Focus on:

Role of the western lowland gorilla (*Gorilla gorilla gorilla*) in seed dispersal in tropical forests and implications of its decline

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Patterns of seed dispersal significantly affect plant demography, dynamics and succession. In the tropics, the majority of tree species bear fruits that are adapted to animal-mediated dispersal. Amongst seed dispersers, the contribution of primates is widely recognized by ecologists as incomparable. However, in lowland Afrotropical forests, the specific role of the largest primate species, the western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman, 1847), has been overlooked. This is of particular relevance as this species seems to fulfill important criteria for effective dispersal, both quantitatively and qualitatively. One trait makes it potentially unique as seed disperser; the regular deposition of seeds in open canopy environments where light will not be a limiting factor for subsequent seedling growth and survival. The magnitude of which this particular trait contributes to forest dynamics remains unexplored though it could be potentially important. It might no longer be the case, however, as the western lowland gorilla is critically endangered. The loss of the ecological services provided by large-bodied seed dispersers may have considerable impacts on the forests. Through dispersal limitation, population dynamics of plants in forests devoid of large frugivores will be strongly impacted. In the long-term, this may lead to shifts in plant community structure, composition and to reduced tree diversity. Currently, forests of the Congo basin face increasing level of deforestation and degradation, which puts already the ecosystem integrity in jeopardy. The additional threat that represents frugivorous wildlife depletion is therefore of forest management concern.
Keywords. Seed dispersal, primate, forest dynamics, Africa.

Le rôle du gorille des plaines de l'Ouest (*Gorilla gorilla gorilla*) dans la dissémination des graines en forêts tropicales et les implications de son déclin. La dissémination des graines par les animaux participe significativement à la démographie, la dynamique et la succession des communautés végétales. En forêts tropicales, la majorité des arbres produisent des fruits adaptés à la consommation et à la dissémination de leurs graines par les animaux. Parmi les différents agents disséminateurs, les primates jouent un rôle inégalable, largement reconnu. Alors que leur rôle fondamental dans la régénération forestière et le maintien de la biodiversité tropicale est accepté, la contribution spécifique du gorille des plaines de l'Ouest (*Gorilla gorilla gorilla* Savage and Wyman, 1847), le plus grand des primates des forêts du Bassin du Congo, reste méconnue. Pourtant, cette espèce semble réunir les conditions fondamentales pour qu'une dissémination très efficace se réalise. Il se distingue notamment par une dispersion régulière des graines dans des micro-habitats caractérisés par une forte ouverture de la canopée où la lumière ne sera pas un facteur limitant à la croissance et la survie des jeunes plants. L'influence sur la dynamique forestière que pourrait jouer cet enrichissement en graines dans les ouvertures forestières par le gorille des plaines de l'Ouest n'a pas encore été explorée malgré son importance potentielle. Elle pourrait cependant ne plus être active compte tenu des menaces critiques qui pèsent sur la survie des populations de gorilles. La perte des services écologiques rendus par la grande faune disséminatrice de graines pourrait avoir des conséquences considérables sur le futur des forêts. En l'absence de dissémination, la dynamique de population de nombreuses espèces serait impactée. Sur le long terme, cela pourrait conduire à une modification de la

structure et composition de la communauté végétale et à un appauvrissement de la diversité. Actuellement, les forêts du bassin du Congo subissent des taux grandissants de déforestation et dégradation qui mettent en péril l'intégrité de l'écosystème. La disparition des frugivores constitue donc une menace additionnelle qui doit être prise en considération dans la gestion des massifs forestiers.

Mots-clés. Dissémination des graines, primate, dynamique forestière, Afrique.

1. INTRODUCTION

Plants bearing fleshy fruits are believed to have a mutualistic relationship with their animal consumers: from an evolutionary perspective, plants take advantage of seed dispersal while animals benefit from the nutritive value of the consumed fruit (Kollmann, 2000). Frugivore-mediated seed dispersal (*i.e.* zoochory) can have significant effects on plant demography, dynamics, succession and spatial distribution at all scale (Kollmann, 2000; Seidler et al., 2006; Blake et al., 2009; Gillespie et al., 2012).

