is a mid-altitude (920–1,590 m), moist-evergreen forest that receives a mean annual rainfall of 1676 mm in two rainy seasons (based on data collected between 1990 and 2016 (measured at Kanyawara, Chapman & Lambert, 2000, Stampone, Hartter, Chapman, & Ryan, 2011)). The park is primarily forest (~60%) with areas of anthropogenic and natural grassland (~15%), and woodlands (~6%) (Chapman & Lambert, 2000).

In April 2016, 10 experimental plots (4 × 4 m) were set up in an area of old-growth forests, with a control plot placed 15 m away (direction randomly determined). Each set of plots (i.e., sites) were separated by 40 m from the next and were at least 10 m away from any trail, tree fall gap, or other type of disturbance. If the random direction chosen for the control plot was within 10 m of a trail, tree fall gap, or any other type of disturbance, or if the slope or habitat type appeared

different, a new random direction was selected. Approximately 200 red colobus defecations were collected from our long-term focal group and dispersed throughout each experimental plot.

Within each of the 4 × 4 m plots, thirty apparently healthy seedlings between 30 and 100 cm in height (average 63.2 cm) were selected on an ad hoc basis and regardless of species. Seedling height was measured from ground level (clearing fallen leaves) to the tip of the main stem, and the number of leaves was counted. To enable the same seedling to be found the next year, we secured a labelled tag on the forest floor next to it. In May 2017, the plots were revisited, the seedlings relocated, their height remeasured and the number of leaves recounted. If the seedling had died, this was noted and no measurements were made.

2.2 | Data analysis

For the analyses of changes in seedling height and leaf number under different treatment conditions, species were either considered as light-demanding or shade-tolerant species (as per (Zanne & Chapman, 2005, Zanne et al., 2005, Hamilton, 1991). In the final analysis, we did not consider plants that died between the two years nor plants for which the species type (light demanding vs. shade tolerant) was unknown. We also sorted out plants that lost height (more than 2 cm) between the two years, because this is more likely explained by damage to the plant and measurement errors rather than stagnant growth. Doing the same analysis while including all plants or choosing 5 cm as a threshold resulted in the same qualitative results. We were able to include 466 plants in the final analysis. For each of the ten plots treated with monkey dung, we included between 17 and 29 plants (mean ± SD = 24.3 ± 3.4) and between 13 and 27 (mean ± SD = 22.3 ± 4.4) for each of the control plots. These 466 plants belonged to 30 species: 12 light-demanding and 18 shade-tolerant species. A total of 57 light-demanding plants and 186 shade-tolerant plants were included in the experimental plots, and 52 light-demanding plants and 171 shade-tolerant plants were included in the control plots.

2.3 | Structure of statistical models

We used mixed models to analyse whether the treatment of plants with monkey dung affected their growth in height and changes in the number of leaves dependent on the type of plant. As dependent variables, we used either height or number of leaves in 2017 (Measurement₂₀₁₇) and as independent variables the Treatment (control or dunged), and the Type of the plant (light demanding or shade tolerant). Furthermore, we included either height or number of leaves in 2016 (Measurement₂₀₁₆) to control for differences between plants in initial size. Because our question was whether treatment affected plant growth dependent on species type, and whether this effect is dependent on the initial size/number of leaves of the plant, we tested for the effect of the three-way interaction Treatment:Type:Measurement₂₀₁₆. Thus, the structure of the model (without random effects) was as follows:

$$\begin{aligned} \text{Measurement}_{2017} &\sim \text{Treatment} + \text{Type} + \text{Measurement}_{2016} \\ &+ \text{Treatment:Type:Measurement}_{2016} \\ &+ \text{Treatment:Type} + \text{Treatment:Measurement}_{2016} \\ &+ \text{Group:Measurement}_{2016} \end{aligned}$$

We included all two-way interactions that were part of the three-way interaction because all terms that are part of higher terms must be included into such a model. With regard to the random effect structure, we included the random intercepts for Species and Site and the random slopes Measurement₂₀₁₆|Species and Measurement₂₀₁₆|Site because plants of different species and plants in different areas may show variation in growth due to their species and unknown environmental factors (e.g., differences in micro-climate or soil composition).

