

Are Primates Ecosystem Engineers?

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Abstract Animals can play important roles in structuring the plant communities in which they live. Some species are particularly influential in that they modify the physical environment by changing, maintaining, and/or creating new habitats; the term ecosystem engineer has been used to describe such species. We here assess the two major foraging strategies of primates, frugivory and folivory, in terms of the potential for primates to function as ecosystem engineers. We argue that whereas the role of primates as seed dispersers has received a great deal of attention, the potential

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role that folivorous primates play in structuring their environment through herbivory has received much less attention. Further, while quantifying if frugivorous primates are ecosystem engineers through their seed dispersal has proved very difficult, it is not as difficult to ascertain whether folivorous primates are ecosystem engineers. We document situations in which folivorous primates act as ecosystem engineers by 1) eating the leaves and/or bark of trees to the extent that they kill trees, 2) feeding on trees to the degree that they slow their growth relative to nonpreferred tree species, 3) eating the flowers of species to the extent that it does not set fruit, or 4) feeding on plants in such a way as to increase their productivity and abundance. Because evidence from the literature is very limited, where possible we present new evidence of these processes from the colobus monkeys at our long-term field site in Kibale National Park, Uganda. We conclude by discussing promising research programs that could be established to refine our understanding of the role primates play in shaping the structure of plant communities, especially tropical forests.

Keywords Herbivory · Keystone modifier · Kibale National Park · Seed dispersal · Tree mortality

Introduction

Animals can play important roles in structuring the plant communities in which they live. Some species are particularly influential in that they modify the physical environment by changing, maintaining, and/or creating new habitats and thus control resource availability for other species in an ecosystem. The term “ecosystem engineer” has been used to describe such species and was first formally applied to animal species by Jones *et al.* (1994). Since the introduction of the term ecosystem engineer concept has generated both considerable interest (Crain and Bertness 2006; Wright and Jones 2006) and controversy (Jones *et al.* 1997; Power 1997; Reichman and Seabloom 2002; Wilby 2002). A recent review critically examines this concept and defines functional groups of ecosystem engineers (Berke 2010). Several classic examples have been used to illustrate this concept. In temperate regions, prairie dogs (*Cynomys* spp.: Van Nimwegen *et al.* 2008), sea otters (*Enhydra lutris*: Estes and Palmisano 1974), and beavers (*Castor Canadensis*: Naiman 1988) are commonly cited for their roles in shaping the structure and composition of plant communities. In the tropics, elephants (*Loxodonta africana*) are perhaps the best known ecosystem engineers given their role in maintaining open wooded grasslands (Dublin *et al.* 1990; Laws 1970) and their ability to shift an area from a forested to a grassland ecosystem (Stuart *et al.* 1985).

The importance of identifying ecosystem engineers lies in their influence over many other species in a given ecosystem through changes in the physical environment. Research in Yellowstone National Park, for example, has demonstrated the cascading effects of elk (*Cervus elaphus*) and beaver browsing on willow (*Salix* spp.) stands (Ripple and Beschta 2005). After the reintroduction of wolves (*Canis lupus*) into this ecosystem, elk numbers declined and they are now less likely to browse intensely on willow stands along streams and rivers, which has resulted in greater abundance of willow that are eaten by beaver (Creel and Christianson 2009). Increased beaver activity has resulted in more dam-building and ponds, which have,

in turn, impacted stream hydrology and created habitat for fish and songbirds. As this example illustrates, if an ecosystem engineer disappears from an area, numerous other species that depend on the altered physical environment will be affected. Therefore, to ensure ecosystems are effectively protected from anthropogenic stressors, identifying and understanding the roles of ecosystem engineers is critical.

Though research on primate feeding ecology has been intensive over the past few decades, the ecological roles primates play in ecosystems remains poorly understood. Thus, our objective is to consider how two foraging strategies, frugivory and folivory, affect primates' potential to function as ecosystem engineers. Research on how primate frugivory affects seed dispersal has received considerable attention since the 1980s (Chapman 1989a; Estrada and Coates-Estrada 1984; Leiberman *et al.* 1979). Despite this, a myriad of postdispersal factors limits our ability to make statements about the roles of primates in forest regeneration (Herrera 1985). Conversely, how primate folivory influences plant ecology has received little attention, despite the fact that folivorous primates make up most of the primate biomass in tropical forests, contributing 48–82 % of the density of diurnal primates (Fashing and Cords 2000). New data from Kibale National Park, Uganda, on colobine foraging behavior and shifts in tree species composition over the last two decades, and data from the literature, lead us to argue that folivores can play an important role in determining the composition of tropical forests. Our hope is that the ideas we generated will serve as a catalyst for future research that will add insights into the significance of primates in their environment.