In the tropics, the majority of tree species bear fruits adapted to animal dispersal. In Neotropical forests, Howe et al. (1982) reported the proportion of animal-dispersed species ranging from 51 to 93% for canopy trees and 77 to 98% for sub-canopy trees. In Paleotropical forests, trees also exhibit adaptations for animal seed dispersal. According to Doucet (2003), about 60% of tree species of Central Gabon are dispersed through endozoochory, and in the Dja region, South-East Cameroon, this value reaches 82% (Letouzey, 1985). Despite the importance of seed dispersal in biodiversity maintenance (Janzen, 1970; Connell, 1971; Harms et al., 2000; Hardesty et al., 2006), mechanisms affecting seed dispersal patterns and recruitment probability of tropical trees remain poorly documented. Furthermore, no generalization intending to predict these parameters for less-known tree species is possible due to the complexity of tropical ecosystems (Müller-Landau et al., 2008).

Fruits and seeds adapted to zoochory vary widely in their shape, size, color, chemical composition, palatability, digestibility and accessibility; therefore they attract and are dispersed by different sets of animal species (Poulsen et al., 2002; Müller-Landau et al., 2008). Behavioral and physiological patterns of frugivorous dispersers, such as activity budget, displacement velocity and distance, retention time and fruit handling, will have consequences on seed viability and spatial patterns of seed deposition (Howe et al., 1982; Lambert et al., 1998; Traveset, 1998; Nathan et al., 2008); factors which greatly influence recruitment probability. Seed dispersal, population dynamics and community structure at a given site are thus dependent on the frugivorous community and plant attributes that attract them.

As primates represent a great proportion of the frugivorous biomass in tropical forests (Garber et al., 1998), in general their contribution to seed dispersal has received much attention and they are believed, as a group, to be incomparable dispersers (Poulsen et al., 2001; Lambert, 2011). That said, for some frugivorous primate species, documentation of their role as seed disperser is lacking, despite their potential effectiveness. If such potentially effective dispersers disappear from forests, there could be long-term detrimental consequences for natural forest regeneration and dynamics (Terborgh et al., 2008; Blake et al., 2009; Poulsen, 2009; Vanthomme et al., 2010). The future of tropical forests is already put in jeopardy by human activities imposing immediate effects on its size, structure and composition, and climate change will further contribute to this (Wright, 2010; de Wasseige et al., 2012). Extirpation of effective dispersers constitutes another major threat for the forests that will remain. This may be the case with the "critically endangered" western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman, 1847) (IUCN, 2012).

Here, we investigate the potential importance and effectiveness of western lowland gorillas as seed dispersers and scrutinize the potential consequences of their removal/extinction for the preservation of the ecosystem integrity. Specifically, the objectives of this review are threefold. First, we aim to describe the advantages and underlying mechanisms of animal-mediated seed dispersal for plant fitness in tropical ecosystems. We then explain the important ecological function of primates as a seed dispersal taxon, we summarize what we know about the contribution of the western lowland gorilla and make expectations of its effectiveness. Finally, we discuss the keystone role of large frugivores and the implications of their decline for the future of tropical forests.

For the purpose of this review of the literature we used the database Scopus provided by Gembloux Agro-Bio Tech. The main keywords entered were "seed dispersal", "western lowland gorilla", "primate", "endozoochory", "tropical forest", "regeneration", "forest degradation" and "Congo Basin". Among relevant references, the most recent were selected, with the exception of publications defining ecological concepts, and illustrations from Central African forests were prioritized.