2.4 | Fitting the Models

We calculated a Gaussian linear mixed models using the lmer function of the lme4 package v1.1-15 (Bates, Mächler, Bolker, & Walker, 2014) in the R programming language v3.4.3. (R Core Team, 2018). Despite the fact that the number of leaves represents a count variable, we did not use a Poisson regression because the number of leaves in the previous year was included as an independent variable. Therefore, using a Poisson model with a log-link function would have assumed that the relationships for leaves between the 2 years is $\log(\text{Leaves}_{2017}) \sim \beta * \text{Leaves}_{2016}$ with β the coefficient estimated by the linear model (all other terms were excluded to simplify the formula). It appeared to us that such a relationship would be less reasonable than a linear relationship for the number of leaves between the 2 years. We used Maximum Likelihood (ML) rather than Restricted Maximum Likelihood (REML) to fit the model (Bolker et al., 2009). Height₂₀₁₇ and Leaves₂₀₁₇ were cube-root transformed before running the model to improve the normality of the model residuals. To maintain the proportional relationship between Height₂₀₁₇ and Height₂₀₁₆ and Leaves₂₀₁₇ and Leaves₂₀₁₆, respectively, we also cube-root transformed these two independent variables. Furthermore, we standardised Height₂₀₁₆ and Leaves₂₀₁₆ after the cube-root transformation by calculating z-scores (i.e., transformed this variable to a mean of 0 and standard deviation of 1) to improve model convergence. We checked the assumption of normally distributed and homogeneous residuals by visually inspecting histograms and a qqplots of residuals, and plots of residuals plotted against fitted values. Furthermore, we visually inspected the distribution of residuals of random effects for a normal distribution. To ensure that no influential cases affected the stability of the models, we excluded subjects one at a time from the data and compared the coefficients of the resulting models (using a function kindly provided by Roger Mundry). To detect potential problems with collinearity, we ran a standard linear model (excluding the random effects) and calculated the variance inflation factor (VIF) using the VIF function of the R-package car v2.1-6 (Fox & Weisberg, 2011). All VIFs were below 1.03, indicating no issues with collinearity.

To establish the significance of the full models, we compared the full with the null models (which only comprised the control variable Measurement₂₀₁₆ and all random effects) by calculating likelihood ratio tests using the R-function ANOVA (with the argument "test = 'Chisq'") (Dobson, 2002; Forstmeier & Schielzeth, 2011). For the effects of individual terms, *p*-values were based on likelihood ratio tests comparing the full model with a model excluding the respective term by using the drop1 function.

3 | RESULTS

Treatment significantly affected growth in height, but the effect was dependent on the plant type and its initial height in 2016: growth of light-demanding species was affected by the dung treatment whereas there was no effect on plant growth for shade-tolerant species (Table 1). This effect on the growth of light-demanding species was dependent on initial size of the plants, and only smaller plants benefited from the dung treatment, (Figure 1). These effects were confirmed when dividing the data into two sets, one that only included light-demanding species, and one that only included shade-tolerant species. We ran the same model as above, but excluded all terms comprising plant type as predictor variable (because each of the two datasets only included plants of one type). For light-demanding species, the full model was significantly better than the null model ($\chi^2 = 14.154$, $df = 2$, $p < 0.001$), and the interaction Treatment:Height₂₀₁₆ showed a significant effect on Height₂₀₁₇ ($\chi^2 = 6.371$, $df = 1$, $p < 0.05$; Table 2). The model predicted that a plant with an initial height of 30 cm would grow to about 31 cm without the addition of dung and to 37.6 cm with the addition of dung. Plants with an initial height of 80 cm were predicted to grow to ~89 cm on average in the second year regardless of the addition of dung, and larger plants treated with dung seemed to have a slight disadvantage: for plants with an initial size of 100 cm, the model predicted a growth to 109 cm when treated with dung and to 113 cm without the addition of dung. Thus, for

the widest range in height of tested plants (30–80 cm) the addition of dung increased the growth between the two years, whereas for some larger plants (80–100 cm) the dung appeared to slow down the growth. For the shade-tolerant species, the full model was not better than the null model ($\chi^2 = 2.0711$, $df = 2$, $p = 0.355$).