Seed Dispersal

Understanding how seeds are handled and moved is critical for determining the composition and dynamics of plant populations (Jordano *et al.* 2011; Lambert and Garber 1998; Nathan and Muller-Landau 2000; Terborgh *et al.* 2002), as well as the population dynamics of animals that feed on those plants (Janson and Chapman 1999). Through seed dispersal, seeds are able to reach new sites for colonization, which influences demography, genetics, spatial distribution, and future vegetation composition (Lambert and Garber 1998; Levey *et al.* 2008). As such, species that are extremely important seed dispersers are possibly ecosystem engineers, and some primates probably fill this influential ecological role (Andresen 2000; Kaplin and Lambert 2002; Lambert and Garber 1998). Primates comprise between 25 % and 40 % of the frugivore biomass in tropical forests (Chapman 1995), eat large quantities of fruit, and defecate or spit large numbers of viable seeds (Lambert 1997; Stevenson 2011; Wrangham *et al.* 1994). For example, on Borneo, a single gibbon group (*Hylobates mulleri* × *agilis*) dispersed a minimum of 16,400 seeds/km² each year from 160 plant species (McConkey *et al.* 2002). If seed dispersing primates are confined to specific routes of travel because of topographical or social constraints, it is possible that they may also contribute to the modification of their habitats and significantly influence the number of food items along their regular travel routes (Di Fiore and Suarez 2007; Milton 1980).

Unfortunately, though claims of the importance of primates as seed dispersers abound (Andresen 2000; Kaplin and Lambert 2002), providing quantitative evidence

that through their seed dispersal they act as ecosystem engineers has proven very difficult to evaluate (Russo and Chapman 2011). The reasons for this difficulty involve at least two critical issues. First, in most situations, large variation in post-dispersal seed fate makes it very difficult to predict accurately how important a primate seed disperser is to a particular tree species. For example, Balcomb and Chapman (2003) demonstrated that *Monodora myristica* has large (16 cm in diameter) thick husked (1.8 cm) fruits and primates were the only animals to open the fruits. Not surprisingly they dispersed >85 % of the seeds. Despite this, of the six sites studied, those with higher frugivorous primate abundance had lower than expected seedling recruitment and lower sapling and pole abundances of this species. Thus, even in a system in which primates are critical for dispersal, spatial and temporal variation in postdeposition processes, such as seed predation from rodents, disease from bacteria or fungi, herbivory by duikers, or competition from already established plants, changed the predictability of frugivore actions on recruitment. Thus, if models are developed to predict changes in plant populations and communities with the loss of primate dispersal services, they must account not only for changes in the seed shadow, but also for the resulting alterations in the transition probabilities between seed, seedling, sapling, and adult stages, the spatial component of these transitions, and the consequences for interspecific interactions among plants, e.g., allelopathy, competition (Balcomb and Chapman 2003; Schupp 1993; Schupp *et al.* 2010). This would be a very difficult and time-consuming endeavor. Some would argue that because there are many processes that could alter the initial pattern that are not linked to the primate seed disperser, primates acting as seed dispersers should not be considered ecosystem engineers (Berke 2010); however, because primates have so often been stated to be critical in forest regeneration patterns (Kaplin and Lambert 2002; Lambert and Garber 1998; Nunes-Iturri and Howe 2007; Pacheco and Simonetti 2000), we take a broader definition and evaluate primate seed dispersers as ecosystem engineers.

Second, the importance of primates will depend on the presence of other species that overlap in dispersal services. Almost universally, fruiting tree species in tropical forests have their seeds dispersed by a variety of species (cf. Chapman *et al.* 1992; Howe and Smallwood 1982). For example, during 61.5 h of observation of *Trichilia gilgiana*, 22 species, including 2 ruminants, 9 rodents, 10 birds, and 2 monkey species, ate fruit from the tree (Gautier-Hion *et al.* 1985). If many nonprimate frugivores are dispersing a species' seeds the importance of primates is likely to be diminished, because the other frugivores will play a role in seedling establishment as well as primates.