2. ENDOZOOCHORY: ADVANTAGES AND DISADVANTAGES

Seed dispersal, regardless of the type of vector, is believed to confer an advantage to the plant through different mechanisms, which increase recruitment probability. It reduces the mortality rate caused by sibling competition (Connell, 1971), intense predation by granivores and grazers that concentrate their activities where food is abundant (Janzen, 1970), and attacks by specific pathogens (Augspurger, 1984). Escape from a density- or distance-dependent mortality is described by the "Escape Hypothesis", better known as the Janzen-Connell hypothesis (Howe et al., 1982). Seed dispersal also enables colonization of particular habitats that are unpredictable in when they will be created or in their location, such as treefall gaps (Howe et al., 1982). This advantage is explained by the "Colonizing Hypothesis". In the specific case of endozoochory, the extra costs involved in producing fruits to attract animals is associated with additional evolutionary advantages, known as the "Directed-Dispersal Hypothesis". This hypothesis considers that non-random movement and habitat preference of some frugivores results in a disproportionate deposition of seeds in sites where specific requirements for seed germination and seedling growth and survival are met (Howe et al., 1982; Wenny, 2001). This evolution of plant traits has further consequences that may improve the fate of dispersed seeds; passage through the gut of a frugivore is normally associated with mechanical and chemical abrasion of the seed coat which, in some cases, impacts positively on germination capacity (*e.g.*, Lieberman et al., 1986; Traveset, 1998; Valenta et al., 2009). Furthermore, when excreted, these seeds are surrounded by fecal material that protects them from hydric stress and offers a nutrient-rich environment that encourages seedling growth and increases survival probability (Nchanji et al., 2003). Finally, dung beetles are attracted to volatile organic compounds emitted from feces and initiate secondary dispersal which can have a huge impact on seed survival, seed predation, germination success and seedling establishment (Shepherd et al., 1998; Andresen et al., 2004).

Despite the numerous potential advantages of endozoochory, attracting frugivores through fruit production is, however, no guarantee for increased plant fitness through higher recruitment success. Some frugivores do not disperse the seeds from some or all species they feed on, they may break the seeds and kill the embryo when mouth-processing or even masticate the seeds on purpose for nutrient intake (Tutin et al., 1993; Lambert et al., 1998). This results in them being seed predators instead. Passage through the gut does not always enhance germination success or rate of all of the fruit items consumed (Traveset, 1998). The level of abrasion of the seed coat and its effect on germination depends on the consumer species and the intrinsic characteristics of seeds, such as thickness and hardness of the seed coat, as well as seed size, which affects the gut transit time; smaller seeds are retained for longer periods than larger ones (Traveset, 1998). A long retention time can enhance germination rate and success through suppressing seed dormancy or by softening the seed coat and increasing its permeability. However, a retention time that is too long can lead in some cases to total seed digestion or germination inhibition (Lieberman et al., 1986; Traveset, 1998). Additionally, the chemical compounds in the feces (*e.g.* fatty acids and phenols) can sometimes act as germination inhibitors (Valenta et al., 2009) and fecal material can reduce germination success by facilitating fungal and bacterial development (Traveset et al., 2007). Similarly, the fruit pulp may also contain germination inhibitors (Robertson et al., 2006) and the presence of pulp surrounding the seeds also increases the risk of fungal and bacterial development that can be lethal to seeds (Baskin et al., 1998). Therefore, undispersed seeds still surrounded by the fruit pulp, either due to dispersal failure (lack of dispersers' visitation) or as a result of seed processing behavior (spitting of seeds not cleared from pulp), are likely to face a high mortality rate. Furthermore, dung beetle activity can result in seed loss, by excessively deep burial in the soil (Shepherd et al., 1998). Finally, the seed deposition pattern exhibited by large frugivores results in a high density of seeds per fecal clump which, to a certain extent, cancels out the advantage of escaping from density-dependent mortality underneath the crown of the parent (Poulsen et al., 2001; Traveset et al., 2007).

Production of fruit attributes that attract animals represents an energy investment by the plant, which would not be cost effective in case of dispersal failure in habitats where animal dispersers are reduced to very low densities or are locally extinct. In general, fruit-bearing plants would have multiple animal dispersers, especially in tropical forests where the frugivore community is highly diverse (Müller-Landau et al., 2008). However, some plants rely on a limited set of dispersers or even a single species and therefore have restricted or no dispersal substitution capacity (Lieberman et al., 1986; Tutin et al., 1991a; Babweteera et al., 2007; Blake et al., 2009). Local extinction of dispersers could therefore lead to important plant population decline through recruitment limitation (Terborgh et al., 2008).

In the tropics, strict one-to-one plant-animal mutualisms occur mainly due to size restriction: big seeds can only be dispersed by large-bodied frugivores with a correspondingly large gut size (Babweteera et al., 2007). The African forest elephant (*Loxodonta cyclotis*

Matschie, 1900) is the largest forest dwelling animal on Earth and it has been reported to be the exclusive disperser of at least 13 tree species at Ndoki Forest, Republic of Congo (Blake et al., 2009). Similarly, the western lowland gorilla is the only regular disperser of seeds of *Cola lizae* N.Hallé (Sterculiaceae), endemic to central Gabon, despite the fact that sympatric chimpanzees occasionally swallow and disperse their seeds (Tutin et al., 1991a). Crucially, both species, western lowland gorillas and African forest elephants, are currently facing considerable population decline throughout their range (IUCN, 2012).

