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Primate Seed Dispersal and Forest Restoration: An African Perspective for a Brighter Future

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Abstract Primate seed dispersal is a vital, but complex, ecological process that involves many interacting agents and plays important roles in the maintenance of old-growth forest, as well as in the development of regenerating forest. Focusing primarily on African examples, in this article we briefly review the ecological process of primate seed dispersal, highlighting understudied and contentious topics, and then we discuss how our knowledge on primate seed dispersal can promote both forest restoration and primate conservation. Though it is frequently claimed that primates are critically important for the maintenance of diverse tropical forest ecosystems, we believe that more empirical evidence is needed to support this claim. Confounding factors can often be difficult to rule out and long-term studies extending beyond the seedling or sapling stage are very rare. In addition, though primates are critical for initial seed dispersal of many tree species, spatial and temporal variation in post-deposition processes, such as secondary seed dispersal and predation by rodents, can dramatically alter the initial patterns generated by primates. However, given the need for immediate conservation action to prevent further primate extinctions, we advocate that the knowledge about primate seed dispersal be used in formulating informed conservation plans. One prominent area where this knowledge will prove extremely valuable is in forest restoration efforts. To aid in the development of such efforts, we

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pose five questions, the answers to which will help facilitate forest restoration becoming a useful tool in strategies designed to conserve primates.

Keywords Primate conservation · Reforestation · Regeneration · Seed fate · Tropical forest

Introduction

The pace of biodiversity loss is increasing, with current extinction rates ca. 1000 times higher than background rates (Pimm *et al.* 2014). Recent estimates suggest that at least 322 vertebrate species have gone extinct since 1500 and that surviving vertebrate species have declined in abundance by 25% since 1970 (Dirzo *et al.* 2014). Overall, 60% of all primate species are currently threatened with extinction (Estrada *et al.* 2017), and though it remains to be confirmed, it seems almost a certainty that with the disappearance of Miss Waldron's red colobus (*Procolobus badius waldroni*) we have lost the first primate to extinction in the twenty-first century (McGraw 2005). The slow life histories and high infant mortality rates of primates makes them especially susceptible to anthropogenic impacts and increasing environmental variability (Van Allen *et al.* 2012).

Humans are clearly responsible for the current decline of primate populations. Between 2000 and 2012, 2.3 million km^2 of forest was lost globally, and in the tropics, forest loss increased each year (Hansen *et al.* 2013). To put this in perspective, this area is approximately the size of Mexico. Another action leading to the decline in primate numbers is bushmeat hunting. Global estimates of the extent of wildlife overexploitation are very poor; however, in Africa, 4 million metric tons of bushmeat are extracted each year from the Congo basin alone (equivalent to ca. 4.5 million cows, or 80 million small (5 kg) monkeys; of course not all bushmeat is primate (Fa and Brown 2009)). Primates are also threatened by a changing climate. Temperatures are predicted to increase by 1.5 °C by the end of the twenty-first century (IPCC 2014), and researchers have projected that by 2100 75% of all tropical forests present in 2000 will experience temperatures that are higher than the temperatures presently supporting closed canopy forests (Peres *et al.* 2016; Wright *et al.* 2009). As forests change, primate populations of many species may decline precipitously. Even if temperature changes were to be somewhat buffered in tropical forests, there is a general agreement that rainfall regimes are already changing and will continue to change over large areas of the tropics (Feng *et al.* 2013; Fu 2015). Altered rainfall patterns are likely to have distressing consequences for the functioning of these diverse ecosystems and the survival of primates.

For endangered primates it is very difficult to predict the combined and potentially synergistic impacts of different dynamic factors on a particular population without long-term data, of which there are unfortunately little available (Chapman *et al.* 2017). For example, a demographic study of a Madagascar lemur, *Propithecus edwardsi*, quantified that hunting and deforestation were (not surprisingly) the most significant threats to this species (Dunham *et al.* 2008). However, the study also revealed that a continued intensification of the El Niño effect and extreme weather events caused by climate change would lead to further declines in the species' populations (Dunham *et al.* 2008, 2011). Such multiple threats create feedbacks that may make the extinction risk faced by primates more severe than currently recognized.