The evidence available to evaluate the importance of primates as seed dispersers that somewhat circumvents these two limitations comes largely from studies of fragmentation and hunting. The impact of these anthropogenic processes depends on the presence of other seed dispersers who can expand their niche to fill the role of the primates that cannot survive in forest fragments or in heavily exploited areas (Peres and Dolman 2000; Wright 2003). Although there can be overlap in the assemblages of fruiting trees that different agents disperse, this overlap may not be enough to promote redundancy when a group of dispersers, such as primates, is lost as a result of hunting (Poulsen *et al.* 2002). Furthermore, density compensation by smaller primates when densities of larger primates fall (Peres and Dolman 2000) is

unlikely to make up for the decline in functional diversity of dispersal services. Evidence of seedling recruitment from hunted and nonhunted sites in Panama suggest that smaller nonhunted animals are not able to expand their niche to disperse large-seeded species, and the seedling communities in hunted areas become dominated by bird, bat, and wind dispersed species (Wright *et al.* 2007). Thus, with the loss of primate dispersal agents, rates of seed dispersal may inevitably decrease and seed shadows may become smaller, which may result in a reduction in species diversity (Stoner *et al.* 2007). For example, in Uganda and Bolivia, reduced numbers of large-bodied primates were correlated with lower seedling densities of large-seeded forest trees species (Chapman and Onderdonk 1998; Pacheco and Simonetti 2000) and higher seedling aggregations around parent trees (Pacheco and Simonetti 2000).

Folivory

Very few studies have examined the potential for folivorous primates to serve as ecosystem engineers; however, there is considerable evidence that other groups of herbivores perform this ecological role. Classic examples include elephants (Laws 1970; Dublin *et al.* 1990), beaver (Naiman 1988), moose (*Alces alces*: Pastor *et al.* 1999), and many insect species, e.g., caterpillar and locust outbreaks (Ludwig *et al.* 1978). However, most folivorous primates have not been considered in this manner (cf. Watts 1987, 1998).

Folivorous primate species could act as ecosystem engineers by 1) eating the leaves and/or bark of trees to the extent that they kill individuals of preferred foraging tree species, thus altering the species composition of the forest; 2) feeding from individuals of preferred food species to the degree that they slow their growth relative to nonpreferred tree species and the forest shifts in composition toward nonpreferred species, or feeding on plants in such a way as to increase the productivity of those plants and potentially increase the abundance of the selected species; 3) eating the flowers of species to the extent that it does not set fruit and thus limiting the recruitment of the species; and 4) modifying nutrient cycling in the forest.

Increased Mortality of Preferred Tree Species

The red colobus of Kibale (*Procolobus rufomitatus*) have been observed since 1970, and C. Chapman and colleagues have been collecting data on them since 1990 (Chapman *et al.* 2010b; Gogarten *et al.* 2012). Based on these long-term observations, we have compiled a list of trees that appear to have been killed by red colobus (Table I). Red colobus often feed on young leaves of a tree to the extent that *ca.* 90 % or more are eaten within a few days; they can do this repeatedly within one year and across years. In addition to leaf consumption, red colobus will consume bark and/or break off terminal branches of some tree species during their foraging such that they are largely removed, resulting in tree death. The number of tree deaths that we report is likely an underestimate of the actual number killed in this way because these were only those individuals that we remembered and could confirm the presence of a dead tree at that location. These trees are limited to the home range of our long-term focal group.

Table 1 Species and number of individuals believed to have been killed by red colobus (*Procolobus rufomitratus*) through their extensive and repetitive foraging on an individual's leaves in Kibale National Park, Uganda

Family	Tree species	No. of individuals killed	Forest	Trend	Density (individuals/ha)		
					1989	1998	2006
Fabaceae	<i>Albizia grandibracteata</i>	5	Yes	Down	3.46	3.27	1.73
Lauraceae	<i>Persea americana</i> (avocado) ^a	19	No	NA	–	–	–
Sterculiaceae	<i>Dombeya mukole</i>	1	Yes	Down	6.35	5.96	5.38
Myrtaceae	<i>Eucalyptus grandis</i> ^a	4	No	NA	–	–	–
Rutaceae	<i>Fagara angolensis</i>	2	Yes	Up	0.38	0.19	0.77
Moraceae	<i>Ficus exasperata</i>	1	Yes	Up	3.08	3.27	3.85
Guttiferae	<i>Harungana</i> <i>madagascariensis</i>	1	No	NA	–	–	–
Bignoniaceae	<i>Markhamia lutea</i>	1	Yes	Down	45.38	35.38	31.73
Euphorbiaceae	<i>Neoboutonia</i> <i>macrocalyx</i>	1	Yes	Down	5.58	4.42	3.08
Fabaceae	<i>Newtonia buchananii</i>	1	Yes	Down	1.73	1.92	1.53
Rosaceae	<i>Prunus africana</i>	13	Yes	Down	0.38	0.38	0.19
Euphorbiaceae	<i>Sapium ellipticum</i>	1	Yes	Down	0.38	0.38	0.19
Fabaceae	<i>Sesbania</i> sp.	1	No	NA	–	–	–