3. PRIMATES AS A KEYSTONE TAXON FOR TROPICAL FORESTS

3.1. Importance of primates as a seed disperser group: generalities

Among animal seed dispersers in tropical ecosystems, the contribution of primates is thought to be of paramount importance (Poulsen et al., 2001; Lambert, 2011). Primates are usually abundant and have a relatively large body size. As most primate species have a high frugivorous diet, they represent a large proportion of the frugivores biomass and are consequently responsible for the removal of a large proportion of the fruit and seed crop (Chapman, 1989; Chapman et al., 1998; Garber et al., 1998; Poulsen et al., 2002; Lambert, 2011). In such cases, diet overlap is common (*e.g.* Chapman, 1989; Tutin et al., 1993; Tutin et al., 1994; Poulsen et al., 2001; Poulsen et al., 2002; Lambert, 2011), resulting in some degree of redundancy among primates in the seed dispersal service for various plant species. Multi-species dispersal of seeds has a great influence on the seed shadow of the plants concerned (*i.e.*, the spatial distribution of seeds around the parental source; Willson, 1993) and subsequently on recruitment probability. Indeed, primates within a community exhibit a variety of feeding strategies, differences in fruit and seed processing, home range size, habitat preference, daily travel distance, gut capacity and retention time of the digesta (Poulsen et al., 2001). As a result, distinct primate species will disperse seeds into different habitat types, at varying distances from the parent plant, and according to a scattered or rather clumped distribution pattern. The probability of encountering suitable conditions for recruitment is therefore higher in case of multi-species seed dispersal (Poulsen et al., 2001).

Contrary to this, some sympatric primate species exhibit diet specialization for certain fruit species, which increases the proportion of seed species in a plant community that is dispersed. For instance, the number of seed species dispersed by each frugivorous primate species in a study site in the Dja Biosphere Reserve, Cameroon, was found to range from 5 to 61, whereas as a whole the primate community dispersed at least 125 seed species through fecal clumps; 77 of them being tree species, which represented 34% of the studied tree flora of the reserve (Poulsen et al., 2001).

These varying dietary, behavioral and ecological characteristics result in a primate community that is diverse yet effective at seed dispersal and therefore able to significantly structure the habitats in which they are found (Poulsen et al., 2001; Lambert, 2011).

Primates are thus essential agents of forest dynamics and regeneration, contributing to the maintenance of high biodiversity of tropical ecosystems. As a consequence, their extirpation could significantly impact on recruitment patterns of many plant species (Lambert, 2011), which would lead to population collapse and in the long term to a shift in the plant community (Terborgh et al., 2008; Babweteera et al., 2009; Poulsen, 2009). It has been argued that large gut-sized birds, such as hornbills, must have a high substitution capacity for primate seed dispersal, by dispersing the same set of seed species. However, hornbills tend to use higher strata of the canopy forest and are attracted by fruits of different colors, feeding more often on reddish fruit species, whereas primates prefer brown and green fruits (Poulsen et al., 2002). Thus, dispersal redundancy between these two taxa is debatable although it seems clear that no one taxon could completely replace the other (Poulsen et al., 2002; Lambert, 2011). Moreover, redundancy among species belonging to closely-related taxa is not always high. In the Dja Biosphere Reserve, apes and Cercopithecines (*Cercopithecus*, *Lophocebus* and *Colobus*) exhibit a small overlap in the seed species they disperse, leading to the conclusion that the loss of seed dispersal services by apes could not be completely fulfilled by Cercopithecines (Poulsen et al., 2001).