Tropical ecosystems are not just losing biodiversity; they are losing ecological processes (Chapman and Peres 2001; Peres and Dolman 2000). One of the processes in which primates play a very significant role is seed dispersal. Primates constitute between 25 and 40% of the frugivore biomass in tropical forests and they defecate or spit out a large number of seeds (Chapman 1995; Lambert and Garber 1998; Wrangham *et al.* 1994). As up to 75% of tropical tree species produce fruits adapted for dispersal by frugivores (Frankie *et al.* 1974; Howe and Smallwood 1982), how forest ecosystems will operate without primate seed dispersal, or with their populations much reduced, is unclear.

Our objectives in this article are to 1) briefly review the ecological process of primate seed dispersal, highlighting areas we view have not received sufficient attention or where there is confusion, focusing on African examples; 2) take what has already been learned about primate seed dispersal and evaluate how this knowledge can support primate conservation efforts, focusing on the role that primates play in forest restoration; and 3) explore what knowledge about seed dispersal will be needed in the future to promote and facilitate restoration efforts. We address these three points based on our years of professional experience in field at sites with very different primate species, and based on our thoughts regarding results found in the literature.

The Ecological Process of Primate Seed Dispersal

When one first considers seed dispersal, it seems to be a deceptively simple, yet vital, ecological process. This process allows seeds to escape the density- and distance-dependent mortality that occurs under or very near the parent tree (Connell 1971; Janzen 1970) and reach new sites for colonization. Thus, the nature of seed dispersal influences plant demography, genetics, plant spatial distribution, and future vegetation composition (Howe and Miriti 2004; Lambert and Garber 1998; Levey *et al.* 2008), which in turn influences primate abundance (Chapman *et al.* 2018). However, though seed dispersal is a vital process, it is not simple. Claims of the importance of primate seed dispersal for plant populations and communities abound (Andresen 2000; Kaplin and Lambert 2002), yet quantitative evidence of this has proven very difficult to obtain (Russo and Chapman 2011), and rarely is the evidence free of confounding factors or involves assessment beyond the seedling stage. In fact, most claims of the importance of primates are often simply based on the number of seeds that a specific primate handles. For example, a single group of gibbons (*Hylobates mulleri* × *agilis*) disperses a minimum of 16,400 seeds per km^2 each year from 160 plant species (McConkey *et al.* 2002), Geoffroy's woolly monkey (*Lagothrix cana*) disperses nearly 1 million *Manilkara bidentata* seeds per km^2 every fruiting season (Levi and Peres 2013), and redtail monkeys (*Cercopithecus ascanius*) disperse 24,492 fruits/ km^2 each day (Lambert 1999).

Though moving such a large number of seeds is an important aspect of seed dispersal, it does not necessarily mean these animals are playing an important role in seedling establishment or subsequent stages of the plant's life history. Other considerations must be taken into account when evaluating the role of primate seed dispersers.

For example, tropical trees often produce hundreds of thousands of seeds during their adult life spans. To be successful, an individual tree has to make one a similarly successful adult, and thus the importance of primates will depend, not just on the quantity of seeds dispersed, but also on the quality of the dispersal service (Schupp 1993; Schupp *et al.* 2010). Almost universally, fleshy fruited tree species have their seeds dispersed by a variety of animal species (cf. Chapman *et al.* 1992). For example, during only 61.5 h of watching fruit removal from *Trichilia gilgiana* in Gabon, 22 species, including two ruminants, nine rodents, ten birds, and two monkey species, ate this species' fruit (Gautier-Hion *et al.* 1985). Such observations contributed to the proposal of the term "diffuse coevolution" to describe the evolutionary relationship between plants and frugivores (Herrera 1985) and later to the refinement of this idea into the concept of coevolving multispecies interaction networks (Guimarães *et al.* 2017; Thompson 2009). If many nonprimate frugivores are dispersing a species' seeds, the relative importance of primates may be low because other frugivores, such as birds, rodents, and ruminants, can play important roles by moving many seeds to high-quality sites for germination and seedling establishment.