In contrast to height, we did not detect an effect of dung treatment on the change in the number of leaves; the model including the three-way interaction Treatment:Type:Height₂₀₁₆ was not significantly better than the null model only comprising Height₂₀₁₆ as fixed effect and all random effects ($\chi^2 = 8.3021$, $df = 6$, $p = 0.2168$). Therefore, we did not further test for the significance of single terms (Forstmeier & Schielzeth, 2011).

4 | DISCUSSION

In this study, we asked: "Do primates create 'hotspots' for seedling growth through their defecations"? Our experiment discovered that small light-demanding species in Kibale benefitted from the augmentation of red colobus dung to the area where they were growing, whereas there was no effect on plant growth for shade-tolerant species. Our expectation was that both light-demanding and shade-tolerant growth forms would benefit from the addition of nutrients in the primate dung. Why the shade-tolerant species did not show an altered growth rate is puzzling. It is possible that the increased N and P provided by the dung was not needed by the plants (i.e. they were not nutrient limited). This seems unlikely for two reasons: first, the soils in the Kibale area are lixic ferralsols which are from geologically old parent materials and low in nutrients and fertility (Majaliwa et al., 2010; Rode, Chapman, Chapman, & Mcdowell, 2003; Rode, Chiyo, Chapman, & Mcdowell, 2006); second, the fact that small light-demanding species show a positive growth effect indicates that growth is nutrient limited, at least under some circumstances.

TABLE 1 Results of a linear mixed model with cube-root transformed Height₂₀₁₇ as the dependent variable

Term	Estimate (SE)	χ^2	<i>p</i>
(Intercept)	4.053 (0.028)	—	—
Treatment (Dung)	0.067 (0.031)		—*
Type (Shade)	0.08 (0.029)		—*
Height ₂₀₁₆	0.459 (0.023)		—*
Treatment (Dung):Type (Shade)	−0.093 (0.036)		—*
Treatment (Dung):Height ₂₀₁₆	−0.072 (0.031)		—*
Group (Understory):Height ₂₀₁₆	−0.087 (0.025)		—*
Treatment (Dung):Type (Shade):Height ₂₀₁₆	0.076 (0.035)	4.563	<0.05

Notes. The full model comprising all variables was significantly better than the null model only comprising Height₂₀₁₆ and all random effects ($\chi^2 = 23.863$, $df = 6$, $p < 0.001$). Treatment and Type were both binary variables with two categories each (Treatment: Control and Dung; Type: Light and Shade). Height₂₀₁₆ was a numerical variable which was cube-root transformed and then standardised by calculating z-scores before running the model. The original mean \pm SD of the cube-root transformed Height₂₀₁₆ was 3.93 ± 0.417 .

*Because the three-way interaction including all variables are significant, the *p*-value of this term has only limited interpretability and is therefore not shown here.