To highlight the importance of primates for seed dispersal, Lambert (2011) used a powerful approach to demonstrate the ecological necessity of conserving primates for forest dynamics and biodiversity maintenance. She applied the multi-species umbrella concept for ecosystem conservation. An umbrella species is by definition "a species for which its conservation confers protection to a large number of naturally co-occurring species" (Roberge et al., 2004, page 77). The originality of her study was to work at higher taxonomic ranks than the species and to implement in her definition the important mutualism existing among plants and animals. In that way, the conservation of an umbrella taxon will benefit many species, both floral and faunal. Based on species richness within taxa, abundance, sensitivity to human disturbance and visitation rate of fruiting trees, primates proved to be the most fitting "umbrella

taxon" compared to birds and squirrels. In terms of seed dispersal and its role in the maintenance of the high biodiversity of tropical forests, conservation efforts targeted towards primates therefore represent an adequate management shortcut in situations where conserving all animal and plant species is economically impossible. Currently, almost half of the world's primate species face conservation challenges (IUCN, 2012). The application of the above management strategy would be therefore highly relevant for the future of many primate species, including the critically endangered western lowland gorilla.

3.2. Western lowland gorilla seed dispersal

To our knowledge, the first documentation of western lowland gorilla seed dispersal activity was published two decades ago (Tutin et al., 1991a). Since then, only a handful of studies have provided further information on this topic, and most of them were conducted at the same study site as the initial study in Lopé National Park, Gabon. Nonetheless, improved knowledge of gorilla ecology contributes to the appreciation of its potential quantitative and qualitative effectiveness in seed dispersal, as discussed below.

Quantitative dispersal. In terms of quantitative seed dispersal, the western lowland gorilla is likely to play an important role for the following reasons:
– They are regular fruit-eaters, feeding on a diverse set of species. In periods of fruit abundance, fruit consumption accounts for up to 70% of feeding time (Doran-Sheehy et al., 2009). Feeding ecology studies conducted across its range (Ndoki, Congo; Lopé, Gabon; Mondika, Congo and Central African Republic; Bai Hokou, C.A.R.) have identified 70 to 115 fruit species in the gorilla diet at each study site (Doran et al., 2002). Fruit remains were found in almost every feces collected over a 7-year period in Lopé (96%, N = 4,301 feces; Tutin et al., 1993). On average, one fecal clump was found to contain remains of three different fruit species;
– With an average body weight reaching 90 and 180 kg for adult females and males respectively (Caldecott et al., 2009), the western lowland gorilla has the largest body size of all primates of the Congo basin. Daily food intake required for metabolism is therefore high and by extension they are responsible for the removal of a large proportion of the fruit/seed crop. In the Dja Biosphere Reserve, Cameroon, despite the low density of western lowland gorillas compared to the six sympatric primate species (the moustached monkey *Cercopithecus cephus cephus*, the white-nosed guenon *Cercopithecus nictitans nictitans*, the crowned guenon *Cercopithecus mona pogonias*, the black-and-white colobus *Colobus guereza occidentalis*, the grey-cheeked mangabey *Lophocebus albigena albigena* and the central chimpanzee *Pan troglodytes troglodytes*), they are assumed to disperse alone almost as many seeds as the rest of the primate community as a whole (Poulsen et al., 2001). With an average of 40.8 intact seeds per fecal unit (SD, ± 262.6), a density of 1.7 weaned individuals·km^{-2} [95% IC, 1.0 –2.9] and 6.7 defecations per day, western lowland gorillas could be dispersing 464.7 seeds per day per km^2 [range, 273.4 – 792.7] compared to 664.2 [422.4 – 955.9] for the remaining primate community.

Qualitative dispersal. From a qualitative perspective, western lowland gorillas may also be effective seed dispersers because:
– They usually process fruits in the mouth and gut without causing damage to seeds; fruit remains in feces consist mainly of intact and still viable seeds (Tutin et al., 1993; Poulsen et al., 2001; Doran et al., 2002). Many seed species have a high concentration of secondary compounds and gorillas lack the specialization of the digestive tract required to metabolize them (Rogers et al., 1990), resulting in the passing of most seeds through the gut undigested (Williamson et al., 1990). Additionally, the gut size of the gorilla is large enough to allow them to swallow the seeds of most fruit species they feed on. The longest-running study investigating western lowland gorilla seed dispersal identified 70 seed species present in feces samples over a 6-year period, encompassing 76.9% of the fruit species known to feature in its diet at this site (N = 91; Lopé National Park, Gabon: Tutin et al., 1991a; Tutin et al., 1991b). While chimpanzees, the second largest primate of Congo Basin forests, systematically expulse seeds exceeding 4.2 cm^3, seeds up to 7 cm^3 can be found in gorilla feces (Tutin et al., 1994). Seeds that pass through western lowland gorilla's digestive tract intact conserve their germination capacity. Poulsen et al. (2001) observed a positive effect on germination success of *Uapaca* seeds from passage through the western lowland gorilla gut. Germination success reached 62% after passage through the gut compared to a 26% germination success for seeds manually extracted from fruit pulp. Among the six primate species tested (five Cercopithecines and the central chimpanzee), the western lowland gorilla conferred the highest germination enhancement for *Uapaca* seeds;
– Seeds are retained for a long period in the western lowland gorilla digestive tract. In addition to the relationship between digestive tract length and body size, the type of food consumed along with the seeds influences seed transit time. For instance, an increase in the amount of fruit consumed results