Another consideration is that the spatial and temporal variation in the fate of the dispersed seeds can be so large as to obscure the initial seed deposition patterns (Schupp 1993; Schupp *et al.* 2010). Thus, while the extinction of one or a few frugivores may alter the number of seeds dispersed and the location where they are deposited (Chapman and Chapman 1996; Gross-Camp and Kaplin 2011; Razafindratsima and Dunham 2015), variation in seed fate may make the demographic consequences of seed dispersal difficult to estimate. For example, in Costa Rica, 98% of the seeds placed at experimental stations were removed or killed within 70 days (Chapman 1989). In Peru, 99% of the *Virola calophylla* seeds naturally dispersed by spider monkeys (*Ateles paniscus*) or ones that had fallen below the parent tree were preyed upon within 15 months (Russo 2003). In Uganda, a detailed study on *Monodora myristica* illustrated how postdispersal processes can overwhelm the patterns of primate seed dispersal for plant populations (Balcomb and Chapman 2003). *M. myristica* has large (16 cm in diameter) thick husked (1.8 cm) fruits, such that primates and elephants are the only animals known to open the fruits and, not surprisingly, primates dispersed >85% of the seeds. Despite this, of the six sites studied, the ones with higher abundance of primate frugivores had lower than expected seedling recruitment and lower sapling and pole abundances. Thus, while primates are critical for the initial dispersal in this system, spatial and temporal variation in postdispersal processes overwhelmed the patterns of dispersal and changed the predictability of frugivore effects on recruitment. These postdispersal processes include seed predation and secondary seed dispersal by rodents, disease from bacteria and fungi, herbivory on seedlings and saplings, and competition from other seedlings and previously established plants (Forget *et al.* 1994; Howe 1990; Jansen and Forget 2001; Schupp 1988; Visser *et al.* 2011).

Apart from studies claiming that primates are important seed dispersers based on the number of seeds they process, the majority of the studies available to evaluate the importance of primates as seed dispersers involve investigations done in areas with reduced primate numbers, either in forests that are fragmented or where primate numbers are diminished by hunting (Chapman and Onderdonk 1998; Poulsen *et al.* 2011). However, in disturbed forests there are many confounding factors that change (e.g., light and soil moisture levels) and these need to be simultaneously studied alongside of the number of seeds primates disperse and when comparing hunted and unhunted forests the situation is complex (Poulsen *et al.* 2011). Studies of hunting indicate that primates are important in maintaining substantial populations of large-seeded tree species in tropical forests (Pacheco and Simonetti 2000; Effiom *et al.* 2013; Vanthomme *et al.* 2010; Wright *et al.* 2007). African forests are of particular concern given the high human population density (Chapman *et al.* 2006) and the heavy levels of hunting of animals that have a seed dispersal role (Abernethy *et al.* 2013; Campbell *et al.* 2011; Covey and McGraw 2014). Though these studies are suggestive of the importance of primates, we encourage researchers to evaluate potential confounding factors, such as changes in microhabitat, seed predators, and other natural enemies. Also, the impacts of hunted or defaunated fragments on primate dispersed trees are likely to be context dependent. Some studies have shown that nonprimate frugivores can expand their niche to fill the role of the primates that cannot survive in forest fragments or in heavily exploited areas (Chapman and Onderdonk 1998; Peres and Dolman 2000; Wright 2003), while in some situations they may be unable to do so (Chaves *et al.* 2015). In Madagascar it was found that a lack of primate dispersers in forest fragments did not hurt recruitment of an animal-dispersed trees species. Instead recruitment was enhanced because of a concomitant decline of seed predators and because the lack of primate frugivores allowed an expanded role of ants that delivered high-quality seed dispersal (Dausmann *et al.* 2008).