The forest column indicates those species typically found growing within the forest (Yes) and those found either outside of the forest (No; plantations of *Sesbania* sp. and *Eucalyptus grandis*). Some species were in edge areas or the area of the field station; thus they were either not in the plots, i.e., *Persea americana*, *Sesbania* sp. and *Eucalyptus grandis*, or were rare in the plots, i.e., *Prunus africana*. An inability to evaluate a population trend for the forest or the sample size for certain species suggests that we should have little confidence in the trend, i.e., *Prunus africana*

^a Indicates a non-native species

To explore the possibility that red colobus shifted the composition of the forest through their foraging behavior, we used long-term data on their foraging behavior and changes in the forest composition. In December 1989, we established 26 permanent vegetation plots in three forestry compartments that had been logged to different degrees. Each plot was 200 m × 10 m, providing a sampling area of 5.2 ha and monitoring an initial sample of 2111 tree (see Chapman *et al.* 2010a for details). We resurveyed plots in May 2000 and September–November 2006 to determine tree mortality. Using this vegetation plot data, we estimated the cumulative diameter at breast height (DBH) of food trees in three areas for each time period. We used red colobus foraging data that were collected from groups using each of the areas, produced area-specific food lists (all foods >1 % of the total foraging time), and calculated the cumulative DBH of these foods in each plot (Chapman and Chapman 1997, 2000). Changes in forest composition were tested using repeated measures analysis of variance tests to evaluate the significance of temporal (across years) and spatial (across compartments) variation and their interactions (see Chapman *et al.* 2010a for more details on the statistical approach). Mauchly's criterion was used to

test for the compound symmetry of the variance–covariance matrix (Potvin *et al.* 1990). When the criterion was rejected, the Greenhouse–Geisser test, which relaxes the symmetry assumption, was used to obtain corrected significance levels (Potvin *et al.* 1990).

There was an effect of time ($F=10.59$, $df=1$, $P=0.002$), but not forestry compartment ($F=1.01$, $df=1$, $P=0.339$). Thus, we pooled areas and contrasted the abundance of the tree species that were known to have individuals killed by red colobus across time. Nine out of thirteen of these species considered to have been killed by red colobus had individuals within our plots; we focused on the death and recruitment of these species between 1989 and 2006. Those four species not evaluated, including avocado (*Persea americana*) and *Sesbania*, occurred only in areas of human activity and are often planted by people and thus they were not present in the plots in the main forest. Of these nine eligible species, seven declined in abundance over the 17 years, which, as predicted, is different from an expected 50/50 distribution ($G=2.942$, $df=1$, $P=0.043$; one tailed). This suggests that these species have higher than expected mortality rates, which may indicate they are susceptible to be killed by extensive red colobus feeding.

Colobus monkeys in Kibale are not the only folivorous monkeys known to defoliate trees and potentially affect their distribution. Several authors have reported that other monkey species have decimated all the leaves on a particular tree, potentially causing its death. For example, one group of purple-faced langurs (*Presbytis senex*) defoliated the young leaves of *Alangium salviifolium* to the point where the trees were dying, and it was suggested that eating one tenth of the young leaves might be the only way for these monkeys to avoid endangering their food species (Hladik 1977). In the mangrove forests of Malaysia, silver leaf monkeys (*Presbytis cristatus*) were responsible for the deaths of *Rhizophora* trees (Jin-Eong 1995). These monkeys select a specific tree on which to feed based upon the size of its leaves (larger ones are preferred) and almost defoliate that tree before moving to the next one. In some situations, monkeys are forced to heavily exploit their food sources. After a cyclone in Sri Lanka, monkeys fed more heavily than normal on the few feeding trees that remained (Dittus 1985). The preferentially consumed trees were rarer than other trees, and the monkeys apparently decimated them to the point that they disappeared from the areas affected by the cyclone, suggesting that, particularly in areas with disturbance, the effects of monkeys on their food tree species may be exacerbated (Dittus 1985; see also Pavelka and Behie 2005; Pavelka *et al.* 2003).