in shorter retention time of the digesta (Traveset, 1998). The diet of the western lowland gorilla, though highly frugivorous, includes non-fruit items such as leaves, pith, shoots, barks and insects year round (Tutin et al., 1993) and in inverse proportion to fruit consumption (Doran-Sheehy et al., 2009). This mixed diet influenced by seasonality and the large body size of gorillas are responsible for relatively long though variable retention times of seeds in the digestive tract regardless of seed size, ranging from a few hours (< 10 h) to 136 h, with a mean of 47.1 h (Remis, 2000). By comparison, central chimpanzees have a mean retention time of 23.6 h (Idani, 1986) and the one of Cercopithecine species ranges from 21.2 h to 25.4 h (Poulsen et al., 2001). The relatively long retention time of the western lowland gorilla may enhance germination, as demonstrated for *Uapaca* seeds (Poulsen et al., 2001), or may conversely inhibit it (Traveset, 1998). Finally, as a consequence of long and variable retention times coupled with long daily path lengths (from < 1 km to 5.3 km; Remis, 1997), western lowland gorillas likely provide a complex heterogeneous seed shadow with an extended tail of long distance dispersal. While such an extended seed shadow increases the probability of encountering suitable conditions for seedling recruitment, long distance dispersal also favors maintenance of genetic diversity and rate of range expansion of the plant populations concerned (Kollmann, 2000; Hardesty et al., 2006). The dispersal and mating system of individual gorillas further contributes to this; when a male leaves the natal group in search of founding a breeding group, this blackback male may travel very long distances (Douadi et al., 2007);

– Seeds dispersed by the western lowland gorilla encounter particular environmental conditions. Western lowland gorillas have a bimodal defecation pattern with half of their feces produced at nest sites and the other half during daily displacement (Todd et al., 2008). Nest sites are not selected randomly and canopy openness seems to be a major determinant. Preference for open canopy areas for nesting, such as tree fall gaps, is a constant feature across the range of the western lowland gorilla (*e.g.*, Tutin et al., 1995; Mehlman et al., 2002; Arnhem, 2008; Willie et al., 2012). Seeds dispersed at nest sites are thus likely to encounter microsites with higher light regimes than seeds dispersed during daily displacement. This seems to be particularly profitable for post-dispersal seed fate as pointed out by Tutin et al. (1991a) in Lopé, Gabon. Seeds of *Cola lizae* dispersed at nest sites had higher germination success, seedling establishment and survival rate than seeds dispersed elsewhere; 71.6% of seedlings survived at nest sites after two months compared

to 13.2% elsewhere. Although not systematically monitored, *Cola lizae* seeds deposited directly beneath parent trees, either through oral expulsion by primates or from fallen fruits, seemed to face a much higher mortality rate than dispersed seeds. The suitability of gorilla nest sites for post-dispersal seed fate was confirmed for two additional species at the same study site (*Ganophyllum giganteum* [A.Chev.] Hauman [Sapindaceae] and *Uapaca guineensis* Müll.Arg. [Euphorbiaceae]: Voysey et al., 1999). Seedling survival and growth of these species were always higher at nest sites after two years than beneath the crown of parent trees or for those scatter dispersed by other primate species at short distances from the parental source. It seems, therefore, that the western lowland gorilla may be a unique disperser in terms of its "directed dispersal" (*i.e.* dispersal of seeds in microsites presenting environmental conditions particularly suitable for recruitment: Howe et al., 1982). Although directed-dispersal is thought to be a rare phenomenon, it leads to a much higher probability of survival to adulthood on a per-seed basis than the other kinds of seed dispersal advantages (Wenny, 2001). In this particular situation, the animal species performing directed dispersal may contribute significantly more to the plant population concerned than all other dispersers. The most explicit example in the tropics comes from male bellbirds perching preferentially in open canopy environment, which improves seedling survival of the tree, *Ocotea endresiana* Mez [Lauraceae] (Wenny, 2001). Regular dispersal of seeds by the western lowland gorilla in open canopy sites is also likely to improve recruitment success of tree species as most of them require at least small canopy gaps to reach adulthood. Interestingly, species requiring a high light regime at seedling stage are most commonly found among timber species (Doucet, 2003).