When evaluating the importance of primate seed dispersers, the ecological processes that are in play between seed dispersal and the establishment of an adult in the next generation play out over hundreds of years. Thus, most trees whose fruits are currently being fed on by primates come from seeds that were dispersed by frugivores dating back 20–100 generations (Herrera 1985). Many canopy-level fruiting trees are shade-tolerant species and often slowly build their way to the canopy (Grubb 1996). For example, seedlings and saplings of *Chrysophyllum* sp. grow extremely slowly in the shaded understory; their mean height only doubling every 27 years (Connell and Green 2000). With this growth rate, a 20-cm seedling could take almost 70 years to reach a meter in height. Similarly, life history modeling has suggested that the population growth rates of several tropical species are relatively insensitive to changes in the transition probabilities of seeds to seedlings, but it is later stages that determine if a population grows or not (Pinero *et al.* 1984). Thus, for such species changing the number of seeds dispersed, by, for example, extensive bushmeat hunting, will have little or no effect on the subsequent population size (Myster 2017).

The extinctions of important seed dispersers that occurred before modern times (Guimarães *et al.* 2008; Janzen and Martin 1982; Pires *et al.* 2014) illustrate that many ecological interactions must be viewed from a long-term perspective. Madagascar lemurs represent a particularly sad and poignant example (Dew and Wright 1998; Overdorff and Strait 1998). After the intensification of human activity on Madagascar roughly 1700 years ago, at least 17 species of lemurs went extinct (Perez *et al.* 2005). Many of these lemurs lived in or near forest and relied on fruit and thus were dispersing seeds (Burney *et al.* 2003). Recently, Federman *et al.* (2016) demonstrated that the extinction of large-bodied lemurs resulted in a significant reduction in the frugivore community's seed dispersal ability. Despite these frugivore extinctions on Madagascar, and similar ones in North and South America (i.e., gomphothere extinctions), there does not seem to have been large extinctions of tree species; rather other animals have taken over the seed dispersal role. Federman *et al.* (2016 *pers. comm.*) suggest that the persistence of these fruiting species, despite the absence of their dispersing megafauna, was due to their long generation times and secondary dispersal agents, such as the introduced *Rattus rattus* or strong winds during cyclones. Combining all of these lines of evidence suggests that thus far there is little long-term empirical data available to evaluate the impact of hunting on forest communities (Poulsen *et al.* 2011; Stoner *et al.* 2007). This means that while it is appropriate to advocate for the protection of primates on moral/ethical grounds or on ecological grounds owing to the many biotic interactions in which they are involved, advocating for primate conservation because their decline will cause the extinction of tree species is currently ungrounded.

Use of Knowledge of Seed Dispersal to Support Primate Conservation and Forest Restoration