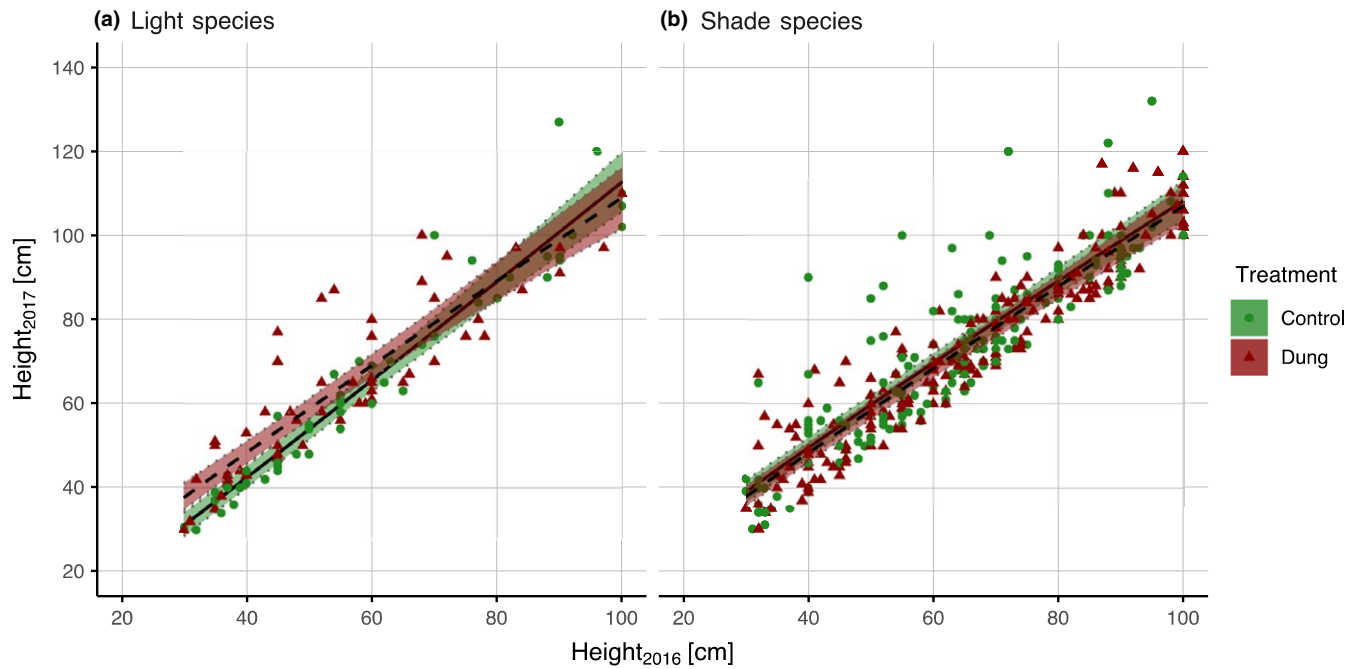


FIGURE 1 Effect of dung treatment on plant growth on a) light-demanding species ($n = 109$ plants) and b) shade-tolerant species ($n = 357$ plants). The solid (control) and dashed (dung treatment) lines show the Height_{2017} predicted by the linear mixed model. The dotted lines depict the bootstrapped 95% confidence intervals ($n = 1,000$ bootstraps). The model was calculated with cube-root transformed Height_{2017} and Height_{2016} values and Height_{2016} was further scaled to a mean of 0 and SD of 1 before running the model. However, to improve the interpretability of the plot both measurements were back-transformed to its original scale [Colour figure can be viewed at wileyonlinelibrary.com]

It is possible that if we had extended the temporal scale of the research, an effect would have been found. Studies of N and P enrichment to soils have found an effect of plant growth in some systems, but the effect was not evident within one growing season (Hatch, Lovell, Antil, Jarvis, & Owen, 2000). The growth process of many shade-tolerant species is often very slow while they build their way to the canopy (Grubb, 1996). For example, *Chrysophyllum* sp. seedlings and saplings grow extremely slowly in the shaded understory; their mean height only doubling every 27 years (Connell & Green, 2000)—thus, a 20 cm seedling could take almost 70 years to reach a metre in height if it survived that long in the understory and did not have the growth advantage of a light gap. The growth rate of saplings (12 species, 331 individuals) that had an initial average height of 1.41 m in 1991 (range: 14 cm–5 m) was analysed in Kibale. When they were first measured, they were judged as being in the shade. After 21 years, their average growth rate was 7.8 cm/year (C. Chapman, unpublished data). This suggests that if monitoring was continued over several years, maybe even decades, a growth effect of nutrient enrichment from dung might be found. It would also be valuable to see if the addition of dung is beneficial to shade-tolerant species when the seed is germinating and the seedling is establishing.