Slowing Growth of Preferred Tree Species

It is conceivable that a folivore could feed on individuals of preferred food species to a degree that they slow their growth relative to nonpreferred species, but not result in their death. This could give nonpreferred species a relative advantage, with the forest gradually shifting in composition toward nonpreferred species. Our research group has previously examined changes in growth rates of preferred colobine foods over time (Chapman *et al.* 2010b). We demonstrated that whereas the cumulative DBH of the food trees for red colobus did not change over time ($F=1.181$, $df=1$, $P=0.312$), it did decline for black-and-white colobus ($F=4.011$, $df=1$, $P=0.034$; repeated measures analysis of variance on log transformed data between three time periods, 1989,

2000, 2006). This is not caused by an overall change in the structure of the forest, i.e., trees dying and thus the cumulative DBH decreasing in general. If we considered each plot as independent, there was no significant change in cumulative DBH of all trees among years ($F=0.430$, $df=1$, $P=0.655$). This suggests that for red colobus food tree mortality is balanced by recruitment, but that this is not so for the food trees of black-and-white colobus. For the black-and-white colobus, this is consistent either with the idea that their foraging slowed the growth rate of preferred species over time or the forest could be in a state of succession and because black-and-white colobus often feed on plant species that are found in disturbed areas (Harris and Chapman 2007; Oates 1974, 1977), this could simply reflect the effect of forest aging (Chapman *et al.* 2010a). A more direct test would be to relate intensity of foraging and growth rate of individual trees. Alternatively, one could examine this idea experimentally and mimic colobus foraging, but vary the intensity of extraction among individuals and quantify variation in growth rate.

In contrast, researchers studying grazers and browsers have shown that moderate structural damage and defoliation can initiate physiological processes in plants that actually stimulate tissue production and, in doing so, alter the plant community structure (Lawes and Chapman 2006; McNaughton 1976, 1977; Persson *et al.* 2007). Gorillas (*Gorilla beringei*) foraging on the dense herbaceous vegetation of the Virunga mountains, caused increased productivity of their food plants (Fossey and Harcourt 1977). A subsequent study compared the growth rates of areas of gorilla feeding to nearby control areas where they did not feed (Watts 1987, 1998). Food species located in feeding areas showed higher growth rates than they did at nearby locations that had not experienced gorilla disturbance and foraging. Further, stem density of herbaceous foods was higher in feeding areas than control areas (Plumptre 1993).

Capuchin monkeys (*Cebus capucinus*) may similarly affect the productivity of their food species (Oppenheimer and Lang 1969). At two sites on Barro Colorado Island, Panama, trees located within the monkeys' home range had more branches than areas without monkeys, suggesting that the capuchins removed terminal buds while feeding, thus promoting branching. This not only increases the amount of foliage available, but was also suggested to increase flower and fruit production depending on the intensity of browsing (Oppenheimer and Lang 1969).

Observations of both the red colobus and black-and-white colobus of Kibale suggest that after extensive feeding on the young leaves of some species, e.g., *Celtis durandii*, *Funtumia latifolia*, the colobus can largely denude a tree of young leaves. However, the tree is then able to recover by putting on a new set of young leaves within *ca.* 1 week. Thus, through colobus monkey foraging, the tree is stimulated to put on more young leaves, which are important colobus food items, rather than having these young leaves develop into less desirable mature leave. We have not quantified such occurrences, but this offers exciting opportunities for future research.

Limiting Fruit Production

The third way a folivore could act as an ecosystem engineer is through overexploitation of the flowers of food species, thereby limiting the fruiting and thus recruitment of that species. For primates, there are limited data to evaluate this idea because long-

term data are needed on both primate foraging and the flowering and fruiting patterns of tree species they feed on. Struhsaker (1978) documented that red colobus frequently eat all or the majority of the flowers of *Markhamia lutea* and hypothesized that this limited fruit set. From 1998 to the present, we have been conducting phenological monitoring of *ca.* 10 individuals of 36 tree species. Here, we use phenological data from June 1998 to May 2011 ($N=150$ month) to test the hypothesis that flower-eating by red colobus limits fruit set of *Markhamia lutea*. We considered only trees greater than the smallest DBH known to be capable of reproduction. The red colobus often eat the flower buds before forming whole flowers and as a result we do not score the tree as flowering because developed flowers never get the chance to form. The chance of a *Markhamia lutea* tree bearing fully developed flowers in a given month was 0.67 %. This is in comparison to the only other species in the Bignoniaceae family, *Spathodea campanulata*, that we monitored for which the chances of having fully developed flowers in a month was 25.2 %, or for any of the species flowering which averaged 14.1 % in a given month. The chance of a *Markhamia lutea* tree fruiting in a given month were 0.65 %, while that of *Spathodea campanulata* was 6.6 %. These data support Struhsaker's original suggestion that the foraging of the red colobus can limit fruit set in this species, and we suggest that by doing so, they likely dramatically reduce the potential for this species to recruit; thereby their foraging alters the composition of the forest. A more direct means of testing this would be to monitor the phenology of *Markhamia lutea* trees in areas without red colobus. These results raise the interesting question of how *Markhamia lutea* established and continues to exist in Kibale.