The seed dispersal interaction network in which primates are involved in is a complex and dynamic system involving many plants and animals, whose connections vary over even short spatial and temporal scales. Causing this ecological network to break down will have cascading, unforeseen, effects. Though extinctions will likely not occur, there may be very negative consequences (Valiente-Banuet *et al.* 2015). Thus maintaining the process of seed dispersal by primates should be a priority. This means maintaining relatively undisturbed intact tropical forests, which calls for effective national parks—an urgent call that is repeatedly made around the world (Laurance *et al.* 2012; Watson *et al.* 2018). Most seed dispersal research makes connections to conservation by stating that maintaining the ecological process of seed dispersal is needed to prevent negative cascading consequences. However, seed dispersal is also essential for the re-creation of tropical forests—forest restoration (Chazdon and Guariguata 2016; Duncan and Chapman 1999; Guariguata and Ostertag 2001; Guevara *et al.* 1986; Holl and Aide 2011; Kaplin and Lambert 2002). Large areas of tropical forests have been converted to agriculture, but with rapid urbanization rates and changing demographics in some countries many lands have been abandoned and left to recover natural forests, creating opportunities for primate conservation (Hansen *et al.* 2013; Jacob *et al.* 2008, 2016). In contrast to the extensive body of research on the relative role of primate seed dispersal in old growth forest, the role of natural seed dispersal for large scale restoration has received little attention, and the role that primates play in this process has largely been overlooked. Conservation projects can involve active restoration, where people plant seedlings or sow seeds into areas, or passive restoration, where the land is allowed to regenerate on its own accord. Typically, the actions of primates aid in both types of restoration projects. To help future efforts and give more attention to the role primates can play in restoration, we consider in this section the significance that forest restoration could play in conservation strategies for primates. Then, in the next section, we outline what knowledge about seed dispersal by primates must be available to reach this goal.

Potential for Forest Restoration to Aid in Primate Conservation

It is clear that in the tropics large areas have been deforested through logging and agricultural expansion and deforestation is increasing at an accelerating rate (Felton *et al.* 2013; Hansen *et al.* 2013). However, these areas do not always remain deforested and estimates suggest secondary forests have replaced at least one of each 6 ha of relatively undisturbed forest deforested in the 1990s (Jacob *et al.* 2008; Wright and Muller-Landau 2006). Furthermore, 2 billion ha in forest and forest/savanna biomes have been identified as opportunities for forest restoration (Chazdon and Guariguata 2016; Laestadius *et al.* 2011); this is an area twice the size of Canada. Estimates of the area covered by regenerating forests range from 500 to 850 million ha (Lamb *et al.* 2005; Pan *et al.* 2011); the upper estimate is the size of Brazil. Moreover, current global trends indicate that the area of regenerating forest is increasing and a great deal of this increase is caused by agricultural land being abandoned as people move to the cities (Wright and Muller-Landau 2006). As of 2008, more people lived in cities than in rural settings. This urbanization trend is increasing, and the UN Population Division estimates that 90% of the world's population growth between 2000 and 2030 will occur in cities of the developing world (United Nations Population Division 2008).

The movement of people from a rural to urban setting offers great conservation opportunities as these abandoned or devalued lands can be restored. But for this opportunity to be grasped to its fullest many questions remain that need to be answered such as the following: 1) What will be the future of lands "abandoned" by rural farmers? Will they become lands of large agricultural industry, such as palm oil (Linder 2013), or be turned into agroecosystems where primate conservation is possible to varying degrees (Estrada *et al.* 2012), or become regenerating natural forest, thereby expanding protected areas or acting as corridors? 2) How does the conservation community illustrate to local and national governments the value of restoring land? Is the carbon value of these lands something that will convince these groups? How do we collect evidence of the carbon value of regenerating forests to convince carbon buyers (Wheeler *et al.* 2016)? Can farmers be convinced of the value of reforested lands by showing them that they increase the abundance and diversity of pollinators coming to their crops? As clean water becomes a scarce resource in many countries, can the fact that forests maintain watersheds and purify polluted waters be used to convince people of their value? How can the aesthetic value of forests and the animals they support be promoted? 3) Can primates be used as "Flagship" or "Guardian Angel" species to promote the value of restoring these lands to a native forest (Bicca-Marques and de Freitas 2010; Simberloff 1998)? The term Guardian Angel has been used by UNESCO to mean that a decline in this species or group of species signals a negative impact for humankind. For example, howlers in Southern Brazil are being called the Guardian Angel of local communities, as they get yellow fever before it erupts in the human population, so they signal that preventative action must be put in place to prevent yellow fever from breaking out in the local communities (Bicca-Marques *et al.* 2017). 4) Finally, can regenerating vegetation be primate habitat? There are only a handful of studies that suggest that forests, and the primate communities they support, can rebound rapidly when left to recover or encouraged to recover. For example, a survey of a site in Korup National Park, Cameroon that was abandoned 7–8 years previously, found populations of all eight species of diurnal primates that occur in the region; in addition, sighting frequency in this recovering area was not significantly different from other sectors of the park (Baya and Storch 2010; Linder 2008). In Kibale National Park, Uganda, 7 years after an area of grassland was replanted with trees as part of a carbon offset program (Omeja *et al.* 2012), all species of diurnal primates were present in high numbers, including the endangered red colobus (*Piliocolobus tephrosceles*) and chimpanzee (*Pan troglodytes*) (Chapman *et al.* 2018). Similarly, 16 years post logging of a pine plantation in Kibale, all primate species except one were present in high numbers (Fig. 1) (Chapman *et al.* 2018). Such studies give hope for the future.