The western lowland gorilla possesses biological and ecological traits required to perform effective seed dispersal. Transportation of many seeds away from the parent plant in open canopy habitats may greatly improve seed and seedling fate of many tropical species, and dispersal of large-seeded species contribute to their spatial distribution. In regards of that, the western lowland gorilla is a good candidate of being a keystone element of the ecosystem, like elephant are considered to be (Blake et al., 2009).

It is worth noting, however, that the western lowland gorilla may also influence its environment by causing damages to recruits of woody species. Although terrestrial herbaceous vegetation composes the majority of gorilla nests, in almost every study site saplings, either bended or broken, are also common

nest building material (Tutin et al., 1995; Mehlman et al., 2002; Willie et al., 2012). The western lowland gorilla is also responsible for damages by breaking the shoots for consumption of the soft inner part, young leaves and the apical bud. For example, Kouadio (2009) observed important seedling and sapling destruction in timber plantations. In order to debate on the real contribution of one animal species on the ecosystem dynamics it is important to consider both the positive and negative effects that the animal species exerts. In the present case, lack of empirical information and quantitative data impede balancing both contributions. However, the loss of the seed dispersal service of the western lowland gorilla is believed to have much more negative impact on the forest than do occasional recruit destruction as discussed in the next section.

4. WILDLIFE DEPLETION AND THE FUTURE OF TROPICAL FORESTS

In the tropics, the high occurrence of zoochory leads to interdependent dynamics between plants and animals, where disturbance affecting one taxon will have an impact on the other (Sodhi et al., 2009); habitat disturbance may result in a decrease in wildlife density (*e.g.* Poulsen, 2009), and depletion of wildlife may alter regeneration patterns of plant communities (*e.g.* Terborgh et al., 2008).

Presently, forests of the Congo basin face increasing rates of degradation through increased anthropogenic pressure on natural resources (forest conversion for farming and agriculture, extractive industries, illegal logging, fuel-wood provisioning; de Wasseige et al., 2012). In addition to this, the bushmeat crisis reached a peak due to an increasing human population, together with the improved road network and the easier access to fire-arms (Wright, 2010). In summary, forests are declining in size and wildlife is declining in abundance. As frugivores represent most of the tropical wildlife biomass it is not surprising that they are the most harvested taxon, encompassing 82% of the carcasses found on western and central African markets (Fa et al., 2005). The same tendency is observed in the Neotropics, where frugivores of the Amazonian basin, regardless of their size, decline faster in abundance with increasing level of hunting pressure than the other dietary specialization groups (Peres et al., 2007). Only rodents seem to increase in abundance with habitat degradation and large vertebrates' depletion (Malcolm et al., 2000; Poulsen, 2009).

Degradation and hunting can lead to local extinctions of frugivores with large-bodied species facing higher risk (Pimm et al., 1988) as 1) they naturally occur at lower densities than smaller species, 2) they often rely on large continuous habitat tracts, 3) they have slow reproductive rates, 4) they give birth to fewer offspring, 5) they are more valuable to hunters and 6) they cannot adjust to persistent hunting pressure by becoming more behaviorally inconspicuous (Babweteera et al., 2007; Babweteera et al., 2009; Poulsen, 2009; Wilkie et al., 2011). Local extirpation of large-bodied frugivores will result in dispersal limitation of large-seeded trees given that remaining smaller-bodied frugivores will not be able to swallow and disperse them (Wang et al., 2007; Blake et al., 2009; Vanthomme et al., 2010). Seeds will then simply fall beneath the crown of the parent plant and risk high density- or distance-dependent mortality (Janzen, 1970; Connell, 1971; Harms et al., 2000; Seidler et al., 2006; Blake et al., 2009; Poulsen, 2009). Without transportation of seeds through the gut of a frugivore, the probability of encountering a favorable site for recruitment is reduced, thus resulting in recruitment limitation (Babweteera et al., 2007). Such altered patterns of tree recruitment could lead in the long-term to shifts in community structure (Seidler et al., 2006; Wright, 2010; Wilkie et al., 2011), composition (Poulsen, 2009; Wright, 2010) and to reduced adult tree diversity (Blake et al., 2009).