Light demanding species typically do not persist in the understory for long. Rather, their strategy is to disperse widely and aim to be deposited in a light gap, such as a tree fall, where they can grow rapidly (Coley & Barone, 1996). The fact that the light-demanding species were able to grow rapidly matches this fast life-history

strategy, and likely, the plants did not invest heavily in plant secondary compounds to deter herbivory or the storage of energy reserves (Grubb, 1996; Zanne & Chapman, 2005). However, the long-term fate of these seedlings is unknown because they would likely have to be exposed to high light conditions, such as a treefall gap, before they could reach the canopy (Denslow, Schultz, Vitousek, & Strain, 1990). Without such an event, the chances of the seedling persisting are low and it may simply be killed by herbivores (Loiselle & Farji-Brener, 2002).

In contrast to light-demanding species with small initial sizes (30–80 cm), the model predicted that the growth of light-demanding species with a larger initial size (80–100 cm) was actually hampered by the addition of dung. These results, however, should be considered with care. The linear nature of our models made it necessary that the

TABLE 2 Results of linear model with cube-root transformed Height_{2017} as the dependent variable for light-demanding species only

Term	Estimate (SE)	χ^2	p
(Intercept)	4.049 (0.027)	—	—
Treatment (Dung)	0.067 (0.03)	—	—*
Height_{2016}	0.47 (0.02)	—	—*
Treatment (Dung): Height_{2016}	−0.076 (0.029)	6.371	<0.05

Note. For details, see footnote of Table 1.

TABLE 3 An estimation of the amount of dung produced by the diurnal primates of Kibale National Park, Uganda

Species	Group/km ²	Group size	Ind/km ²	Dung weight (kg)	#/day	Dung(kg)/day
<i>Colobus badius</i>	3.4	8	27.2	0.016	6.0	2.61
<i>Ptilocolobus tephrosceles</i>	7	47	329	0.015	6.0	29.61
<i>Cercopithecus ascanius</i>	7	19	133	0.009	12.8	15.32
<i>Cercopithecus mitis</i>	1.8	11	19.8	0.011	10.4	2.27
<i>Lophocebus albigena</i>	3.4	17	57.8	0.025	6.0	8.67
<i>Papio anubis</i>	0.3	33	9.9	0.07	6.0	4.16
<i>Pan troglodytes</i>			1.5	0.109	6.6	1.08
					Total	63.72

Notes. Group density from Chapman, Bortolamiol et al. (2018), group size from Gogarten et al. (2015), chimpanzee density from Emery-Thompson, Kahlenberg, Gilby, and Wrangham (2007). Dung weight and defecation rate from Lambert (2002), Wrangham et al. (1994), and C. Chapman, unpublished data (for the colobines).

lines for the growth rate of dung treated versus control plants would have to intersect at one point, and a model with another (more complex) structure might have predicted that growth rate actually converge for plants larger than 80 cm. Furthermore, this effect was only seen for a small part of the range for which we had fewer data points (see Figure 1). Thus, to investigate whether larger plants treated with dung really had a disadvantage would require to measure plants over a larger range of initial height and implement a model that allows the growth lines to converge.

Our results show that some tropical seedlings benefit from the nutrients that result from monkey dung being deposited in their vicinity. This can have important consequences for plant communities. For example, let us consider Kibale, where primate abundance and ecology has been extensively studied (Chapman, Struhsaker, & Lambert, 2005; Chapman, Valenta, Bonnell, Brown, & Chapman, 2018). Here previous studies provide data on the weight of an average defecation for each common diurnal primate species, the number of times they defecate daily, and primate density (Table 3). From this, we estimate that primates in Kibale are defecating 63.7 kg of dung over an area of one square kilometre every day (Table 3). Thus, primates are depositing a substantial amount of dung each day and, since their ranging tends to focus on important feeding and sleeping sites (Anderson, 1984; Di Fiore & Suarez, 2007), they are creating nutrient hotspots in the forest. However, it is unclear what the long-term impacts of these hotspots will be on the tree community as shade-tolerant species did not show an increased growth, while small light-demanding species did; it is not clear if they can be successful without exposure to high light conditions, such as a treefall gap. Differences in life expectancy under a closed forest canopy are likely to be critical to the relative value of nutrient additions to both light-demanding and shade-tolerant species (Denslow et al., 1990). Since shade-tolerant species often have slow growth rates this requires long-term monitoring as is often the case in ecological studies.

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