What Knowledge about Seed Dispersal Is Needed to Promote Forest Restoration?

Seed dispersal is a stepwise process: primates eat fruits and ingest the seed; they move away from the parent tree; defecate or spit out the seed; the seed on the ground is or is not destroyed, the seed germinates or does not; the seedling survives or does not; and so on. This progression of steps can be used to formulate a set of questions that can guide the procurement of information needed to construct informed conservation and restoration plans. Using this stepwise progression, we propose five questions, the answers to which, we believe, will be important in understanding the role primates play in forest restoration programs:

1) *What primate species use deforested lands and why?*

   It is important to know which of the primate species in a community will leave the protection of the forest to venture into deforested lands and which will not, as only those species that leave the old-growth forest will bring seeds into deforested lands to promote tree regeneration. Deforested lands are often a dangerous

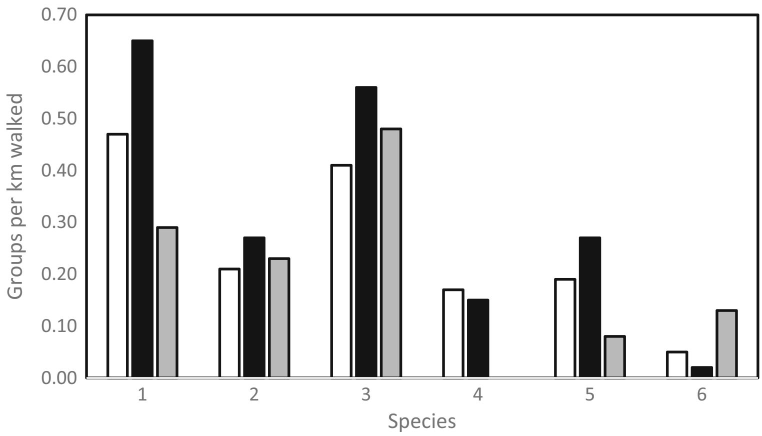

Fig. 1 The number of groups per km walked for the following species (1 = red colobus [*Piliocolobus tephrosceles*], 2 = black-and-white colobus [*Colobus guereza*], 3 = redtail monkey [*Cercopithecus ascanius*], 4 = blue monkey [*Cercopithecus mitis*], 5 = mangabey [*Lophocebus albigena*], 6 = baboon [*Papio Anubis*]) monitored in the old-growth forest of Kanyawara, Kibale National Park, Uganda in 2005, 2014 (white and black bars) and the adjoining regenerating forest block (Nyakatojo, 2014, gray bar) that was a pine plantation before being logged starting in 1993. Further information on this research can be found in Chapman *et al.* (2018).

environment for primates largely because of the presence of dogs (Farris *et al.* 2017; Pozo-Montuy *et al.* 2013). Terrestrial or semiterrestrial species, such as baboons, vervets, and ring-tailed lemurs will likely readily use these deforested habitats as they naturally cross and forage in grasslands, but for other species it may be difficult to predict if they use deforested habitats or not. For example, blue monkeys in southwestern Uganda are not found along forest edges or in fragments (Worman and Chapman 2006), while in South Africa they are common in fragments and frequently move among fragments (Lawes 2004).