Recruitment limitation of large-seeded species will have another disruptive effect on the ecological function of tropical forests. Large seed size is generally associated with shade-tolerant long-lived species because seedlings will rely on seed resources for establishment in a shaded environment, while small seeds are associated with light-demanding, fast-growing and short-lived species (Queenborough et al., 2009). Moreover, seed size is correlated to wood density (Queenborough et al., 2009), which is a good predictor of carbon storage capacity (Ruiz-Jaen et al., 2011). Therefore, recruitment limitation of large-seeded long-lived tree species may result in a plant community shift towards a higher density of small-seeded short-lived tree species (Terborgh et al., 2008; Vanthomme et al., 2010), resulting in turn in a lower rate of carbon sequestration (Kirby et al., 2007).

Like the other two charismatic largest frugivores of Central Africa (elephants and chimpanzees), the western lowland gorilla is at risk of extinction, with hunting pressure and habitat loss/degradation being the most widespread threats (IUCN, 2012); a risk which could render the preceding possibilities a reality. Not only large-seeded tree species will be affected by the loss of the service provided by these threatened large frugivores but also zoochorous species, which recruit disproportionately, better in open canopy sites where gorillas produce most of their feces. If the strong declining trend of these keystone dispersers continues, the effects on the Congo basin ecosystem presented above will be inevitable (Blake et al., 2009). Obviously, survival of tropical forests is compromised first and foremost by much more direct threats

imposing immediate effects on them. Satellite image comparisons over time report a net annual deforestation rate in Central Africa of 0.17% per year and an additional 0.09% of dense forest is degraded annually (de Wasseige et al., 2012). Considering all the services provided by forests to humans, such as provisioning of food, timber and non-timber forest products, and carbon sequestration, the loss and degradation of tropical forests is of great concern. In contrast to the external threats, wildlife depletion impacts on the forest from the inside. Although the degradation through dispersal limitation is subtler with effects that require years before being manifests, consequences on ecosystem goods and services are real. Tree cover alone is therefore not a satisfying measure of the ecosystem health. Instead, equilibrium of the dynamics existing between plants and animals should also be taken into account (Terborgh et al., 2008).

5. CONCLUSION

The effectiveness of primates as seed dispersal agents is widely recognized and the western lowland gorilla should not be excluded. Although poorly documented, an initial review of the physiology and ecology of this African great ape shows that this species fulfills the main requirements for effective seed dispersal, both from the quantitative as well as the qualitative point of view.

A distinctive trait of the western lowland gorilla, which highlights its value as seed disperser, is its specific dispersal-related relationship with at least one tree species, *Cola lizae*, an extremely rare phenomenon, which might be prejudicial in case of disperser loss. At present, it is unknown how many such relationships might exist between the western lowland gorilla and other plant species in tropical forests.

By dispersing seeds regularly in treefall gaps, the western lowland gorilla might be an active vector of seed dispersal in light of the directed-dispersal hypotheses (Wenny, 2001). Empirical demonstration of this particular advantage on the fitness of species dispersed by the western lowland gorilla would make it a strong candidate for being a keystone species for its ecosystem.

The limited yet revealing information available on western lowland gorilla seed dispersal, considered alongside the inherent biological and ecological traits of the gorilla, clearly lead to the suggestion that this ape plays a substantial role in Afrotropical forest dynamics, population structure, and maintenance of biodiversity and ecosystem function. As the western lowland gorilla is critically endangered and needs immediate action to be taken to prevent its extinction, the emphasis on its ecological role within its ecosystem

may be used in addition to its flagship status for fund raising and public awareness.

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