The foraging of spider monkeys (*Ateles geoffroyi*) has also been described to cause a massive destruction of the flowers and thereby limit fruit set (Riba-Hernandez and Stoner 2005). For 3 month the flowers of *Symphonia globulifera* represented between 86 % and 100 % of the focal groups monthly foraging time and their feeding resulted in the complete detachment of the flowers in 80 % of their feeding episodes. In the subsequent fruiting season none of the trees that the spider monkeys ate flowers from set fruit; however, 70 % of the trees that were outside of the range of the group fruited. These examples suggest that more attention should be placed on understanding the long-term effects of such foraging on the population structure of tropical trees.

Modifying Nutrient Cycling

The role of herbivores or folivores in the cycling of nutrients in tropical forest systems is poorly understood. In contrast, grasslands herbivores, through grazing, defecating, and urinating, have been documented to both alter the size of the nutrient pool and change their fluxes (McNaughton 1976, 1977; Singer and Shoenecker 2003). It is possible that primates can improve soil quality where they tend to defecate. In this way, a low to moderate level of herbivory may be tolerable as long as the benefit of a limiting nutrient from elsewhere in the forest outweighs the cost of the nutrients taken through consumption of its leaves. Trees that are repeatedly used over years as sleep sites would benefit most (Anderson 1984; Chapman 1989b), especially if they are not used as food. This "fertilizer" hypothesis has been suggested for sloths, which are known to bury their dung at the base of their food trees (Forsyth and Miyata 1984; Gilmore *et al.* 2001; Montgomery and Sunquist 1975).

Feeley and Terborgh (2005) quantified howler (*Alouatta seniculus*) density and soil nutrients on forested islands. They documented that howler density was positively related to the annual increase in basal area, which is an indicator of above-ground productivity and they predicted that high levels of herbivory on preferred tree species would eventually lead to the dominance of nonpreferred trees. In a subsequent study of these forested islands, it was documented that such changes in nutrient cycling can indirectly impact bird communities and thus the activities of howlers can have cascading effects on the plant and animal communities (Feeley and Terborgh 2006). Similarly, the soil under red howler monkey (*Alouatta seniculus*) latrines has been shown to have stimulated root penetration, increased microbial and earthworm activity, and improved soil fertility (Neves *et al.* 2010)

Conclusions and Future Research Directions

Simply given their abundance and biomass, it is likely that primates play an important role in structuring tropical forest ecosystems, not only in terms of seed dispersal, but also as folivores. One important distinction is that while seed dispersal is mutualistic, folivorous primate–plant interactions are instead predator–prey interactions with very different natural selection pressures, with direct consequences for survivorship, as well as fecundity. However, just as we now know that certain microorganisms can shift from providing benefits to being parasites depending upon their prevalence and the state of the host; it is possible that lower levels of folivory may provide benefits to certain tree species. A second important distinction is that at many locations folivorous primates make up much more of the biomass of tropical forests than frugivorous primates, so their overall effects on the ecosystem are likely to be greater. Thus, we argue here that folivorous primates are likely important ecosystem engineers in tropical forests. Future research investigating how folivorous primates affect tropical trees through their foraging can take both observational and experimental approaches. Investigators can relate the intensity of foraging to the growth rate of trees and likelihood of tree survival. From an experimental approach, researchers can simulate folivore foraging activity and document the fate of the trees under different levels of exploitation. It should also be relatively easy to remove arboreal pathways leading to specific trees that one expects folivores are affecting, while controlling for light levels and other potentially confounding effects, and document whether growth rate and survival probability are elevated in a set of isolated trees vs. trees in which the folivores can still forage. Obtaining a better understanding of the significance of the role primates play in their environment will enhance the effectiveness of tropical forest conservation practices, which is critically needed at a time when these forests are seriously threatened by human actions.

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