All too often conservation strategies developed for a given context are applied to other contexts worldwide without considering their suitability for those other contexts (e.g., extractive reserve concepts developed for areas with low human densities are often applied without modification to areas with high human densities). This leads to inefficiencies, unsatisfied local communities, and project failure. Thus, it is important that this is not done when applying a conservation strategy of promoting primates as agents of reforestation. As a result, it will be important to consider the pool of local primate seed dispersers and this will vary by region. For example, Victor Arroyo-Rodriguez (*unpubl. data*) made a detailed study of the species using deforested areas (the matrix among fragments) and found that Africa had on average 3 times the percentage of the community's species that used the matrix when compared to Madagascar, which was the lowest of any region. The Neotropics and Asia were intermediate. This shows the importance of the continental scale, but the local scale is also important. For example, in Kibale vervets are absent from the north of the park, as were baboons until recently, while to the south both species are abundant. Thus it seems likely that because both of these species are often found in grasslands and very young regenerating forests, the rate of regeneration would differ between the north and the south of the park.

2) *How can primates be "encouraged" to use deforested lands?*

To increase the rate of natural restoration or to improve the tree diversity in areas in which seedlings have been planted, research is needed into ways to encourage seeds from old-growth forest to be dispersed to deforested lands and primates can play a major role in this process (Chazdon *et al.* 2009; Omeja *et al.* 2016). In general, we have a poor understanding of how seed dispersal services can be positively affected (McConkey and O'Farrill 2016); however, there are likely to be many ways that this can be naturally done. One simple and well-tested means is to leave abandoned structures where primates can seek refuge from predators or leave introduced tree species in which the animals can feed (Duncan and Chapman 1999). Often when land is being restored buildings are levelled; crops are cleared; and nonnative trees, such as fruit or timber trees, are cut to allow the land to return to its natural state. However, leaving such structures and trees in place for a time will encourage primates to leave the forest (Jacob *et al.* 2016). More research on conditions under which primates move across open matrices would improve our view of the relative importance of primates in the regeneration of fallow fields and pastures.

3) *What seeds are dispersed into deforested lands by primates and what is their fate?*

The most valuable type of seed disperser to use deforested lands would be one that brought a diversity of seeds into degraded lands and deposited them in a fashion that they germinated and survived. Thus, to provide scientific support for the idea that primates can be important in restoration efforts, knowledge of what plant species they are dispersing into these areas and the fates of these seeds is important. The diversity of fruits eaten by most primates (Chapman and Rothman 2009) make them potentially important for restoring a diverse forest community. However, typically the disappearance/mortality rate of seeds in primate dung is very high (ca. 75–100%), making determining the fate to the seedling stage difficult and requiring large sample sizes, particularly when seeds that disappear cannot be monitored. Such high seed mortality rates also mean that monitoring a suitable sample of seedlings to determine seedling survivorship will require germinating seeds in a greenhouse setting, allowing the seedlings to grow, and transplanting them to the deforested area to evaluate seedling fate.

Research into the role of primates in aiding restoration of deforested lands is in the pioneering stages, as there are few existing studies. Yet, the conservation/management community needs general information now. This is a dilemma for the research community as recommendations must be made based on very limited data. To facilitate generalization from one area to the next, it would help if tree species are categorized into regeneration niches (i.e., early successional to old-growth species) (Grubb 1977). Thus, for researchers attempting to make generalizations, rather than trying to compare species or genera, they can evaluate that in one location some percentage of a specific regeneration niche did well, while in another location it did not, and explore reasons for such differences. However, defining a species regeneration niche is often a difficult task (Zanne and Chapman 2005). Despite this difficulty, it is our opinion that conducting analysis on regeneration niches is the right course of action.

4) *What is the fate of seedlings that establish?*

Most research on primate seed dispersal only follows the process of seed dispersal to seed deposition (Chapman 1989; Lambert 2001; cf. Andresen 1999); however, with respect to conservation and management needs, this is clearly insufficient. Wherever possible, it would be desirable to follow seedlings to determine their fate. Though difficult, it is possible to germinate seeds that have been defecated by primates, grow them to the seedling stage, and determine their fate through the seedling to sapling stage (Balcomb and Chapman 2003), and we suggest that such an approach should be considered in future research efforts.

One particularly important element affecting seed and seedling fate in many systems is fire. Evidence from a variety of sites clearly indicates that if fire is not controlled, regeneration of seedlings will not progress (Buechner and Dawkins 1961;Omeja *et al.* 2012; Struhsaker 2002; Vargas *et al.* 2008). While controlling fire seems like an obviously necessary management practice, other practices that seem logical may have unanticipated results. For example, in a system where the deforested lands are dominated by aggressive grasses that can grow to 3 m in height, a management practice that would be apparently useful would be to weed around a seedling to remove competition with the grasses and allow the seedling to receive more sunlight. However, in an experimental examination of such a strategy Omeja *et al.* (2009) discovered that such weeding led to the desiccation and death of many seedlings in the dry season. This example illustrates the need for careful evaluation of management practices before they are broadly applied.

5) *What happens at later stages of succession?*

Financial and logistic constraints make long-term research very difficult, but of course the longer the research, the more useful it is for providing accurate information for conservation/management plans. With respect to regeneration, it is well documented that the rates of biomass accumulation subsequent to disturbance is highly variable (Omeja *et al.* 2012; Uhl *et al.* 1982); thus whenever possible it will be useful to place a study done at one site into a more general framework and attempt to understand factors affecting the recovery. This is needed to compare sites where primates are thought to contribute to the initial forest regeneration to different degrees. For example, variation among pioneer species between regions may be very important to explain decadal patterns of regeneration. Although the structure of trees that become established after disturbance can be variable (Grubb and Metcalfe 1996), Richards (1996) and others have noted the existence of a guild of large-leafed, fast-growing, widely dispersed pioneer species typically with umbrella-like crowns (e.g., *Cecropia* [Neotropics], *Musanga* [Africa], and some *Macaranga* [Africa, Asia, and Australia]). In the course of succession, these pioneers establish a canopy beneath which less light-tolerant species can establish and prosper. However, in some regions these large-leafed, fast-growing pioneer species are rare or absent and thus while initial regeneration in such regions can be rapid, once the smaller-leafed pioneers age and die, regeneration can be slow as shade-tolerant species have to establish (Chapman *et al.* 1999). Understanding such patterns will greatly advance the accuracy with which managers can predict the recovery of the plant and animal communities.

In conclusion, our article illustrates that primate seed dispersal is a complex process that plays a crucial role in plant regeneration, both in conserved and disturbed forests. Furthermore, while claims of the importance of primates in shaping the long-term future of forest ecosystems abound, providing quantitative evidence of their importance has proven difficult and rarely is the evidence independent of confounding factors or involves examinations beyond the seedling stage. We have demonstrated that while primates move many seeds away from the parent trees, spatial and temporal variation in post-deposition processes, such as seed dispersal and predation by rodents, can change the initial patterns generated by the frugivores' actions. Such complexity is intriguing, demonstrates the need to maintain all of the interactants in the process to prevent unanticipated negative cascading events, and calls for careful science that makes cautious claims of conservation significance until systems are well studied. However, the habitats in which primates live are all affected by anthropogenic change; thus the role that primates as seed dispersers needs to be reinvestigated with a fresh eye.

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Compliance with Ethical Standards

Ethical Note: The nature of the paper does not involve direct the use of animals, rather we rely on published literature and the synthesis of ideas.

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